BIOLOGY AND CONSERVATION OF FLORIDA TURTLES

EDITED BY

PETER A. MEYLAN

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CHELONIAN RESEARCH MONOGRAPHS

Contributions in Turtle and Tortoise Research

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Biology and Conservation of Florida Turtles

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COVER ILLUSTRATIONS

Front Cover**:** Leatherback sea turtle, *Dermochelys coriacea*, nesting in the daytime (0845 hrs) near 25th Street in Miami Beach, 30 March 1999. Although most sea turtle nesting occurs at night, some species will nest during daylight hours. Photo by DAVID CALDERIN, MIAMI BEACH POLICE DEPARTMENT.

Frontispiece**:** Two adult gopher tortoises, *Gopherus polyphemus,* in front of the mouth of a gopher tortoise burrow, Duval Co., Florida. Photo by BARRY MANSELL.

Back Cover (Upper)**:** Alligator eating a Florida softshell turtle, *Apalone ferox*, Eco-Pond, Everglades, Florida. Photo by KEVIN T. KARLSON.

Back Cover (Lower)**:** Gopher tortoise, *Gopherus polyphemus*, from Florida, showing nasal discharge and palpebral edema (swollen eyelids), common symptoms of Upper Respiratory Tract Disease (URTD). Photo by LORI WENDLAND.

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Walter Auffenberg in his office at the Florida State Museum (now Florida Museum of Natural History) on the University of Florida campus ca.1979. Photo by Peter Meylan.

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Dedication

In Memory of Walter Auffenberg

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Walter Auffenberg (1928–2004) was a leading figure in Florida herpetology from the early 1950s through the end of the century. His contributions to the study of herpetology in the broadest sense and his significant conservation efforts deserve recognition. Thus, it is with great pleasure that the authors of this volume dedicate their collected efforts to him.

Walt was a complex individual. He was not always easy to work with and he knew it. In January 1987, after one of us (PM) had finished a Ph.D. under his direction, Walt asked for a candid letter to a prospective graduate student who needed to know more about what he was getting himself into. This is what was said about Walt in 1987:

> "Walt Auffenberg is an amazing guy. He has established his expertise in a variety of fields in herpetology (land tortoises, fossil snakes, snake musculature, fossil salamanders, etc.), and then moved on to other things. His grasp of any subject he chooses to pursue is rapid and complete, including his hobbies. He is more than willing to give advice and discuss ideas of common interest, but he does not lead graduate students by the hand through graduate school.
>
> All of Walt's students have worked on their dissertation and thesis projects independently from each other and fairly independently from Walt. He does not have a "group" that works as a unit. His most significant contribution is, as in your case, the identification of good projects and funding to undertake them. Although he provides guidance and support, he has always stressed the need for good, independent thinking. He is a realist about the future of herpetologists in the job market and feels that students have to start developing their own career (and not that of their advisors) as soon as possible.
>
> He spends a lot of time in the field during which his availability is, of course, minimal. Also, when in Gainesville, he will at times sequester himself at home in order to write or analyze data. At these times he usually makes himself available to those who need to see him a few times a week. He has always been punctual about important deadlines like orals, defenses, and letters of various kinds. You should not be surprised, however, to have a variable level of interaction with him. If things are not as they should be on any given day, I only suggest that you not let it bother you and try again a day or two later."

Most people know Walt Auffenberg for his work on the monitor lizard genus, *Varanus*. His three books on the Komodo monitor, Gray's monitor, and Bengal monitor clearly established him as an authority on the behavioral ecology of these large lizards. The public's interest in the largest of lizards brought him much acclaim in this area.

Those who really knew Walt are aware that he was much more than an extraordinary herpetologist—he was a paleontologist, taxonomist, behaviorist, ecologist, conservationist, a great teacher, a fantastic artist and scientific illustrator, an accomplished roller skater, guitarist, pianist, and motorcyclist. Whatever Walt did, he made sure he did well.

Walt's story began in Dearborn, Michigan on 6 February 1928. He grew up there under the strict supervision of his father. Even in his teenage years he began to assemble a collection of preserved snakes, which eventually came to the Florida Museum of Natural History. During these early years he traveled far and wide to collect. As a high school student, he would hitchhike and ride the bus as far as Mexico. Apparently he would leave Detroit with friends in tow, but one by one they would give up on the long trip and he would carry on by himself. It was during one of these trips that he first visited Florida.

In 1945, Walt finished High School and joined the Navy as a medical corpsman. He was stationed in south Texas where he met and married his wife, Elinor, in 1947. During this time he published his first paper, on the occurrence of the scarlet snake in south Texas. While there, he made pocket money by playing ragtime piano in the bars of Corpus Christi. In 1949 he wrote a key to proteroglyphus snakes of the world and sent it to Doris Cochran, then Curator of Herpetology at the Smithsonian.

She said it was great, but that he needed to go to college and get a degree in herpetology.

At about this same time Walt's father bought a small tavern in central Florida in Astor Park, between DeLand and Ocala. The Forest Tavern would later be made famous by Walt's mother for its smoked turkey sandwiches. When Walt finished his service he moved to Florida and attended Stetson University in DeLand, completing his undergraduate studies in 1951. He played piano at local taverns and dance halls to make ends meet. He said he was always careful to position the piano near a window in order to make a quick escape when fights broke out. Even at that time, in the early 50s, he had made connections at the University of Florida (UF) and was donating specimens to the collections of the Florida State Museum (now the Florida Museum of Natural History). Through the museum he met a series of herpetologists who were important influences on him. They included Coley Goin, then a curator at the museum, Louis Hall Babbitt, a herpetologist from Massachusetts who was a frequent field companion, and Arnold Grobman, who became his graduate advisor at UF and under whom he completed a Master's in 1953. Archie Carr was at UF in those days and he and Walt were good friends but Walt felt that Archie was gone too much to be a good major professor.

Walt continued to spend a lot of time in the field during these years. He often organized collecting trips with fellow students. He was a great field man, a great snake catcher. If you got one bag of snakes, Walt got three. He liked to collect water snakes and moccasins by grabbing them by the tail, swinging them around to avoid a bite, and then tossing them up to high ground where he would catch them. On one occasion, poor Babbitt, who was deaf, could not hear the commotion and was hit in the chest by a flying moccasin. On another occasion, Walt was alone with Elinor in a remote area of south Georgia and was bitten by a moccasin that he had grabbed from under a creek bank. Elinor had not learned to drive so they waited a few days for the pain to subside and the swelling to go down so that Walt could drive home. Walt also survived bites by a copperhead and a coral snake. Walt even had a dog that had learned to find snakes. "Mr. Jones" was a smart mongrel. When Duke Campbell first came to Gainesville and wanted to see an indigo snake, he and one of us (LO) borrowed Walt's snake-hunting dog and went to Tuscawilla Prairie near Micanopy. Mr. Jones found what we were looking for. This interest in snakes led to Walt's Master's degree on the species that was very abundant everywhere in those days, *Coluber constrictor*. His work on the geographic variation of this species is a classic and we will debate his named subspecies far into the future.

But snakes and snake hunting were not enough. At UF he had classes with the renowned bird paleontologist, Pierce Brodkorb. He discovered the joy of finding microfossils by sifting dirt. Among them were the fossils of many amphibians and reptiles. He did not want to study fossil birds, but instead helped to develop the field of paleoherpetology. This was the next major focus of his career, one that he never gave up. Many of the fossils he studied were microfossils picked from bags of matrix that were collected and carried back to the museum for washing, picking, and sorting. In addition to picking matrix, Walt and his colleagues started cave diving for fossils. J.C. Dickinson, then director of the museum, decided that these students were in danger when they began using a commercial rebreathing apparatus to go deep into caves. The contraption disappeared.

In the mid- to late 1950s Walt produced many publications on fossil reptiles and amphibians. He served as Associate Curator of Vertebrate Paleontology at the Charleston Museum during 1954 and 1955 and then returned to UF in 1956 as an Assistant Professor in Biology and Associate Curator of Vertebrate Paleontology at the Florida State Museum. Among the papers he published were half a dozen on extinct salamanders, including the description of a new but extinct family of salamanders, and another on several kinds of extinct sirens with Coley Goin. He collected, reassembled, and described the entire skeleton of a long-snouted crocodile of the genus *Gavialosuchus*. He also published on fossil frogs, snakes, lizards, and turtles, including *Macroclemys* (= *Macrochelys*) and *Terrapene*. During this period he became interested in the musculature of limbless tetrapods and published on the axial musculature of the salamanders, *Siren* and *Amphiuma*, and the boid snake, *Sanzinia*. He wrote a review of the trunk musculature in limbless land vertebrates that appeared in the American Zoologist in 1962. But much of his time during this period was spent working on his dissertation on the fossil snakes of Florida, which he finished in 1959 and published in Tulane Studies in 1963. This remains a classic paper in snake paleontology.

It was during this period that he received an invitation from A.S. Romer to attend Harvard on a graduate fellowship. But there was some kind of mix-up and when he got to Harvard, there was no funding. Ernest Williams helped Walt get a job at Brandeis and they worked together at the Museum of Comparative Zoology. Walt apparently amazed Williams with his ability to identify snakes from isolated vertebrae.

Walt illustrated the Fossil Snakes of Florida and, in fact, nearly all of his own publications. He simply could not wait for someone else to complete the work. It was during his paleontological period that he developed his skill with line and stipple drawings, shaded drawings, and finally scratch techniques, the last of which he apparently learned from Sam McDowell.

At some point in the early 60s he added land tortoises to his growing list of interests. Beginning in 1961, and until he quit publishing, the Testudinidae was a regular subject. Between 1961 and 1969 he published 13 papers on fossil land tortoises, mostly from North America. His interest in tortoises also led to him keeping live tortoises. From this time, until they were replaced *by Varanus bengalensis* in about 1978, he kept live tortoises in groups in his yard in Gainesville for long periods. During the same year that he published his dissertation, he also published a note on the drinking habits of some tortoises, his first foray into behavioral ecology. It was followed by a series of papers on the behavior and ecology of living land tortoises.

In 1959, Arnold Grobman asked Walt to join him at the Biological Sciences Curriculum Studies in Boulder, Colorado, as Associate Director. Walt was the leg man. He found writers for BSCS textbooks and he sold the program around the world. In this capacity he made his first trips to Asia. He spent a fair amount of time in India and soon became fascinated by India's herpetofauna and culture. From that point on, the herpetology and culture of Asia were among his primary interests. When he returned to the Florida State Museum in 1963 as Curator of Herpetology and Chairman of the Natural Sciences Department, the options for working in Asia continued.

It was after this return that he set to work with J.C. Dickinson and Liz Wing on developing the funds to build a new natural history museum building on the University of Florida campus. He wrote much of the NSF grant proposal that resulted in much of the construction money for the only free-standing museum building that NSF has ever funded (Dickinson Hall).

In the late 1960s, Wayne King, then a curator at the Bronx Zoo, developed an interest in the biology and conservation of the Komodo monitor. He asked Walt if he had any graduate students who might want to go to live on Komodo Island and study its dragon. Walt decided this was too good an opportunity and packed up his family and left for a year on Komodo. This was a new focus for him, the behavioral ecology of large reptiles, especially varanid lizards. Since the beginning of the 1970s, varanids were a major part of Walt's research interests. But he also took a new interest in large, island-dwelling iguanids, especially the West Indian rock iguanas of the genus *Cyclura*. This was the only time that Walt assembled a working group of students around him. Walt led the team, consisting of Tom Wiewandt, John Iverson, Dave Auth, Dagmar Werner, and Jose Ottenwalder.

Although much of his time and effort were spent on varanids and iguanids, he continued to publish on land tortoises. In 1969 be published an extensive study on *Gopherus berlandieri* of south Texas with Bill Weaver and in 1974 he published a checklist of fossil tortoises—nothing like it exists for any other turtle family. In 1976, he published a complete osteology of *Gopherus* and during the mid-70s he produced several papers on tortoise behavior. But about half of his papers during this decade were on monitor lizards and they led up to his first book on a monitor lizard, *The Behavioral Ecology of the Komodo Monitor*, which appeared in 1981.

Early in the 1970s Walt revealed his feelings about the condition of his own species with a paper entitled *Mankind: a population out of balance*. In 1973, he stepped down as Chairman of the Natural Sciences Department to pursue research full time.

As if all of his existing interests were not enough, he also started working in Africa around this time. Mary Leakey asked if he would examine the fossil turtles from Olduvai Gorge. This led to additional research on fossil turtles from Laetoli, Lake Turkana, Rusinga, and several localities in South Africa.

In 1978 he rediscovered Gray's monitor and through careful museum sleuthing, determined where in the Philippines it would be found. After some preliminary surveys, he packed up his family for a second time and lived in southeastern Luzon and studied this unusual species for over a year. This work resulted in his second book, on the biology of Gray's monitor. At this stage in his career he traveled regularly to Asia and collected data on *Varanus* at many localities. On one of these trips he had to come home early. A small water monitor bit him on the thumb and it got infected. Despite several courses of antibiotics he could not control the infection and he had to return to Florida for intravenous antibiotics. On another occasion he caught the tip of a finger in the sprocket of a riding lawn mower and lost a piece of it about a week before he was due to leave for the Philippines. He decided the skin graft would heal just fine in the field and left in spite of his new injury. He said that he was starting to be as scarred as an old alligator.

By the late 1970s he had also started working on the Bengal monitor. He stopped at European museums to examine monitor specimens, especially *Varanus bengalensis*, during trips to and from Asia. He compiled significant amounts of data on this widely distributed species and published eight papers on it before producing a book on the subject in 1994. In the 1980s he traveled back and forth to Asia all the time. This resulted in a rumor that he was a CIA operative and herpetology was just a cover.

His interest in land tortoises and their predicament also resulted in serious efforts on their behalf. In 1979, he and Dick Franz produced five catalogue accounts for the Society for the Study of Amphibians and Reptiles, as well as a landmark paper on the status and distribution of *Gopherus polyphemus*. In 1978 he inspired the first All Florida Herpetology Conference. As it closed he invited a small group of interested folks into his office for an informal meeting that led to the formation of the Gopher Tortoise Council, which remains an important voice for gopher tortoises and conservation of upland habitats more than 25 years later.

He was always enthusiastic about fieldwork and was convinced that one could work with large reptiles safely if one was careful. He convinced Kent Vliet that alligators were not so dangerous and that one could swim with them with only a short piece of board to bump them away when they came too close. He wrote great letters back from the field, one of which apparently so entertained the post-doc application committee at the American Museum of Natural History in New York, that it got one of us (PM) a postdoctoral position there. He had sent them a handwritten aerogram that stood out among the stacks of clean, white letterhead. Gene Gaffney says that the committee was fascinated by the following story about the family of turtles that was to be the subject of the applicant's work (the family Trionychidae). [From a letter written by Walt Auffenberg, 2 June 1985]:

> "In rivers they [large trionychid turtles] occur in deeper parts (now 10'–20'), on sandy bottom, near cremation ghats, for they eat largely dead bodies, or parts thereof leftover after cremation. The Taj Mahal area is one such ghat. Both [*Chitra indica* and *Aspideretes gangeticus*] are common only in that part of the river where such ghats are located and where the water is deep. The body-eating has undoubtedly contributed to living humans (usually small) being dragged underwater and drowned and eaten! Two this year – one a 10 year old boy."

Along with the monographic treatments of *Varanus*, he produced other papers on the herpetofaunas were he stayed for long periods to study the monitors. These included a herpetofauna of Komodo, notes on an Indian snake, *Xenochrophis*, and turtle, *Lissemys*, and, with his son Troy, papers on resource partitioning and reproductive patterns among five species of skinks in Luzon.

By the late 1980s he had discovered "PL480 money", US funds loaned to foreign governments that they could pay back to the US in their own currency by hiring US researchers to work within their borders. He used this source of funds and a Fulbright Fellowship to undertake a series of major projects in Pakistan. Between 1988 and his retirement in 1993, he produced a series of four papers on the herpetofauna of Pakistan, including major contributions on saw-scaled vipers, *Echis*, and the agamid lizard, *Calotes versicolor*. His travels in Pakistan also allowed him to add significantly to the data set used for his book on the Bengal monitor that appeared in 1994.

Walt was working on a monographic treatment of the Herpetology of Pakistan when he had a major stroke in December 1995. The stroke left him with little sight and severe ataxia which made it difficult for him to finish this project. His son Kurt, with the help of a host of colleagues, is working on finishing this Pakistan book. But other ideas will never come to fruition. In the late 1980s he was getting interested in cladistics and thought that he might be able to use the method to study the evolution of dragons of myth. Work on living dragons had led him to collect data on the morphology of mythical dragons throughout the world and he was fascinated with the changes in dragons across cultures and through time. The energy of this man was incredible and there is little doubt that he would have succeeded with this next major turn in his career as he had so many times before, if only his health had held out.

As we were getting organized to assemble this volume, we wrote to the approximately 35 authors who were then signed on to contribute. We suggested that even though Walt had roughed some of us up over the years, he deserved recognition for what he has done for herpetology and for Florida. The authors were unanimous in their support of dedicating this volume to Walt. One of them offered this candid observation:

> "Walt Auffenberg has indeed roughed many of us up over the years, but he is the perfect person for the dedication. You and I would not be in the positions we are without him—he made our lives as professional herpetologists possible. Walt's contributions to the conservation of reptiles and amphibians have also been greatly under appreciated, due in part to his own lack of self-promotion, but also [because of] his intensely focused approach to life which made even those closest to him outsiders.
>
> He was a very interesting and complex mix of behaviors: extreme administrative and scientific effort and success, fabulous memory, visual sensory superiority, understanding of what draws people to science and how to project that essence to others, grand enthusiasm, always saying what he thought, and intensity followed by abandonment of many good ideas. It is past due for more PR for this exceptional man who made it possible for professionalism to finally reign for herpetology in Florida, India, Indonesia and Pakistan, some of the most densely populated and biologically threatened areas of the earth."

For their help in checking facts and preparing this dedication we thank Kurt Auffenberg, Dave Auth, and Wayne King.

Bibliography of Walter Auffenberg

1948. Airplane introduces *Cemophora coccinea* to Texas. Herpetologica 3(4):23.
1948. Range extension of *Farancia abacura reinwardtii* in Texas. Herpetologica 3(6):61.
1949. The racer, *Coluber constrictor stejnegerianus* in Texas. Herpetologica 4(2):53-58.
1950. A new subspecies of the mud snake, *Liodytes alleni*. Herpetologica 5(3):13-16.
1953. A new subspecies of the snake *Coluber constrictor* from Florida. Copeia 1953(1):44-45. (with L.H. Babbitt).
1954. Additional specimens of *Gavialosuchus americanus* (Sellards) from a new locality in Florida. The Quarterly Journal of the Florida Academy of Sciences 17(4):185-209.
1955. A reconsideration of the racer, *Coluber constrictor*, in eastern United States. Tulane Studies in Zoology 2(6):89-155.
1955. Glass lizards (*Ophisaurus*) in the Pleistocene and Pliocene of Florida. Herpetologica 11:133-136.
1955. The status of the fossil snake *Coluber acuminatus*. Copeia 1955(1):65-67.
1955. The fossil salamanders of the family Sirenidae. Bulletin of the Museum of Comparative Zoology 113(7):497-514. (with C.J. Goin).
1956. Remarks on some Miocene anurans from Florida, with a description of a new species of *Hyla*. Breviora 52:1-11.
1956. Additional records of Pleistocene lizards from Florida. The Quarterly Journal of Florida Academy of Sciences 19:157-167.
1957. The status of the fossil turtle *Macroclemys floridana* Hay. Herpetologica 13:123-126.
1957. A new fossil salamander of the genus *Siren* from the Eocene of Wyoming. Copeia 1957(2):83-85.
1957. A new species of *Bufo* from the Pliocene of Florida. The Quarterly Journal of Florida Academy of Sciences 20(1):14-20.
1957. Notes on fossil crocodilians from southeastern United States. The Quarterly Journal of Florida Academy of Sciences 20(2):107-113.
1957. A note on an unusually complete specimen of *Dasypus bellus* (Simpson) from Florida. The Quarterly Journal of Florida Academy of Sciences 20(4):233-237.
1958. A new genus of colubrid snake from the Miocene of North America. American Museum Novitates 1874:1-16.
1958. The trunk musculature of *Sanzina* and its bearing on certain aspects of the myological evolution of snakes. Breviora 82:1-12.
1958. Fossil turtles of the genus *Terrapene* in Florida. Bulletin of the Florida State Museum, Biological Series 3(2):53-92.
1958. New salamanders of the family Sirenidae from the Cretaceous of North America. Fieldiana, Geology 10(33):449-459. (with C.J. Goin).
1958. A new family of Miocene salamanders from the Texas Coastal Plain. The Quarterly Journal of Florida Academy of Sciences 21(2):169-176.
1958. A small fossil herpetofauna from Barbuda, Leeward Islands, with a description of a new species of *Hyla*. The Quarterly Journal of Florida Academy of Sciences 21(3):248-254.
1959. The status of the salamander genera *Scapherpeton* and *Hemitrypus* of Cope. American Museum Novitates 1979:1-12. (with C.J. Goin).
1959. The epaxial musculature of *Siren*, *Amphiuma*, and *Necturus* (Amphibia). Bulletin of the Florida State Museum, Biological Sciences 4(8):253-265.
1959. A Pleistocene *Terrapene* hibernaculum, with remarks on a second complete box turtle skull from Florida. The Quarterly Journal of Florida Academy of Sciences 22(1):49-53.
1959. *Anomalophis bolcensis* (Massalongo), a new genus of fossil snake from the Italian Eocene. Breviora 114:1-16.
1961. Additional remarks on the evolution of trunk musculature in snakes. The American Midland Naturalist 65(1):1-16.
1961. A new genus of fossil salamander from North America. The American Midland Naturalist 66(2):456-465.
1961. A correction concerning the phalangeal formula of the turtle, *Stylemys nebrascensis* Leidy. Copeia 1961(4):496-498.
1962. A new species of *Geochelone* from the Pleistocene of Texas. Copeia 1962(3):627-636.
1962. A redescription of *Testudo hexagonata* Cope. Herpetologica 18(1):25-34.
1962. The status of *Testudo anyangensis* Ping. Herpetologica 18(1):58-59.
1962. *Testudo amphithorax* Cope referred to *Stylemys*. American Museum Novitates 2120:1-10.
1962. A review of the trunk musculatue in the limbless land vertebrates. American Zoologist 2:183-190.
1963. Present problems about the past. Biological Sciences Curriculum Study, Pamphlet 6:1-35.
1963. The fossil snakes of Florida. Tulane Studies in Zoology 10(3):131-216.
1963. *Testudo hypselonota* Bourret referred to *Geochelone radiata* (Shaw). Journal of the Bombay Natural History Society 60(2):462-465.
1963. A note on the drinking habits of some land tortoises. Animal Behaviour 11(1):72-73.
1963. Fossil testudinine turtles of Florida genera *Geochelone* and *Floridemys*. Bulletin of the Florida State Museum, Biological Sciences 7(2):53-97.
1964. A first record of breeding colour changes in a tortoise. Journal of the Bombay Natural History Society 61(1):191-192.
1964. A redefinition of the fossil tortoise genus *Stylemys* Leidy. Journal of Paleontology 38(2):316-324.
1964. A new fossil tortoise from the Texas Miocene, with remarks on the probable geologic history of tortoises in eastern U.S. The Pearce – Sellards Series, Texas Memorial Museum, University of Texas 3:1-10.
1964. Notes on the courtship of the land tortoise *Geochelone tranvancorica* (Boulenger). Journal of the Bombay Natural History Society 61(2):247-253.
1964. Guidebook for the 1964 Field Trip of the Society of Vertebrate Paleontology in Central Florida, 52 pp. (Edited with W.T. Neill, T.H. Patton, and S.D. Webb).
1964. The Reddick 1 site, a Pleistocene fissure and cave complex. In: Auffenberg, W., Neill, W.T., Patton, T.H., and Webb, S.D. (Eds.). Guidebook for the 1964 Field Trip of the Society of Vertebrate Paleontology in Central Florida, pp. 31-50.
1965. Sex and species discrimination in two sympatric South American tortoises. Copeia 1965(3):335-342.
1965. Reptiles in the Quaternary of North America. In: Wright, H.E., Jr. and Frey, D.G. (Eds.). The Quaternary of the United States. Princeton University Press, pp. 557-568. (with W.W. Milstead).
1966. The carpus of land tortoises (Testudininae). Bulletin of the Florida State Museum, Biological Sciences 10(5):159-191.

1966. On the courtship of *Gopherus polyphemus*. Herpetologica 22(2):113-117.

1966. A new species of Pliocene tortoise, genus *Geochelone*, from Florida. Journal of Paleontology 40(4):877-882.

1966. The vertebral musculature of *Chersydrus* (Serpentes). The Quarterly Journal of Florida Academy of Sciences 29(2):155-162.

1967. Notes on West Indian tortoises. Herpetologica 23(1):34-44.

1967. Further notes on fossil box turtles of Florida. Copeia 1967(2):319-325.

1967. The fossil snakes of Florida. The Plaster Jacket, Florida State Museum, No. 3, 7 pp.

1967. What is a plaster jacket? The Plaster Jacket, Florida State Museum, No. 6, 10 pp.

1969. Tortoise behavior and survival. Patterns of Life Series, Rand McNally, Chicago, 38 pp.

1969. Social behavior of *Geochelone denticulata*. The Quarterly Journal of Florida Academy of Sciences 32(1):50-58.

1969. *Gopherus berlandieri* in southeastern Texas. Bulletin of the Florida State Museum, Biological Sciences 13(3):141-203. (with W.G. Weaver, Jr.)

1969. Land of the Chaco tortoise *Geochelone chilensis*. International Turtle and Tortoise Society Journal 3(3):16-19,36-37.

1970. A day with number 19. Report on a study of the Komodo monitor. Animal Kingdom 1970(Dec):18-23.

1971. A new fossil tortoise, with remarks on the origin of South American testudinines. Copeia 1971(1):106-117.

1971. We lived with dragons. Science Digest 1971(Aug):32-38.

1971. A world of ecosystems. In: Biology, an Inquiry into Life, Vol. 1. Tata McGraw-Hill Publishing Co., Bombay-New Delhi, pp. 315-338.

1971. Mankind: a population out of balance. In: Biology, an Inquiry into Life, Vol. 1. Tata McGraw-Hill Publishing Co., Bombay-New Delhi, pp. 339-352.

1972. Komodo dragons. Natural History 81(4):52-59.

1972. Fossil turtles. The Plaster Jacket, Florida State Museum, No. 16,10 pp.

1973. Growth records of wild, recaptured Komodo monitors (*Varanus komodoensis*). HISS News-Journal 1(2):41-42. (with I.S. Darevsky).

1974. Checklist of fossil land tortoises (Testudinidae). Bulletin of the Florida State Museum, Biological Sciences 18(3):121-251.

1975. The Dragon Isles: West Indian rock iguanas. The Bahamas Naturalist 1(1):2-7.

1976. The genus *Gopherus* (Testudinidae): Pt. 1. Osteology and relationships of extant species. Bulletin of the Florida State Museum, Biological Sciences 20(2):47-110.

1976. The effect of large body size on the temperature regulation of the Komodo dragon, *Varanus komodoensis*. Comparative Biochemistry and Physiology 55A:345-350. (with B.K. McNabb).

1976. The gopher tortoise. In: Layne, J.N. (Ed.). Inventory of Rare and Endangered Biota of Florida. Florida Audubon Society, pp. 467-470.

1976. First description of an adult *Varanus grayi*. Copeia 1976(3):586-588.

1976. Bahamas rock iguanas, part two. Bahamas Naturalist 1976(Summer):9-16.

1977. Display behavior in tortoises. American Zoologist 17:241-250.

1978. Social and feeding behavior in *Varanus komodoensis*. In: Greenberg, N. and MacLean, P.D. (Eds.). Behavior and Neurology of Lizards. National Institute of Mental Health.

1978. Courtship and breeding behavior in *Geochelone radiata* (Testudines: Testudinidae). Herpetologica 34(3):277-287.

1978. Suwannee cooter *Chrysemys concinna suwanniensis* (Carr). In: McDiarmid, R.W. (Ed.). Rare and Endangered Biota of Florida. Vol. 3. Amphibians and Reptiles. University Presses of Florida, Gainesville, pp. 32-33.

1978. Gopher tortoise *Gopherus polyphemus* (Daudin). In: McDiarmid, R.W. (Ed.). Rare and Endangered Biota of Florida. Vol. 3. Amphibians and Reptiles. University Presses of Florida, Gainesville, pp.33-35.

1978. Gray's monitor lizard, Project 1396, status survey. World Wildlife Yearbook 1977-1978:129-131.

1978. *Gopherus* Rafinesque, gopher tortoises. Catalogue of American Amphibians and Reptiles 211:1-2. (with R. Franz).

1978. *Gopherus agassizii* (Cooper), desert tortoise. Catalogue of American Amphibians and Reptiles 212:1-2. (with R. Franz).

1978. *Gopherus berlandieri* (Agassiz), Texas tortoise. Catalogue of American Amphibians and Reptiles 213:1-2. (with R. Franz).

1978. *Gopherus flavomarginatus* Legler, Bolson tortoise. Catalogue of American Amphibians and Reptiles 214:1-2. (with R. Franz).

1978. *Gopherus polyphemus* (Daudin), gopher tortoise. Catalogue of American Amphibians and Reptiles 215:1-2. (with R. Franz).

1979. The gopher tortoise: a declining species. Symposium on Threatened and Endangered Wildlife of Southeast United States, pp. 61-63. (with L.R. Franz).

1979. Detective Auffenberg gets his beast. International Wildlife 1979(Mar-Apr):12-15.

1979. A monitor lizard in the Philippines. Oryx 15(1):38-46.

1979. The butaan: world's rarest lizard? Topic, Philippines 1979(Jan-Feb):14-16.

1979. Demography of terrestrial turtles. In: Harless, M. and Morlock, H. (Eds.). Turtles: Perspectives and Research. John Wiley & Sons, New York, pp. 541-569. (with J.B. Iverson).

1979. Intersexual differences in behavior of captive *Varanus bengalensis* (Reptilia, Lacertilia, Varanidae). Journal of Herpetology 13(3):313-315.

1979. Research on monitor lizards. Tiger Paper 4(4):20-21.

1980. The butaan: the world's rarest lizard? In: Sitwell, N. (Ed.). Wildlife '80, Grolier Enterprises Co., London, pp. 70-75.

1980. The herpetofauna of Komodo, with notes on adjacent areas. Bulletin of the Florida State Museum, Biological Sciences 25(2):39-156.

1980. Autecological notes on *Xenochrophis piscator* (Reptilia: Serpentes) from Keoladeo Ghana Sanctuary. International Journal of Ecology and Environmental Science 6:77-82.

1981. The Behavioral Ecology of the Komodo Monitor. University Presses of Florida, Gainesville, 406 pp.

1981. Florida environments and their herpetofaunas. Part I. Environmental characteristics. Florida Herpetologist, Florida State Museum 2:1-36.

1981. Combat behaviour in *Varanus bengalensis* (Sauria: Varanidae). Journal of the Bombay Natural History Society 78(1):54-72.

1981. Behaviour of *Lissemys punctata* (Reptilia, Testudinata, Trionychidae) in a drying lake in Rajasthan, India. Journal of the Bombay Natural History Society 78(3):487-493.

1981. The fossil turtles of Olduvai Gorge, Tanzania, Africa. Copeia 1981(3):509-522.

1982. A la dÈcouverte des dragons de Komodo. Science et Vie

1978:40-43,150-151.

1982. We lived with dragons. In: Discoveries, Scott Foresman Reading Systems, Scott, Foresman and Co., Glenview, IL, pp. 59-65.

1982. Catch a lizard, use a lizard. International Wildlife 1982(Nov-Dec):16-19.

1982. The status and distribution of the gopher tortoise (*Gopherus polyphemus*). In: Bury, R.B. (Ed.). North American Tortoises: Conservation and Status. U.S. Fish and Wildlife Service, Wildlife Research Report No. 12, pp. 95-126. (with R. Franz).

1982. Florida environments and their herpetofaunas. Part II. Changes in the environment. Florida Herpetologist, Florida State Museum 3:1-28.

1982. Florida environments and their herpetofaunas. Part III. Herpetogeography. Florida Herpetologist, Florida State Museum 4:1-36.

1982. Feeding strategy of the Caicos ground iguana, *Cyclura carinata*. In: Burghardt, G.M. and Rand, A.S. (Eds.). Iguanas of the World: Their Behavior, Ecology, and Conservation. Noyes Publications, Park Ridge, NJ, pp. 84-116.

1983. The burrows of *Varanus bengalensis*: characteristics and use. Records of the Indian Museum 80:375-385.

1983. Courtship behavior in *Varanus bengalensis* (Sauria: Varanidae). In: Rhodin, A.G.J. and Miyata, K. (Eds.). Advances in Herpetology and Evolutionary Biology. Museum of Comparative Zoology, Cambridge, MA, pp. 535-551.

1983. The food and feeding of juvenile Bengal monitor lizards (*Varanus bengalensis*). Journal of the Bombay Natural History Society 80(1):119-124. (with I.M. Ipe).

1984. Notes on feeding behaviour of *Varanus bengalensis* (Sauria: Varanidae). Journal of the Bombay Natural History Society 80(2):286-302.

1985. Rub gently with a little lizard balm. The Reader's Digest, Asia Edition, pp. 6-10.

1986. New land tortoises (Testudines: Testudinidae) from the Miocene of Africa. Zoological Journal of the Linnean Society 86:279-307. (with P.A. Meylan).

1986. The Indian monitor lizard. Sanctuary 6(4):326-333.

1986. Shelter use in gopher tortoises. Gainesville Herpetological Society Newsletter 2(3):10-14.

1987. Spotted turtle. Florida Living 1987(Oct):84.

1987. Canebrake rattlesnake. Florida Living 1987(Nov):77.

1987. The chelonians of the Laetolil Beds. In: Leakey, M.D. and Harris, J.M. (Eds.). Laetoli – A Pleistocene Site in Northern Tanzania. Clarendon Press, Oxford, pp. 62-78. (with P.A. Meylan).

1988. Gray's Monitor Lizard. University Presses of Florida, University of Florida Press, Gainesville, 419 pp.

1988. A new species of *Geochelone* (Testudinata: Testudinidae) from the Pleistocene of Florida (U.S.A.). Acta Zoologica Cracoviensis 31(23):591-604.

1988. New reptile records for Pakistan. Herpetological Review 19(3):61. (with Z. Perveen and F. Iffat).

1988. Resource partitioning in a community of Philippine skinks (Sauria: Scincidae). Bulletin of the Florida State Museum, Biological Sciences 32(2):151-219. (with T. Auffenberg)

1989. Reproductive patterns in sympatric Philippine skinks (Sauria: Scincidae). Bulletin of the Florida State Museum, Biological Sciences 34(5):201-247. (with T. Auffenberg).

1989. A study of *Varanus flavescens* (Hardwicke and Gray) (Sauria: Varanidae). Journal of the Bombay Natural History Society 86(3):286-307. (with H. Rahman, F. Iffat and Z. Perveen).

1989. Utilization of monitor lizards in Pakistan. Traffic Bulletin, WWF 11(1):8-12.

1990. Notes on the biology of *Varanus griseus koniecznyi* Mertens (Sauria: Varanidae). Journal of the Bombay Natural History Society 87(1):26-36. (with H. Rahman, F. Iffat and Z. Perveen).

1990. The reptile tick *Aponomma gervaisi* (Acarina: Ixodidae) as a parasite of monitor lizards in Pakistan and India. Bulletin of the Florida Museum of Natural History 35(1):1-34. (with T. Auffenberg).

1991. Preferred habitat, home range and movement patterns of *Varanus bengalensis* in southern Pakistan. Mertensiella 2:7-28. (with Q.N. Arain and N. Khurshid).

1991. Studies on Pakistan reptiles Pt. 1. The genus *Echis* (Viperidae). Bulletin of the Florida Museum of Natural History 35(5):263-314. (with H. Rehman).

1991. Studies of Pakistan reptiles – notes on *Kachuga smithi*. Hamadryad 16(1/2):25-29. (with N.A. Khan).

1993. Studies on Pakistan reptiles. Pt. 3. *Calotes versicolor*. Asiatic Herpetological Reseach 5:14-30. (with H. Rehman).

1994. The Bengal Monitor. University Press of Florida, Gainesville, 560 pp.

1995. *Calotes versicolor nigrigularis* Auffenberg and Rehman 1993 a junior primary homonym. Asiatic Herpetological Research 6:27.

1997. Geographic variation in *Bufo stomaticus*, with remarks on *Bufo olivaceus*: biogeographical and systematic implications. In: Mufti, S.A., Woods, C.A., and Hasan, S.A. (Eds.). Biodiversity of Pakistan. Pakistan Museum of Natural History, Islamabad and Florida Museum of Natural History, Gainesville, pp. 351-372.

2002. Introduction: the past to now. In: Murphy, J.B., Ciofi, C., La Panouse, C. de, and Walsh, T. (Eds.). Komodo Dragons: Biology and Conservation. Smithsonian Institution Press, Washington, DC, pp. 1-19. (with K. Auffenberg).

2004. Studies on Pakistan lizards: *Cyrtopodion stoliczkai* (Steindachner, 1867) (Gekkonidae: Gekkoninae). Asiatic Herpetological Research 10:151-160. (with K. Auffenberg and K. Krysko).

2004. Studies on Pakistan lizards: observations on the scincid lizard *Mabuya dissimilis* (Hallowell, 1860) with comments on two other species in the genus. Hamadryad 28(1/2):66-72. (with A. Greer and K. Auffenberg).

2004. Behavioural ecology of *Ophiomorus tridactylus* (Indian sand swimmer) from Uthal, District Bela, Balochistan, Pakistan. Journal of Natural History and Wildlife 3(1):33-35. (with H. Rehman).

Gulf coast shore of Egmont Key, Tampa Bay, Florida, with two sets of gopher tortoise (*Gopherus polyphemus*) tracks and a set of human footprints. The future paths and survival prospects for turtles and tortoises are inextricably intertwined with and dependent on habitat and wildlife conservation efforts by humans. Photo by Anders Rhodin.

Biology and Conservation of Florida Turtles – Peter A. Meylan, Ed.
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Foreword

Turtles and Humans in Florida and the World: a Global Perspective on Diversity, Threats, and Economic Development

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As I prepared this book for publication, and read and reviewed all the contributions, it became increasingly clear that turtles in Florida face major threats and conservation challenges as a direct result of the rapid development, urbanization, and habitat loss occurring in the State. Some might even say that turtles are being bulldozed into oblivion in Florida, and in many ways, this would not be far from the truth. I felt that this development problem was pervasive enough that I even suggested to Peter Meylan that he consider changing the title of this book to *Turtles of Florida: Biology and Conservation in a Developed Landscape*. Peter gently declined and correctly pointed out that Florida is in fact a complex mosaic of both developed and undeveloped areas, and he preferred his original title.

Fair enough, but it made me consider more closely the challenges that turtles face in Florida, and how those challenges are inter-related with humans and their complex developmental pressures. I thought about Florida in the context of the rest of the world, and how threatened Florida's turtles might be in comparison to other areas, notably Asia, where turtles have been in terrible trouble for decades (van Dijk et al., 2000) as a result of massive direct exploitation for food, medicine, and the pet trade, in addition to habitat loss. I wondered how Florida would compare to Asia and elsewhere in terms of the threat levels to its turtles and the conservation challenges posed by its levels of urbanization and development.

Clearly, turtles in Florida face major threats from rapid development caused by the incredibly rapid growth of its human population and the concomitant rapid expansion of its percent and extent of urbanization (Reynolds, 2001; Enge et al., 2006). Huge parts of Florida's native habitat are literally disappearing under the trappings of development: asphalt, concrete, and artificial landscapes. Urban sprawl, malls, housing developments, roads and highways, industrial parks, agricultural orchards and fields, silvicultural forests, hydrological engineering, and other anthropogenic habitat alterations are rapidly impacting and destroying the remnants of available turtle habitat. And with the increasing loss of these habitats, Florida also increasingly loses its turtles (Enge et al., 2006).

I decided to analyze how Florida would rank globally in terms of conservation prioritization for its turtles if one compared it to other areas of the world. Such an analysis was recently performed by Stuart and Thorbjarnarson (2003) for several nations in Asia, using turtle diversity, endemism, and threat level per species as the basis for a ranking system for turtle conservation prioritization among nations. In addition, I wanted to try to correlate the threat levels faced by turtles all over the world with some measure of human economic development to attempt to better understand the complex interactions between turtles and humans.

Methods. — I analyzed diversity, endemism, and threat levels for turtles for all 155 global nations and territories that have native freshwater turtles or tortoises, with or without marine turtles, including the State of Florida as if it were a separate nation. Nations with only marine turtles were excluded from the analysis. Analysis of the USA as a whole nation included Florida, despite also treating Florida as a separate entity.

Analysis included all turtle taxa (freshwater turtles, tortoises, marine turtles; species and subspecies) most widely and currently recognized as distinct (updated from Iverson, 1992, 2006; Fritz and Havas, in review; TTWG, in review; as well as all recent turtle taxonomic literature). All data were compiled into an unpublished database (Rhodin, unpubl. data). I followed a liberal interpretation of what constitutes a distinct and recognized taxon of turtle, accepting most recent taxonomic revisions unless reasonably refuted by subsequent analysis (published or not).

Turtle diversity (= richness) was defined as the number of taxa (species and subspecies) of freshwater turtles, tortoises, and marine turtles occurring (living or extinct since 1500 AD) per nation. Marine turtles were excluded from the earlier analysis by Stuart and Thorbjarnarson (2003), but I included them in this analysis because of their importance in Florida, so that global comparisons reflected total turtle faunas, rather than just freshwater turtles and tortoises. Presence of marine turtles in nations was recorded as per their listing in the 2006 IUCN Red List, which is based on primarily nesting rather than just foraging presence.

Endemism was recorded per nation as (a) percent endemism, and (b) total number of endemic taxa. Taxon density was defined as number of taxa per 1000 sq.km. national area.

Threat levels used for all taxa in all nations (except Florida) were the most recent 2006 IUCN Red List global status determinations (EX = Extinct; EW = Extinct in the Wild; CR = Critically Endangered; EN = Endangered; VU = Vulnerable) (IUCN, 2006). A potential problem with this analysis is that not all IUCN Red List evaluations are up-to-date, with many species not re-evaluated since 1996, especially the turtle taxa of North and South America, Africa, and Australia. The taxa that have had the most recent and thorough evaluations are the Asian species, which were all evaluated in late 1999 (TFTSG and ATTWG, 2000), making it likely that they have somewhat higher average status listings than species that have not been evaluated since 1996. For example, the species of African turtles and tortoises appear to be under significant threat from the bushmeat trade (Lawson, 2000; Luiselli et al., 2006), but only a few species have been re-evaluated recently, and average threat levels for African nations are most likely under-listed.

For Florida turtles, the current IUCN Red List evaluations are all from 1996 and not reflective of the rapid development and habitat loss that have occurred in the state over the last decade. Therefore, the threat levels for four Florida turtle taxa used in this analysis were adjusted higher to reflect recent regional evaluations and determinations, using Enge et al. (2006) plus all chapters in this volume, including Table 1 on p. 30 of the Introduction. These adjustments, as provisionally suggested below, were made in order to provide more accurate up-to-date threat levels for Florida turtles as the basis for this global comparison.

The gopher tortoise, *Gopherus polyphemus*, has been listed by IUCN as VU since 1982. However, a recent thorough evaluation of its status in Florida using IUCN-based criteria (IUCN, 2001) has led to its recent uplisting in the state to Threatened (Enge et al., 2006; Mushinsky et al., this volume). The primary basis for the uplisting was an inferred population size reduction state-wide of between 50 and 60% over the past three tortoise generations (60–93 yrs), based on an observed 50–60% decline in the area of occupancy through loss of available habitat (Enge et al., 2006). Those same criteria would qualify the species as EN by the IUCN Red List criteria (IUCN, 2001) (if similar reductions have occurred in other parts of its range, which they apparently have), and I have therefore adjusted the threat level for the species to EN for Florida for this analysis.

The two species of map turtles in Florida, *Graptemys barbouri* and *G. ernsti*, are both currently classified as Near Threatened (NT) by IUCN. All species of *Graptemys* were recently listed on CITES Appendix III by the USA. Both *G. barbouri* and *G. ernsti* are classified as Globally Imperiled by Florida Natural Areas Inventory (Ewert et al., this volume; Aresco and Shealy, this volume) and both probably warrant at least a VU classification by IUCN, and I therefore rank them that way for Florida for this analysis. The Suwannee cooter, *Pseudemys concinna suwanniensis*, is considered a Species of Special Concern by the State of Florida (Jackson, this volume) and also probably warrants a VU classification, which is how I rank it for Florida for this analysis.

The two other Florida non-marine turtles already listed as threatened by IUCN retain their current rankings without adjustment for this analysis: the alligator snapper, *Macrochelys temminckii* (VU), and the spotted turtle, *Clemmys guttata* (VU). Other Florida non-marine turtles are listed by IUCN as either NT or not listed (implying a Least Concern status as of 1996), and at this time there do not appear to be compelling reasons to uplist them. In addition, all five species of marine turtles in Florida are listed globally by IUCN as either CR or EN.

Though four taxa of turtles were provisionally adjusted for threat level for Florida in this analysis, no such changes were made for analysis of the USA as a whole.

Threat level was recorded as (a) Total Threat Level [TTL] = (No. EX taxa x 3.0) + (No. EW taxa x 2.0) + (No. CR taxa x 2.0) + (No. EN taxa x 1.0) + (No. VU taxa x 0.5), and (b) Average Threat Level [ATL] = (TTL / number of taxa). These formulas used the methodology developed by Stuart and Thorbjarnarson (2003) with modifications for assessing EW and VU taxa (which they did not assess) and assigned similar modifier values. EW was valued at the same modifier level as CR (2.0) and VU was valued at a modifier of 0.5, half the value for EN. These modifiers are arbitrary, but generally reflective of the relative values of the different threat levels (see Stuart and Thorbjarnarson, 2003).

Prioritizations for turtle conservation action were analyzed through two separate methods. Method A was similar to that developed by Stuart and Thorbjarnarson (2003), ranking the sums of ranks of richness, percent endemism, and average threat level. It differed from their method by including subspecies in addition to species, and VU species in addition to the more threatened categories. Method B differed from that developed by Stuart and Thorbjarnarson (2003), ranking the sums of ranks of richness, total endemism, and total threat level, as well as including subspecies and VU taxa. In terms of prioritizing nations for turtle conservation action, either method may be applied, with method A focusing on areas of highest percent endemism and average threat levels, and method B focusing on areas of greatest total endemism and total threat levels.

Finding a relevant global measure of "development" in order to compare other nations with Florida was problematic. There is no available global index of development that quantifies extent of urbanization and loss of natural habitat due to physical development, as is occurring so rampantly in Florida. The United Nations provides global measures of human population percentages that inhabit urban areas (www.unfpa.org/swp/2006), but these numbers are not directly correlated with habitat loss or extent of urbanization. Measures of human population density are also available globally, but do not measure development.

Although in Florida we are concerned mainly with the threats from physical development with resultant habitat loss, one can also consider the meaning of "development" in human social and economic terms. In fact, the meaning of the designations "developed" and "developing" for the nations of the world is traditionally defined more by their development in human social and economic terms rather than what we typically call development in the physical sense, as is occurring in Florida, with urbanization and destruction of natural habitats.

A widely available index for the degree of human social and economic development is the Human Development Index

Table 1. Diversity (Richness). Top 20 ranking of 155 global nations and territories (including Florida) with the highest richness of taxa of turtles and tortoises (species and subspecies). Nation color indicates Human Development Index (HDI); green = developed, orange = developing, red = underdeveloped, black = no data (see text and Appendix). Nations in italics have lost all their non-marine turtle taxa to extinction (none in this table).

	Nations and Territories	Taxa Present
1	United States of America	88
2	Mexico	63
3	Australia	42
4	Brazil	39
5	**Florida, USA**	**38**
5	India	38
7	Indonesia	36
8	Colombia	32
9	Myanmar	30
10	China (People's Republic of China)	29
10	Thailand	29
10	Vietnam	29
13	Ecuador	28
14	South Africa	26
15	Bangladesh	25
15	Venezuela	25
17	Malaysia	23
18	Congo (Democratic Republic of the Congo)	18
19	Guatemala	17
20	Laos	16

(HDI) provided by the United Nations (UNDP, 2005). This index ranks nations according to criteria of average achievements in several basic dimensions of human social and economic development, including: a long and healthy life, as measured by life expectancy at birth; knowledge, as measured by the adult literacy rate and the combined gross enrollment ratio for primary, secondary, and tertiary schools; and a decent standard of living, as measured by GDP per capita in purchasing power parity in US dollars. "High development" (= developed) areas have HDI ≥ 0.80, "medium development" (= developing) areas have HDI < 0.80 and ≥ 0.50, and "low development" (= underdeveloped) areas have HDI < 0.50. This index has come to be accepted as a means of comparing standard-of-living in the nations of the world (http://en.wikipedia.org/wiki/Human_Development_Index).

I chose to use HDI as an available means to compare Florida with the rest of the world in terms of how this aspect of human economic development might correlate with threat levels to turtles. As no separate HDI value has been calculated for Florida, the one for the USA was used instead (which may or may not be entirely accurate, depending on the average life expectancy, education level, and standard of living in Florida as compared to the rest of the USA).

The use of HDI as a measure of human economic development does not necessarily correlate with the degree of physical development and urbanization, but is more a measure of social progress and may correlate more with quality-of-life factors such as social responsibility, environmental ethics, and conservation awareness. As such, its use in this analysis should correlate more with a national ethic for prevention and lessening of threats to turtles than with the actual threats of direct exploitation or physical development leading to urbanization and habitat loss.

Results. — My analysis covered 475 taxa (species and subspecies) of turtles and tortoises. Since the analysis covered all turtle taxa extant since 1500 AD, it also included a few extinct taxa (11), most of which disappeared relatively long ago (e.g., Indian Ocean island tortoises of the genus *Cylindraspis*). All data in the analysis are summarized in the Appendix.

Diversity (or richness) of turtle taxa is ranked by nation in Table 1. The most turtle-rich nation in the world is the USA (88 taxa), with Mexico ranked No. 2 (63 taxa), Australia No. 3 (42 taxa), Brazil No. 4 (39 taxa), and Florida ranked No. 5 (38 taxa), tied with India. This emphasizes how important Florida's turtle fauna is on a global scale. In fact, fully 8.0% of the world's turtle diversity occurs in Florida, which represents just 0.1% of the area of all nations with turtles. The many turtle-rich nations of Asia are well represented on the top of this list also, including Indonesia (No. 7), Myanmar (No. 9), and China, Thailand, and Vietnam (tied at No. 10).

Percentage of endemism of turtle taxa is ranked by nation in Table 2a. The highest ranked nations on this list

Table 2a. Percentage Endemism. Top 20 ranking of 155 global nations and territories (including Florida) with the highest percentage of endemic taxa of turtles and tortoises (species and subspecies). Color-coding of nations by HDI category and italicization as per Table 1.

		Endemic Taxa	
	Nations and Territories	%	No.
1	Australia	83.33%	35
2	*Mauritius (incl. Rodrigues)*	*80.00%*	*4*
3	Seychelles	77.78%	7
4	United States of America	67.05%	59
5	Madagascar	57.14%	8
6	Mexico	49.21%	31
7	Morocco	44.44%	4
7	Japan	44.44%	4
9	Ecuador	35.71%	10
10	Italy	33.33%	3
10	*Réunion*	*33.33%*	*1*
12	China (People's Republic of China)	31.03%	9
13	Brazil	28.21%	11
14	**Florida, USA**	**23.68%**	**9**
15	Myanmar	23.33%	7
16	South Africa	23.08%	6
17	Libya	20.00%	1
17	Puerto Rico	20.00%	1
19	Turkey	18.75%	3
20	India	18.42%	7

Table 2b. Total Endemism. Top 20 ranking of 155 global nations and territories (including Florida) with the most endemic taxa of turtles and tortoises (species and subspecies). Color-coding of nations by HDI category and italicization as per Table 1.

	Nations and Territories	Endemic Taxa
1	United States of America	59
2	Australia	35
3	Mexico	31
4	Brazil	11
5	Ecuador	10
6	**Florida, USA**	**9**
6	China (People's Republic of China)	9
8	Madagascar	8
9	India	7
9	Myanmar	7
9	Seychelles	7
12	South Africa	6
13	Indonesia	5
13	Vietnam	5
15	Morocco	4
15	Japan	4
15	*Mauritius (incl. Rodrigues)*	*4*
18	Colombia	3
18	Venezuela	3
18	Turkey	3

Table 3a. Average Threat Level. Top 20 ranking of 155 global nations and territories (including Florida, ranked No. 90) with the highest average threat level per taxon of freshwater turtles and tortoises (species and subspecies, not including marine turtles). Color-coding of nations by HDI category and italicization as per Table 1.

	Nations and Territories	Threat Level
1	*Mauritius (incl. Rodrigues)*	*2.600*
2	*Réunion*	*2.000*
3	Seychelles	1.944
4	China (People's Republic of China)	1.328
5	Puerto Rico	1.200
5	Bahrain	1.200
7	Taiwan (Republic of China)	1.167
8	Jamaica	1.125
9	Bahamas	1.083
9	Haiti	1.083
9	Dominican Republic	1.083
12	Philippines	1.056
13	Vietnam	1.052
14	Cuba	1.000
14	Maldives	1.000
14	Yemen	1.000
17	Japan	0.944
18	Malaysia	0.935
19	Myanmar	0.900
20	Indonesia	0.847
90	**Florida, USA**	**0.303**

Table 3b. Total Threat Level. Top 20 ranking of 155 global nations and territories (including Florida) with the highest total threat level for its taxa of freshwater turtles and tortoises (species and subspecies, not including marine turtles). Color-coding of nations by HDI category and italicization as per Table 1.

	Nations and Territories	Threat Level
1	China (People's Republic of China)	38.5
2	Vietnam	30.5
2	Indonesia	30.5
4	Myanmar	27.0
5	Thailand	24.0
6	India	23.0
7	Ecuador	22.5
8	Mexico	21.5
9	Malaysia	21.5
10	United States of America	18.0
11	Seychelles	17.5
11	Bangladesh	17.5
13	*Mauritius (incl. Rodrigues)*	*13.0*
13	Colombia	13.0
13	Laos	13.0
16	Australia	12.0
16	Brazil	12.0
18	**Florida, USA**	**11.5**
19	Cambodia	11.0
20	Taiwan (Republic of China)	10.5

are the island nations with most of their turtle taxa endemic. Australia tops the list at 83% of its 35 taxa; Mauritius (including Rodrigues) is at 80% but all 4 of its endemic taxa are already extinct (Gerlach, 2004); Seychelles is at 78%, but 3 of its endemic taxa are extinct (Gerlach, 1977). Both the USA and Madagascar also have high percentages of endemism. Florida ranks No. 14 on the list, fairly high, and most similar to Myanmar and South Africa.

Total endemism of turtle taxa is ranked by nation in Table 2b. Here, the USA tops the list with 59 endemic taxa, far ahead of Australia (35) and Mexico (31). China and Florida are tied at No. 6, each with 9 endemic taxa, Florida's all being subspecies. Of the island nations with high percentages of endemism, only Australia, Madagascar, and Seychelles have high total endemism.

Average threat level of turtle taxa is ranked by nation in Table 3a. The two nations with all their non-marine turtles EX top the list, with Mauritius at 2.600 and Réunion at 2.000. Seychelles, with 3 taxa EX, ranks at No. 3 with a score of 1.944. China ranks at No. 4 with 1.328 points, topping all major nations with rich turtle faunas and the highest average

Table 4a. Prioritization A. Ranking methodology similar to that developed by Stuart and Thorbjarnarson (2003). Top 25 ranking of 155 global nations and territories (including Florida) for conservation prioritization for taxa of turtles and tortoises (species and subspecies), as measured by the sum of ranks of rankings for Richness (Table 1), Percentage Endemism (Table 2a), and Average Threat Level (Table 3a). Color-coding of nations by HDI category and italicization as per Table 1.

	Nations and Territories	Sum of Ranks
1	China (People's Republic of China)	27.0
2	Myanmar	43.0
3	Vietnam	46.0
4	Ecuador	47.0
5	Indonesia	56.0
6	Seychelles	63.0
7	India	65.5
8	Madagascar	68.0
9	Japan	81.5
10	Bangladesh	90.5
11	Mexico	93.0
12	Taiwan (Republic of China)	97.0
13	Australia	100.5
14	Philippines	102.0
15	Papua New Guinea	104.0
16	Brazil	106.0
17	*Mauritius (incl. Rodrigues)*	*106.5*
18	United States of America	109.0
19	**Florida, USA**	**109.5**
20	Turkey	110.5
21	Colombia	116.0
22	Sri Lanka	118.0
23	Bahamas	121.5
24	Venezuela	123.5
25	Puerto Rico	126.5

Table 4b. Prioritization B. Ranking methodology different from that developed by Stuart and Thorbjarnarson (2003). Top 25 ranking of 155 global nations and territories (including Florida) for conservation prioritization for taxa of turtles and tortoises (species and subspecies), as measured by the sum of ranks of rankings for Richness (Table 1), Total Endemism (Table 2b), and Total Threat Level (Table 3b). Color-coding of nations by HDI category and italicization as per Table 1.

	Nations and Territories	Sum of Ranks
1	Indonesia	9.5
2	Mexico	10.5
3	United States of America	11.0
4	India	11.5
5	China (People's Republic of China)	12.0
6	Myanmar	13.0
7	Vietnam	13.5
8	Thailand	16.0
9	Australia	19.5
10	Ecuador	20.0
11	Brazil	20.5
12	Colombia	22.0
13	**Florida, USA**	**23.5**
14	Malaysia	25.5
15	Bangladesh	27.0
16	Laos	35.5
17	Venezuela	38.5
18	Guatemala	45.5
19	Cambodia	50.0
20	Nicaragua	51.5
21	Madagascar	52.0
21	Honduras	52.0
23	Papua New Guinea	54.0
24	Panama	55.5
25	Turkey	56.5

threat levels for Asia. Florida ranks No. 90 among 155 nations, indicating a relatively average threat level on a global comparative scale.

Total threat level of turtle taxa is ranked by nation in Table 3b. Here, China tops the list with 38.5 total points, followed closely by several Asian nations (Vietnam, Indonesia, Myanmar, Thailand, and India) at Nos. 2–6. Ecuador ranks No. 7 due to its many threatened and extinct subspecies of Galapagos tortoises, *Geochelone nigra* (Pritchard, 1996). Florida ranks No. 18 out of 155 nations on the list, indicating a high total threat level on a global comparative scale.

Prioritization of turtle conservation action by Method A is ranked by nation in Table 4a. Method A utilized a ranking methodology similar to that developed by Stuart and Thorbjarnarson (2003) and measured the sum of ranks of rankings for Richness (Table 1), Percentage Endemism (Table 2a), and Average Threat Level (Table 3a). The top nation here is China, as it was when analyzed by Stuart and Thorbjarnarson (2003), confirming their recommendation that China should be prioritized for turtle conservation efforts, at least when using these criteria. That the country still ranks No. 1 when compared globally as opposed to just within Asia is powerful testament to the need for turtle conservation efforts there. Many of the other developing nations of Asia rank right below China, with Myanmar, Vietnam, Indonesia, and India being highly prioritized. Ecuador comes in high due to its Galapagos tortoises, most of which are already receiving considerable conservation action and protection (Pritchard, 1996). Mexico, Madagascar, and Australia also rank high on this list, indicating need for focused turtle conservation action in those turtle-rich nations. Florida ranks No. 19, high on a global basis, also indicating the need for heightened conservation action for its turtle taxa.

Prioritization of turtle conservation action by Method B is ranked by nation in Table 4b. Method B utilized a ranking methodology different from that developed by Stuart and Thorbjarnarson (2003) and measured the sum of ranks of rankings for Richness (Table 1), Total Endemism (Table 2b), and Total Threat Level (Table 3b). As a result, the turtle-rich nations gravitate to the top of the list, with Indonesia, Mexico, and the USA ranked Nos. 1–3, respectively. India ranks No. 4, and China still manages to rank No. 5, followed closely by other major Asian nations (Myanmar, Vietnam, and Thailand). Florida now ranks No. 13 on the list, indicating its high importance in terms of considerations for conservation action based on its rich turtle fauna.

Density of turtle taxa is ranked by nation in Table 5. The first listing includes all nations of the world, including very small ones that have disproportionately high turtle densities by virtue of their very small size. Several small island nations (Seychelles, Singapore, Cayman Islands, and Maldives) top this list, despite those nations having relatively few turtle taxa. Florida ranks No. 24, indicating a relatively high density of turtle taxa, even when compared to some of these smaller nations. The second listing separates out the larger nations and territories with national areas > 100,000 sq. km. These are the nations with the highest densities of turtle taxa over relatively large areas. Coming in at the No. 1 ranking is Florida, further testament to how special and important the turtle fauna of Florida is on a global scale.

Table 5. Taxon Density. Top 20 ranking of global nations and territories (including Florida) with the highest density of taxa of turtles and tortoises (species and subspecies). First listing for all 155 nations; second listing for the 99 largest nations with land areas > 100,000 sq. km. Color-coding of nations by HDI category and italicization as per Table 1.

	Nations and Territories	Density of Taxa per 1000 sq. km.
1	Seychelles	19.780
2	Singapore	11.713
3	Cayman Islands	11.538
4	Maldives	10.067
5	Bahrain	7.205
6	São Tomé and Príncipe	2.997
7	*Mauritius (incl. Rodrigues)*	2.451
8	Trinidad and Tobago	2.145
9	Brunei	1.214
10	*Réunion*	1.197
11	Gambia	0.655
12	Puerto Rico	0.549
13	Lebanon	0.481
14	Belize	0.479
15	Bahamas	0.430
16	Israel	0.392
17	Jamaica	0.364
18	Swaziland	0.346
19	Cyprus	0.324
20	El Salvador	0.285

	Nations and Territories with Area > 100,000 sq. km.	
1	**Florida, USA**	**0.223**
2	Bangladesh	0.169
3	Guatemala	0.156
4	Honduras	0.133
5	Nicaragua	0.123
6	Ecuador	0.103
7	Nepal	0.088
7	Vietnam	0.088
9	Suriname	0.079
10	Cambodia	0.077
11	Eritrea	0.074
12	Malaysia	0.070
12	Benin	0.070
14	Laos	0.068
14	Malawi	0.068
16	Guyana	0.065
17	Thailand	0.057
18	Senegal	0.056
19	Cuba	0.054
20	Dominican Republic	0.048

Correlation betwen threat levels and human social and economic development (HDI group ranking) was then analyzed. The average threat level per turtle taxon is ranked by nation in Table 6 for the 51 global nations and territories (including Florida) with the richest turtle faunas (≥ 10 taxa). These turtle-rich nations were analyzed so as to minimize possible variation based on disproportionately high threat levels for nations with only a few turtle taxa. However, an analysis was also run for all nations with turtles.

Of note is that China heads this group of turtle-rich nations, having the highest average threat level (1.328), with the other developing nations of Asia ranked closely right behind (Vietnam, Malaysia, Myanmar, Indonesia, Thailand, and Laos, with Cambodia and Bangladesh right below). Only two non-Asian nations rank in the top 10 (Ecuador and Madagascar). Florida, with an average threat level of 0.303, ranks at No. 36 out of 51, indicating relatively lower average threats on its turtles when compared to other nations with turtle-rich faunas.

Table 6. Average Threat Level, Turtle-Rich Nations. Ranking of 51 global nations and territories (including Florida) with ≥ 10 taxa of turtles and tortoises (species and subspecies), ranked by average threat level per taxon. Color-coding of nations by HDI category and italicization as per Table 1.

	Nations and Territories	Threat Level
1	China (People's Republic of China)	1.328
2	Vietnam	1.052
3	Malaysia	0.935
4	Myanmar	0.900
5	Indonesia	0.847
6	Thailand	0.828
7	Laos	0.813
8	Ecuador	0.804
9	Cambodia	0.786
10	Madagascar	0.714
11	Bangladesh	0.700
12	Papua New Guinea	0.679
13	India	0.605
14	Trinidad and Tobago	0.591
15	Belize	0.545
16	Suriname	0.538
17	French Guiana	0.536
17	Costa Rica	0.536
19	Honduras	0.533
20	Panama	0.500
20	Guyana	0.500
20	Senegal	0.500
23	Guatemala	0.471
24	Nicaragua	0.469
25	Mozambique	0.467
26	Iran	0.462
26	Nepal	0.462
28	Turkey	0.438
29	Colombia	0.406
30	Kenya	0.385
31	Venezuela	0.380
32	Peru	0.375
33	Pakistan	0.364
34	Mexico	0.341
35	Brazil	0.308
36	**Florida, USA**	**0.303**
37	Tanzania	0.300
38	Canada	0.292
39	Australia	0.286
39	Angola	0.286
41	Ghana	0.273
42	Togo	0.250
42	Sudan	0.250
44	United States of America	0.205
45	South Africa	0.192
46	Congo (Democratic Republic of the Congo)	0.139
47	Argentina	0.136
47	Bolivia	0.136
49	Namibia	0.115
50	Nigeria	0.091
51	Uganda	0.000

Table 7. Significance levels (two-tailed t-tests) comparing degree of economic development (HDI) per nation with turtle diversity, endemism, and threat levels. Analysis for 50 nations with ≥ 10 taxa (see Table 6). Developed (Dd) nations, $n = 9$; developing (Dg), $n = 33$; underdeveloped (Ud), $n = 8$. * = significant at $t < 0.05$.

	mean	comparison	t-test
Diversity			
Developed (Dd)	32.667	Dd vs Dg	0.9563
Developing (Dg)	19.788	Dd vs Ud	0.0535
Underdeveloped (Ud)	13.875	Dg vs Ud	0.0001 *
Total Endemism			
Developed (Dd)	15.111	Dd vs Dg	0.2336
Developing (Dg)	2.273	Dd vs Ud	0.1018
Underdeveloped (Ud)	1.375	Dg vs Ud	0.0125 *
Percent Endemism			
Developed (Dd)	0.268	Dd vs Dg	0.5440
Developing (Dg)	0.083	Dd vs Ud	0.2742
Underdeveloped (Ud)	0.096	Dg vs Ud	0.2635
Average Threat Level			
Developed (Dd)	0.354	Dd vs Dg	0.0014 *
Developing (Dg)	0.538	Dd vs Ud	0.8013
Underdeveloped (Ud)	0.360	Dg vs Ud	0.0067 *
Total Threat Level			
Developed (Dd)	9.944	Dd vs Dg	0.0085 *
Developing (Dg)	11.864	Dd vs Ud	0.0380 *
Underdeveloped (Ud)	4.938	Dg vs Ud	0.0003 *

This small group of turtle-rich nations was analyzed based on their HDI group ranking (developed, developing, or underdeveloped) (Table 7). The mean for average threat level for developed nations ($n = 9$) was 0.354, for developing nations ($n = 33$) it was 0.538, and for underdeveloped nations ($n = 8$) it was 0.360. The average threat level in developed nations differed significantly from that in developing nations (Table 7), and in developing nations it differed significantly from underdeveloped nations, but developed and underdeveloped nations were not significantly different.

Mean total threat levels differed significantly among all three HDI developmental categories (Table 7); diversity and total endemism differed significantly only between developing and underdeveloped nations; percent endemism was not significantly different among any categories. The differences observed in threat levels between developmental categories were not apparently due to differences in turtle diversity or endemism, except perhaps when comparing developing with underdeveloped nations.

The same analysis for all HDI-ranked nations with any turtles (≥ 1 taxon) yielded similar but less significant results: the mean for average threat level for developed nations ($n = 40$) was 0.405, for developing nations ($n = 74$) it was 0.500, and for underdeveloped nations ($n = 32$) it was 0.262. The average threat level in developed nations did not differ significantly from that in developing nations ($p = 0.126$), but in developing nations it differed significantly from underdeveloped nations ($p = 0.006$), and developed and underdeveloped nations were not significantly different ($p = 0.398$).

Based on these data, it appears that socially and economically underdeveloped nations have relatively low threat levels per turtle taxon, developing nations have very high threat levels per turtle taxon, and developed nations intermediate threat levels.

Discussion. — This analysis has demonstrated how remarkably diverse and globally important Florida's turtles are. Florida ranks among the world's most important areas for turtles, with very high diversity, endemism, and density of taxa, being listed at or near the top in all categories.

At the same time, Florida's turtles are facing increasing threats from physical development, primarily rapid urbanization and habitat loss. The threat levels to Florida's turtles place them at moderate to high levels of global prioritization for turtle conservation action. Florida's turtle fauna is not yet as threatened as in Asia, where massive direct exploitation coupled with habitat loss have combined to reduce those turtle faunas to mere remnants of their former abundance. However, if habitat loss and other threats in Florida are not addressed, the threat levels here will contine to increase. Fortunately, at this time, Florida's turtles are still abundant enough that, with appropriate conservation action, we should be able to successfully preserve them into the future.

The analysis of correlation between turtle threat levels and human social and economic development (HDI) demonstrated that "developing" nations tend to have more highly threatened turtles than either "developed" or "underdeveloped" nations. In general, the initial "developing" expansion of human social and economic development is usually associated with increased exploitation of turtles by growing human populations, as in Asia (van Dijk et al., 2000) and Africa (Lawson, 2000; Luiselli et al., 2006), leading to unsustainable use. As developing countries become more economically developed, a gradual shift occurs away from subsistence utilization of turtles towards alternate sources of protein, leading to lesser direct threats on turtle populations (though those threats are often replaced by loss of habitat and urbanization caused by industrial and community development). Threats in developing nations come first as part of a general liquidation of resources for development, protection follows as the situation settles into a secure, developed context. The speed and intensity of these processes determine whether turtles weather the storm or are eliminated faster than they are protected (P.P. van Dijk, *pers. comm.*).

What this analysis also showed is that there appears to be what one might call a "dilemma of development." The dilemma is that depending on how one defines the term "development" it can either threaten or help to protect turtles. Physical development, such as is occurring in Florida with urbanization and habitat loss, threatens turtles, but human social and economic development may help engender improved protection for threatened turtles through an enhanced public conservation ethic and recognition of the importance of adequate native habitats and protected areas and decreased exploitation of native species.

In terms of comparing the two methods of prioritization for turtle conservation, I believe Method B offers a more meaningful way of identifying those nations where the greatest conservation needs would benefit the most from focused conservation efforts. However, political will and available opportunities usually drive the selection process.

Conclusions. — The bottom line here is that Florida is a very special place for turtles when one places it in the global context of what the rest of the world has to offer. The human residents of Florida are indeed fortunate to be living in this global epicenter of high turtle richness and density, where threat levels are still relatively moderate, providing opportunities to enjoy these animals in the wild, both in community-based habitats and conservation-focused protected areas. Though physical development and urbanization with habitat loss threaten many of the species here, the levels of threats are still comparatively moderate on a global scale. This should be cause for celebration as well as continued vigilance and advocacy lest those development pressures push turtles into higher and higher threat levels, from which they may never recover.

We do not wish Florida's landscape to become devoid of turtles, where the only turtles we would ever see would be in zoos and special exhibits and a few protected areas. We need turtles in our midst in their native habitats and it is our responsibility to keep them there. Let us not allow to happen here what has already happened in that other major epicenter of turtle richness, Asia, where overwhelming threats to turtles have tipped the balance to the point where hardly anyone ever sees a wild turtle anymore.

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LITERATURE CITED

ENGE, K.M., BERISH, J.E., BOLT, R., DZIERGOWSKI, A., AND MUSHINSKY, H.R. 2006. Biological status report – gopher tortoise (*Gopherus polyphemus*). Tallahassee, FL: Florida Fish and Wildlife Conservation Commission, 60 pp. http://www.myfwc.com/imperiledspecies/reports/Gopher-Tortoise-BSR.pdf.

FRITZ, U. AND HAVAS, P. In review. CITES checklist of chelonians of the world. Submitted to CITES.

GERLACH, J. 1997. Seychelles Red Data Book – 1997. Victoria, Seychelles: The Nature Protection Trust of Seychelles, 130 pp.

GERLACH, J. 2004. Giant Tortoises of the Indian Ocean. The genus *Dipsochelys* inhabiting the Seychelles Islands and the extinct giants of Madagascar and the Mascarenes. Frankfurt: Edition Chimaira, 207 pp.

IUCN. 2001. IUCN Red List Categories and Criteria: Version 3.1. Gland, Switzerland: IUCN Species Survival Commission, 30 pp.

IUCN. 2006. 2006 IUCN Red List of Threatened Species. http://www.redlist.org.

IVERSON, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately printed, 363 pp.

IVERSON, J.B. 2006. A Checklist of the Turtles of the World. http://www.earlham.edu/biology/documents/Checklist/pdf.

LAWSON, D.P. 2000. Local harvest of hingeback tortoises, *Kinixys erosa* and *K. homeana*, in southwestern Cameroon. Chelonian Conservation and Biology 3(4):722-729.

LUISELLI, L., POLITANO, E., AND LEA, J. 2006. Assessment of the Vulnerable status of *Kinixys homeana* (Testudines: Testudinidae) for the IUCN Red List. Chelonian Conservation and Biology 5(1):130-138.

PRITCHARD, P.C.H. 1996. The Galápagos Tortoises: Nomenclatural and Survival Status. Chelonian Research Monographs No. 1, 85 pp.

REYNOLDS, J.E. 2001. Urbanization and land use change in Florida and the South. In: Bergstrom, J.C. (Ed.). Current Issues Associated with Land Values and Land Use Planning. Proceedings of a Regional Workshop. Southern Rural Development Center, pp. 28-49. http://srdc.msstate.edu/publications/220_ch2.pdf.

STUART, B.L. AND THORBJARNARSON, J. 2003. Biological prioritization of Asian countries for turtle conservation. Chelonian Conservation and Biology 4(3):642-647.

TFTSG AND ATTWG (IUCN/SSC TORTOISE AND FRESHWATER TURTLE SPECIALIST GROUP AND ASIAN TURTLE TRADE WORKING GROUP). 2000. Recommended changes to 1996 IUCN Red List status of Asian turtle species. In: van Dijk, P.P., Stuart, B.L., and Rhodin, A.G.J. (Eds.). Asian Turtle Trade: Proceedings of a Workshop on Conservation and Trade of Freshwater Turtles and Tortoises in Asia. Chelonian Research Monographs 2:156-164.

TTWG (TURTLE TAXONOMY WORKING GROUP). In review. A list of modern turtle terminal taxa (with comments on areas of instability and recent change). Submitted to Chelonian Research Monographs.

UNDP (UNITED NATIONS DEVELOPMENT PROGRAMME). 2005. Human Development Report 2005. http://hdr.undp.org/reports/global/2005.

VAN DIJK, P.P., STUART, B.L., AND RHODIN, A.G.J. (Eds.). 2000. Asian Turtle Trade: Proceedings of a Workshop on Conservation and Trade of Freshwater Turtles and Tortoises in Asia. Chelonian Research Monographs No. 2, 164 pp.

Appendix. Data for all 155 global nations and territories (including Florida) as used in this analysis. HDI = Human Development Index; nations in green are "high development" (= developed) areas with HDI ≥ 0.80, nations in orange are "medium development" (= developing) areas with HDI < 0.80 and ≥ 0.50, nations in red are "low development" (= underdeveloped) areas with HDI < 0.50, nations in black are unranked areas without adequate HDI data. Turtle richness includes all species and subspecies of freshwater turtles, tortoises, and marine turtles, living or extinct since 1500 AD (*n* = 475) currently most widely recognized as distinct (interpreted from Iverson, 1992, 2006; Fritz and Havas, in review; TTWG, in review; Rhodin, unpubl. data). Turtle density is richness per 1000 sq.km national area. Endemism is recorded as total number of endemic taxa and percent endemism. Threat level is recorded as TTL = (No. EX taxa x 3.0) + (No. EW taxa x 2.0) + (No. CR taxa x 2.0) + (No. EN taxa x 1.0) + (No. VU taxa x 0.5) or ATL = (TTL / number of taxa). Threat levels are per 2006 IUCN Red List, but adjusted for Florida as a stand-alone entity (see text). Prioritizations are sums of ranks of richness, endemism, and threat level, with Method A similar to that developed by Stuart and Thorbjarnarson (2003), ranking richness, percent endemism, and average threat level, and Method B different, ranking richness, total endemism, and total threat level. Nations in italics have lost all their native non-marine turtle taxa to extinction.

			Turtle	Turtle	Endemism		Threat Level		Prioritization	
	HDI	sq. km.	Richness	Density	Total	Percent	Total	Average	A	B
Afghanistan	—	652,225	2	0.003	0	0.00%	1.0	0.500	292.0	242.0
Albania	0.780	28,703	6	0.209	0	0.00%	3.0	0.500	243.0	160.5
Algeria	0.722	2,381,741	5	0.002	0	0.00%	2.0	0.400	276.5	190.0
Angola	0.445	1,246,700	14	0.011	0	0.00%	4.0	0.286	226.5	91.5
Argentina	0.863	2,780,092	11	0.004	2	18.18%	1.5	0.136	177.0	139.0
Armenia	0.759	29,743	4	0.134	0	0.00%	1.0	0.250	316.5	221.5
Australia	0.955	7,692,030	42	0.005	35	83.33%	12.0	0.286	100.5	19.5
Austria	0.936	83,858	1	0.012	0	0.00%	0.0	0.000	387.0	288.0
Azerbaijan	0.729	86,600	4	0.046	0	0.00%	1.0	0.250	316.5	221.5
Bahamas	0.832	13,939	6	0.430	1	16.67%	6.5	1.083	121.5	127.5
Bahrain	0.846	694	5	7.205	0	0.00%	6.0	1.200	208.0	150.0
Bangladesh	0.520	147,570	25	0.169	1	4.00%	17.5	0.700	90.5	27.0
Belarus	0.786	207,595	1	0.005	0	0.00%	0.0	0.000	387.0	288.0
Belize	0.753	22,965	11	0.479	0	0.00%	6.0	0.545	188.5	91.0
Benin	0.431	114,760	8	0.070	0	0.00%	4.0	0.500	222.0	127.0
Bolivia	0.687	1,098,581	11	0.010	0	0.00%	1.5	0.136	255.0	139.0
Bosnia and Herzegovina	0.786	51,129	4	0.078	0	0.00%	0.0	0.000	354.0	255.0
Botswana	0.565	581,730	9	0.015	0	0.00%	0.0	0.000	295.0	196.0
Brazil	0.792	8,547,404	39	0.005	11	28.21%	12.0	0.308	106.0	20.5
Brunei	0.866	5,765	7	1.214	0	0.00%	4.5	0.643	211.5	130.5
Bulgaria	0.814	287,413	4	0.014	0	0.00%	0.5	0.125	328.5	232.5
Burkina Faso	0.317	274,400	5	0.018	0	0.00%	0.5	0.100	318.5	220.0
Burundi	0.378	27,816	5	0.180	0	0.00%	0.0	0.000	341.5	242.5
Cambodia	0.571	181,035	14	0.077	0	0.00%	11.0	0.786	157.0	50.0
Cameroon	0.497	475,442	7	0.015	0	0.00%	0.5	0.071	295.0	191.0
Canada	0.949	9,970,610	12	0.001	0	0.00%	3.5	0.292	234.0	105.5
Cayman Islands	—	260	3	11.538	0	0.00%	2.0	0.667	261.0	212.5
Central African Republic	0.355	622,436	6	0.010	0	0.00%	0.0	0.000	325.5	226.5
Chad	0.341	1,284,000	6	0.005	0	0.00%	0.5	0.083	305.5	204.0
China (People's Republic of China)	0.755	9,572,900	29	0.003	9	31.03%	38.5	1.328	27.0	12.0
Colombia	0.785	1,141,568	32	0.028	3	9.38%	13.0	0.406	116.0	22.0
Congo (Democratic Republic of the Congo)	0.385	2,344,858	18	0.008	1	5.56%	2.5	0.139	169.0	99.5
Congo (Republic of the Congo)	0.512	342,000	7	0.020	0	0.00%	0.0	0.000	312.5	213.5
Costa Rica	0.838	51,100	14	0.274	0	0.00%	7.5	0.536	177.5	61.0
Croatia	0.841	56,542	4	0.071	0	0.00%	0.0	0.000	354.0	255.0
Cuba	0.817	110,861	6	0.054	1	16.67%	6.0	1.000	126.5	134.0
Cyprus	0.891	9,251	3	0.324	0	0.00%	2.0	0.667	261.0	212.5
Czech Republic	0.874	204,260	1	0.005	0	0.00%	0.0	0.000	387.0	288.0
Djibouti	0.495	23,200	1	0.043	0	0.00%	0.5	0.500	304.5	265.5
Dominican Republic	0.749	126,060	6	0.048	0	0.00%	6.5	1.083	196.5	127.5
Ecuador	0.759	272,045	28	0.103	10	35.71%	22.5	0.804	47.0	20.0
Egypt	0.659	997,690	6	0.006	0	0.00%	4.0	0.667	222.5	148.0
El Salvador	0.722	21,041	6	0.285	0	0.00%	3.0	0.500	243.0	160.5
Equatorial Guinea	0.655	28,051	6	0.214	0	0.00%	3.5	0.583	230.0	153.0
Eritrea	0.444	121,100	9	0.074	0	0.00%	7.5	0.833	177.0	87.0
Estonia	0.853	43,431	1	0.023	0	0.00%	0.0	0.000	387.0	288.0
Ethiopia	0.367	1,133,882	7	0.006	0	0.00%	0.5	0.071	295.0	191.0
Florida, USA	0.944	170,306	38	0.223	9	23.68%	11.5	0.303	109.5	23.5
France	0.938	543,965	6	0.011	1	16.67%	2.0	0.333	198.5	174.0
French Guiana	—	86,504	14	0.162	0	0.00%	7.5	0.536	177.5	61.0
Gabon	0.635	267,667	8	0.030	1	12.50%	0.0	0.000	235.5	205.5
Gambia	0.470	10,689	7	0.655	0	0.00%	0.0	0.000	312.5	213.5
Georgia	0.732	69,700	5	0.072	0	0.00%	2.5	0.500	259.0	185.0
Germany	0.930	357,021	1	0.003	0	0.00%	0.0	0.000	387.0	288.0
Ghana	0.523	238,533	11	0.046	0	0.00%	3.0	0.273	241.5	117.5
Greece	0.912	131,957	6	0.045	0	0.00%	1.5	0.250	288.0	182.0
Guatemala	0.663	108,889	17	0.156	0	0.00%	8.0	0.471	182.0	45.5
Guinea	0.466	245,857	5	0.020	0	0.00%	0.0	0.000	341.5	242.5
Guinea-Bissau	0.348	36,125	4	0.111	0	0.00%	0.0	0.000	354.0	255.0
Guyana	0.720	215,083	14	0.065	0	0.00%	7.0	0.500	186.5	66.0
Haiti	0.475	27,700	6	0.217	0	0.00%	6.5	1.083	196.5	127.5
Honduras	0.667	112,492	15	0.133	0	0.00%	8.0	0.533	173.5	52.0
Hungary	0.862	93,030	1	0.011	0	0.00%	0.0	0.000	387.0	288.0
India	0.602	3,166,414	38	0.012	7	18.42%	23.0	0.605	65.5	11.5
Indonesia	0.697	1,922,570	36	0.019	5	13.89%	30.5	0.847	56.0	9.5
Iran	0.736	1,629,918	13	0.008	2	15.38%	6.0	0.462	130.5	83.5
Iraq	—	435,052	5	0.011	0	0.00%	1.5	0.300	295.0	198.0
Israel	0.915	20,425	8	0.392	0	0.00%	6.5	0.813	189.0	106.5
Italy	0.934	301,277	9	0.030	3	33.33%	4.0	0.444	136.5	117.5
Ivory Coast (Cote d'Ivoire)	0.420	322,463	9	0.028	0	0.00%	3.0	0.333	243.0	130.0
Jamaica	0.738	10,991	4	0.364	0	0.00%	4.5	1.125	223.0	172.0

	HDI	sq. km.	Turtle Richness	Turtle Density	Endemism		Threat Level		Prioritization	
					Total	Percent	Total	Average	A	B
Japan	0.943	377,837	9	0.024	4	44.44%	8.5	0.944	81.5	82.0
Jordan	0.753	89,342	2	0.022	0	0.00%	0.0	0.000	374.5	275.5
Kazakhstan	0.761	2,724,900	4	0.001	0	0.00%	1.5	0.375	295.0	210.5
Kenya	0.474	582,646	13	0.022	1	7.69%	5.0	0.385	150.5	90.0
Kuwait	0.844	17,818	2	0.112	0	0.00%	1.0	0.500	292.0	242.0
Kyrgyzstan	0.702	199,900	2	0.010	0	0.00%	1.0	0.500	292.0	242.0
Laos	0.545	236,800	16	0.068	0	0.00%	13.0	0.813	144.0	35.5
Latvia	0.836	64,589	1	0.015	0	0.00%	0.0	0.000	387.0	288.0
Lebanon	0.759	10,400	5	0.481	0	0.00%	2.5	0.500	259.0	185.0
Lesotho	0.497	30,355	2	0.066	0	0.00%	0.0	0.000	374.5	275.5
Liberia	—	97,754	7	0.072	0	0.00%	3.0	0.429	245.0	147.5
Libya	0.799	1,757,000	5	0.003	1	20.00%	4.0	0.800	147.0	164.0
Lithuania	0.852	65,300	1	0.015	0	0.00%	0.0	0.000	387.0	288.0
Macedonia	0.797	25,713	4	0.156	0	0.00%	0.5	0.125	328.5	232.5
Madagascar	0.499	587,041	14	0.024	8	57.14%	10.0	0.714	68.0	52.0
Malawi	0.404	118,484	8	0.068	0	0.00%	0.0	0.000	304.5	205.5
Malaysia	0.796	329,845	23	0.070	0	0.00%	21.5	0.935	134.0	25.5
Maldives	0.745	298	3	10.067	0	0.00%	3.0	1.000	240.0	199.0
Mali	0.333	1,248,574	6	0.005	0	0.00%	0.5	0.083	305.5	204.0
Mauritania	0.477	1,030,700	5	0.005	0	0.00%	1.5	0.300	295.0	198.0
Mauritius (incl. Rodrigues)	*0.791*	*2,040*	*5*	*2.451*	*4*	*80.00%*	13.0	2.600	106.5	117.5
Mexico	0.814	1,964,375	63	0.032	31	49.21%	21.5	0.341	93.0	10.5
Moldova	0.671	33,700	1	0.030	0	0.00%	0.0	0.000	387.0	288.0
Morocco	0.631	710,850	9	0.013	4	44.44%	3.5	0.389	139.5	122.5
Mozambique	0.379	812,379	15	0.018	0	0.00%	7.0	0.467	190.5	60.5
Myanmar	0.578	676,577	30	0.044	7	23.33%	27.0	0.900	43.0	13.0
Namibia	0.627	825,118	13	0.016	1	7.69%	1.5	0.115	189.5	131.5
Nepal	0.526	147,181	13	0.088	0	0.00%	6.0	0.462	203.5	83.5
Nicaragua	0.690	130,373	16	0.123	0	0.00%	7.5	0.469	185.5	51.5
Niger	0.281	1,186,408	3	0.003	0	0.00%	0.5	0.167	332.5	242.5
Nigeria	0.453	923,768	11	0.012	0	0.00%	1.0	0.091	260.5	150.0
North Korea	—	122,762	2	0.016	0	0.00%	1.5	0.750	265.5	231.0
Pakistan	0.527	796,095	11	0.014	1	9.09%	4.0	0.364	163.5	105.0
Panama	0.804	74,979	15	0.200	0	0.00%	7.5	0.500	181.0	55.5
Papua New Guinea	0.523	462,840	14	0.030	1	7.14%	9.5	0.679	104.0	54.0
Paraguay	0.755	406,752	6	0.015	0	0.00%	0.5	0.083	305.5	204.0
Peru	0.762	1,285,216	16	0.012	0	0.00%	6.0	0.375	200.5	68.0
Philippines	0.758	300,076	9	0.030	1	11.11%	9.5	1.056	102.0	80.0
Poland	0.858	312,685	1	0.003	0	0.00%	0.0	0.000	387.0	288.0
Portugal	0.904	92,365	2	0.022	0	0.00%	0.0	0.000	374.5	275.5
Puerto Rico	—	9,104	5	0.549	1	20.00%	6.0	1.200	126.5	150.0
Réunion	—	*2,507*	*3*	*1.197*	*1*	*33.33%*	6.0	2.000	138.5	172.5
Romania	0.792	237,500	3	0.013	0	0.00%	0.5	0.167	332.5	242.5
Russia	0.796	17,075,400	7	0.000	1	14.29%	3.0	0.429	173.5	147.5
Rwanda	0.450	26,338	6	0.228	0	0.00%	0.0	0.000	325.5	226.5
São Tomé and Príncipe	0.604	1,001	3	2.997	0	0.00%	1.0	0.333	312.0	231.5
Saudi Arabia	0.772	2,248,000	5	0.002	0	0.00%	3.0	0.600	243.5	176.5
Senegal	0.458	196,712	11	0.056	0	0.00%	5.5	0.500	200.0	95.5
Seychelles	0.821	455	9	19.780	7	77.78%	17.5	1.944	63.0	68.5
Sierra Leone	0.298	71,740	8	0.112	0	0.00%	3.0	0.375	245.5	139.5
Singapore	0.907	683	8	11.713	0	0.00%	5.0	0.625	204.5	119.5
Slovakia	0.849	49,035	1	0.020	0	0.00%	0.0	0.000	387.0	288.0
Slovenia	0.904	20,273	2	0.099	0	0.00%	0.0	0.000	374.5	275.5
Somalia	—	637,000	8	0.013	0	0.00%	3.0	0.375	245.5	139.5
South Africa	0.658	1,219,090	26	0.021	6	23.08%	5.0	0.192	135.0	67.0
South Korea	0.901	99,461	2	0.020	0	0.00%	1.5	0.750	265.5	231.0
Spain	0.928	505,990	7	0.014	1	14.29%	2.5	0.357	186.0	156.0
Sri Lanka	0.751	65,610	9	0.137	1	11.11%	7.0	0.778	118.0	92.0
Sudan	0.512	2,503,890	10	0.004	0	0.00%	2.5	0.250	250.5	131.5
Suriname	0.755	163,820	13	0.079	0	0.00%	7.0	0.538	182.0	72.0
Swaziland	0.498	17,364	6	0.346	0	0.00%	0.0	0.000	325.5	226.5
Switzerland	0.947	41,284	1	0.024	0	0.00%	0.0	0.000	387.0	288.0
Syria	0.721	185,180	6	0.032	0	0.00%	3.5	0.583	230.0	153.0
Taiwan (Republic of China)	0.910	36,188	9	0.249	1	11.11%	10.5	1.167	97.0	77.0
Tajikistan	0.652	143,100	2	0.014	0	0.00%	1.0	0.500	292.0	242.0
Tanzania	0.418	942,799	15	0.016	1	6.67%	4.5	0.300	158.0	81.5
Thailand	0.778	513,115	29	0.057	0	0.00%	24.0	0.828	132.0	16.0
Timor Leste (East Timor)	0.513	14,609	2	0.137	0	0.00%	1.5	0.750	265.5	231.0
Togo	0.512	56,785	10	0.176	0	0.00%	2.5	0.250	248.0	131.5
Trinidad and Tobago	0.801	5,128	11	2.145	0	0.00%	6.5	0.591	185.5	84.5
Tunisia	0.753	164,150	4	0.024	0	0.00%	1.5	0.375	295.0	210.5
Turkey	0.750	779,452	16	0.021	3	18.75%	7.0	0.438	110.5	56.5
Turkmenistan	0.738	488,100	5	0.010	0	0.00%	1.5	0.300	295.0	198.0
Uganda	0.508	241,038	10	0.041	0	0.00%	0.0	0.000	288.0	189.0
Ukraine	0.766	603,700	3	0.005	0	0.00%	0.5	0.167	332.5	242.5
United States of America (including Florida)	0.944	7,710,721	88	0.011	59	67.05%	18.0	0.205	109.0	11.0
Uruguay	0.840	176,215	6	0.034	0	0.00%	1.0	0.167	294.0	193.0
Uzbekistan	0.694	447,400	2	0.004	0	0.00%	1.0	0.500	292.0	242.0
Venezuela	0.772	916,445	25	0.027	3	12.00%	9.5	0.380	123.5	38.5
Vietnam	0.704	331,041	29	0.088	5	17.24%	30.5	1.052	46.0	13.5
Yemen	0.489	472,099	3	0.006	0	0.00%	3.0	1.000	240.0	199.0
Yugoslavia (Serbia and Montenegro)	—	102,173	4	0.039	0	0.00%	0.0	0.000	354.0	255.0
Zambia	0.394	752,614	8	0.011	0	0.00%	0.0	0.000	304.5	205.5
Zimbabwe	0.505	390,757	9	0.023	0	0.00%	0.0	0.000	295.0	196.0

Biology and Conservation of Florida Turtles – Peter A. Meylan, Ed.
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Introduction

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As this world becomes a more crowded place we will have to make specific provisions for those animals and plants that we would like to take with us into the future. Most of the biodiversity that survives around us today does so by accident. The species that we have not used up and species whose habitats we have not used up are what we have for company. Clearly there are valiant efforts to preserve significant parcels of natural habitat, and individual species, but the native plants and animals that most of us see on a daily basis remain with us largely by accident. They are the survivors of our success as a species.

As we humans continue to fill more and more of the planet and demand the use of more of its resources, this "default" option for conserving the other species that live on this planet will work for fewer and fewer of them. This is certainly the case for turtles in Florida. The turtle species that flourish in drainage ditches and retention ponds are very likely to remain common and those that get along with alligators may already benefit from the economic interest in that species and the resultant management decisions. But, there are no turtles that flourish in subdivisions, shopping malls, pine plantations, or tomato fields. Instead, upland species are losing out rapidly to development and so, too, are species whose habitat requirements include uplands adjacent to wetlands. Riverine species face a variety of threats, not the least of which is the degradation of their limited, linear habitats. Sea turtles in Florida share a series of threats, the most pressing of which is the squeeze they face on Florida's nesting beaches between rising sea levels on the one hand and rapid rates of beach armoring on the other (L. Ehrhart, *pers. comm.*). In total, there are 25 species of turtles that are native to Florida, 18 of them have been considered to be in need of conservation attention (Table 1).

Although none of the turtle species that inhabited Florida when Europeans arrived in the 15th century have gone extinct, we probably lost our giant tortoises with the arrival of humans about 10,000 years ago. Two extinct land tortoises, *Hesperotestudo incisa* and *H. crassiscutata*, relatives of the living gopher tortoise, were almost certainly still living in Florida when the first humans arrived (Holman, 1978). There is good evidence that paleoindians dined on the larger of the two species (Clausen et al., 1979).

Kemp's ridley (*Lepidochelys kempii*) probably came very close to extinction in the early 1970s when the harvest of nesting females and their eggs on the only known nesting beach in Tamaulipas, Mexico, combined with loss to shrimp trawls throughout the Gulf of Mexico reduced the species to a few hundred females nesting annually. But timely action by the Mexican Government, National Marine Fisheries Service, U.S. Fish and Wildlife Service, and the U.S. National Park Service prevented this extinction. By putting Mexican marines on the nesting beach and turtle excluder devices (TEDs) in the mouths of shrimp nets, the smallest of the living sea turtles was snatched from the jaws of extinction.

Florida's sea turtles are the most seriously threatened turtle species in our state. Kemp's ridley appears to be started down the road to recovery (Márquez et al., 2005) but the leatherback (*Dermochelys coriacea*) seems to be in serious decline, at least in the Pacific (Spotila, 1996, 2000). The hawksbill turtle (*Eretmochelys imbricata*) has recently been confirmed to be critically endangered (Meylan and Donnelly, 1999). Nesting beach populations are flourishing at only five sites worldwide where they have been protected for 10 years or more. At some protected sites they are not increasing and there is a continuing threat that international trade in hawksbill shell could reopen.

Gopher tortoises (*Gopherus polyphemus*) were originally found in every county in Florida, but it appears that the most populated counties may be seeing the last of their gophers disappear now. Furthermore, a respiratory disease has decimated populations even in the most remote parts of the state. Box turtles also occur throughout the state and are still common at a few select sites. But they are now uncommon over parts of their former range. The diamondback terrapin (*Malaclemys terrapin*) should be common all along Florida's coasts but appears to have suffered the fate of this species in other states. Many have been drowned in crab traps and the species is quite rare in places. The spotted turtle (*Clemmys guttata*) has only recently been confirmed as native to Florida and is known from fewer than 50 records spread across the state from just south of Tallahassee to just north and west of Orlando.

Even relatively common freshwater species suffer serious impact from human development. For example, roadways dice up their habitat. This is particularly problematic in Florida because wetlands and lakes throughout the state are highly dynamic, drying and filling at irregular intervals. Turtles are often forced to move because of these fluctuations and in doing so are threatened by the need to cross roads. Nowhere has this been as dramatically documented as in Tallahassee during a recent drying event at Lake Jackson. Over a 43-month period that included a major dry-down event, Aresco (2003) recorded 8833 attempts by turtles to cross U.S. Hwy. 27 between Lake Jackson and Little Lake Jackson, in Leon Co. During a 40-day period before fencing was put up to keep migrating turtles off of the roadway, 343

Figure 1. Turtles and tortoises are well-liked members of the Floridian fauna and need to be preserved. Photo by George Heinrich.

turtles were found dead on the road. A temporary silt fence barrier was constructed along the portions of the roadway at which most animals were crossing. It intercepted 8466 attempts by turtles of nine different species to cross the highway over the remaining period. The fencing reduced the rate of mortality from 9.7 turtles/km/day to 0.08 turtles/km/day. Aresco (2003) estimated that without the barrier, turtles would have died at a rate of 1294 turtles/km/year over the course of his 3.5 years of study. This is just one 2 km segment of one road crossing one corner of one Florida lake. How many similar stretches of highway exist in Florida?

Although the situation for turtles in Florida is not yet desperate, the outlook is for more development with more habitat fragmentation and loss, and these are coming rapidly. The human population of Florida grew by 23.5% between 1990 and 2000 and is on pace to increase at the same rate between 2000 and 2010 (U.S. Census Bureau, 2004). So it is time to formulate a plan to save all of Florida's turtles and to save them over as much of the state as possible. If we don't, we will all live poorer lives. People like turtles, they like to see and hold turtles (Fig. 1). Turtles are not like crocodiles or other species for which one has to provide economic incentives for conservation. We can get people to save turtles for turtles' sake and we don't have to try to develop economic excuses for their saving. But in order to save turtles in Florida and elsewhere, we must educate people, spur their interest in these ancient creatures, inform them of the conservation issues, and educate decision-makers about their plight and what can be done. That is the purpose of this book.

About Florida Turtles. — Turtles are an ancient group with ancient diversity and much of that diversity is represented in Florida. The two basic types of turtles, side-necks (Pleurodira), and hidden-necks (Cryptodira), started down independent evolutionary pathways in the Triassic, at the beginning of the age of dinosaurs, but unlike the dinosaurs, both survive today. Side-necks have never been reported from Florida but it is only a matter of time before a fossil of the group is collected in the state. There are records of side-necks in the Miocene of Maryland and the Pliocene of North Carolina and there are several records of fossils from around the Caribbean during this time. These all probably represent an extinct marine radiation of side-necks (the *Shweboemys* Group of the Podocnemididae, see Gaffney and Wood, 2002). Turtles of this group must have been present in Florida waters in the Miocene and Pliocene and fossils will one day be found in Florida.

Florida's living turtles are all cryptodires. They belong to 7 of the 11 living cryptodire families. Three of the families that are not found in Florida are each represented by a single living species (Carettochelyidae, Dermatemydidae, and Platysternidae). Only one large family of hidden-necked turtles does not have representatives in Florida, the Geoemydidae. All seven of the cryptodire families in Florida are ancient lineages. Five of seven can be dated back to the Cretaceous, the last portion of the age of dinosaurs. The two youngest families are at least 52 million years old. Details about the evidence for the great age of the families of Florida turtles are given in each of the family introductions in this volume.

The living turtle fauna of Florida is significant on a global scale. The 25 species belong to 7 of 14 living turtle families (Table 2); so, in a sense, half of the major kinds of turtles in the world are represented in Florida. At present about 275 turtle species are recognized worldwide, so just less than 10% of the world's turtle species are found in our

Table 1. Listed species, subspecies, and populations of turtles from Florida.

Scientific Name	FNAI Global Rank[1]	FNAI State Rank[2]	Federal Status[3]	State Status[4]	CITES Status[5]	FWC Bioscore[6]
Lepidochelys kempii	G1	S1	LE	E	App. I	28
Chelonia mydas	G3	S2	LE	E	App. I	27.6
Dermochelys coriacea	G2	S2	LE	E	App. I	25.6
Eretmochelys imbricata	G3	S1	LE	E	App. I	
Caretta caretta	G3	S3	LT	T	App. I	18.3
Graptemys barbouri	G2	S2	N	SSC	App. III	28.3
Graptemys ernsti	G2	S2	N	N	App. III	22.3
Gopherus polyphemus	G3	S3	N	T	App. II	27.3
Macrochelys temminckii	G3G4	S3	N	SSC	App. III	17
Malaclemys terrapin rhizophorarum	G4T2	S2	N	N		33.6
Clemmys guttata	G5	S3?	N	N		18.7
Kinosternon baurii (pop. 1)[7]	G5T2Q	S2	N	E		
Pseudemys nelsoni (pop. 1)[8]	G5T2Q	S2	N	N		
Pseudemys concinna suwanniensis	G5T3	S3	N	SSC		30
Apalone mutica calvata	G5T5	S1	N	N		12.3
Malaclemys terrapin tequesta						33.6
Malaclemys terrapin centrata						29.6
Malaclemys terrapin macrospilota						29.6
Malaclemys terrapin pileata						26.3
Terrapene carolina major					App. II[9]	22
Terrapene carolina bauri[10]					App. II[9]	20
Deirochelys reticularia[10]						9
Kinosternon subrubrum steindachneri[10]						12

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[1] Florida Natural Areas Inventory (FNAI) global rank is based on an element's worldwide status. G1 = Critically imperiled globally because of extreme rarity or extreme vulnerability to extinction due to some natural or man-made factor. G2 = Imperiled globally because of rarity or because of vulnerability to extinction due to some natural or man-made factor. G3 = Either very rare and local throughout its range or found locally in a restricted range or vulnerable to extinction from other factors. G4 = Apparently secure globally. G5 = Demonstrably secure globally. G#G# = Range of rank; insufficient data to assign specific global rank (e.g. G3G4). G#T# = Rank of a taxonomic subgroup such as a subspecies or variety; the G portion of the rank refers to the entire species and the T portion refers to the specific subgroup; numbers have same definition as above (e.g., G4T2). G#T#Q = Same as above, but validity as subspecific rank or variety is questioned.

[2] Florida Natural Areas Inventory (FNAI) state rank is based on the status of the element in Florida. S1 = Critically imperiled in Florida because of extreme rarity (5 or fewer occurrences or less than 1000 individuals) or because of extreme vulnerability to extinction due to some natural or man-made factor. S2 = Imperiled in Florida because of rarity (6 to 20 occurrences or less than 3000 individuals) or because of vulnerability to extinction due to some natural or man-made factor. S3 = Either very rare and local throughout its range (21-100 occurrences or less than 10,000 individuals) or found locally in a restricted range or vulnerable to extinction from other factors. S4 = Apparently secure in Florida. S5 = Demonstrably secure in Florida.

[3] Federal legal status. These definitions are derived from the U.S. Endangered Species Act of 1973. The federal status given here is that for Florida populations. LE = Endangered: species in danger of extinction throughout all or a significant portion of its range. LT = Threatened: species likely to become endangered with the foreseeable future throughout all or a significant portion of its range. N = Not currently listed, nor currently being considered for listing as Endangered or threatened.

[4] State legal status. Data from FNAI. E = Endangered: species, subspecies, or isolated population so few or depleted in number or so restricted in range that it is in imminent dater of extinction. T = Threatened: species, subspecies, or isolated population facing a very high risk of extinction in the future. SSC = Species of Special Concern is a species, subspecies, or isolated population which is facing a moderate risk of extinction in the future. N = Not currently listed, nor currently being considered for listing.

[5] Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Appendix I (App. I) includes those species in danger of extinction for which all commercial trade is prohibited. Appendix II (App. II) are not necessarily threatened with extinction but may become so unless trade is strictly regulated. Appendix III (App. III) are species listed by the USA only. These include species that are in international trade and are vulnerable to overexploitation. Regulated trade is allowed provided that the exporting country issues a permit that includes findings that the specimens were legally acquired, and the trade will not be detrimental to the survival of the species or its role in the ecosystem. http://www.cites.org/eng/resources/species.html

[6] FWC Bioscore is an attempt to measure seven biological variables that can be considered indicators of vulnerability to extinction: population size, population trend, range size, distribution trend, population concentration, reproductive potential and ecological specialization (Millsap et al., 1990),

[7] Florida Keys population only. See account for *Kinosternon baurii*.

[8] Florida panhandle population only. See account for *Pseudemys nelsoni*.

[9] Listed as all members of the genus *Terrapene.*

[10] These three turtles were added to a list of "Species of greatest conservation need" during a Florida Comprehensive Wildlife Conservation Strategy Workshop held 3–4 November 2004.

Table 2. The species treated in this volume and their geographic distribution.

Family	Scientific Name	Common Name	Florida Distribution	Global Distribution
Chelydridae	*Chelydra serpentina*	snapping turtle	statewide	Canada to northern South America
Chelydridae	*Macrochelys temminckii*	alligator snapping turtle	panhandle and northern peninsula	southern US
Dermochelyidae	*Dermochelys coriacea*	leatherback	along both coasts	world wide
Cheloniidae	*Chelonia mydas*	green turtle	along both coasts	world wide
Cheloniidae	*Eretmochelys imbricata*	hawksbill	along both coasts	world wide
Cheloniidae	*Caretta caretta*	loggerhead	along both coasts	world wide
Cheloniidae	*Lepidochelys kempii*	Kemp's ridley	along both coasts	North Atlantic and Gulf
Trionychidae	*Apalone ferox*	Florida softshell	statewide	southeast US
Trionychidae	*Apalone mutica*	smooth softshell	small part of panhandle	central US
Trionychidae	*Apalone spinifera*	spiny softshell	panhandle and northern peninsula	eastern US
Kinosternidae	*Kinosternon baurii*	striped mud turtle	peninsula	southeast US
Kinosternidae	*Kinosternon subrubrum*	eastern mud turtle	statewide	eastern US
Kinosternidae	*Sternotherus minor*	loggerhead musk turtle	panhandle and northern peninsula	southeast US
Kinosternidae	*Sternotherus odoratus*	musk turtle	statewide	eastern US
Emydidae	*Terrapene carolina*	box turtle	statewide	eastern US
Emydidae	*Clemmys guttata*	spotted turtle	northern peninsula	eastern US and Canada
Emydidae	*Trachemys scripta*	yellow-bellied slider	panhandle and northern peninsula	eastern US to South America
Emydidae	*Graptemys barbouri*	Barbour's map turtle	small part of panhandle	AL, FL, GA
Emydidae	*Graptemys ernsti*	Ernst's map turtle	small part of panhandle	AL, GA
Emydidae	*Malaclemys terrapin*	diamondback terrapin	along both coasts	Massachusetts to Texas (coastal)
Emydidae	*Deirochelys reticularia*	chicken turtle	statewide	southeast US
Emydidae	*Pseudemys floridana*	Florida cooter	statewide	southeast US
Emydidae	*Pseudemys nelsoni*	red-bellied cooter	peninsula	FL, GA
Emydidae	*Pseudemys concinna*	river cooter or Suwannee cooter	panhandle and northern peninsula	eastern US
Testudinidae	*Gopherus polyphemus*	gopher tortoise	statewide	southeast US

state. By carefully examining the distributions of all of the world's turtles, Iverson (1992a,c) identified two centers of global diversity for turtles. One of them is in Bangladesh at the mouth of the Ganges River; the other is in the southeastern United States, with the highest diversity reached in the panhandle of Florida and adjacent Mobile Bay. Drainage basins in the southeastern U.S. have some of the highest numbers of species found in any single river drainage in the world. Iverson (1992a) listed the Ganges River as the most diverse basin with 19 species known. But southeast U.S. rivers such as the Mississippi, Mobile, Apalachicola, Savannah, and Suwannee are close behind with 15 to 18 species each. When sea turtles and terrestrial species are considered in addition to the freshwater forms, Florida stands out as an extremely important center of worldwide turtle diversity.

Although there are no turtle species whose distribution is entirely restricted to Florida, there are many for which the greatest part of their range, and probably the majority of their populations, occur in Florida. These include the Florida red-bellied turtle (*Pseudemys nelsoni*), the Florida cooter (*Pseudemys floridana*), the Florida softshell (*Apalone ferox*), the striped mud turtle (*Kinosternon baurii*), the gopher tortoise (*Gopherus polyphemus*), and possibly the chicken turtle (*Deirochelys reticularia*). The loggerhead sea turtle (*Caretta caretta*), which is the most commonly encountered sea turtle species on Florida beaches, has just two major nesting areas worldwide; Florida is one and Oman the other. A recent review of the status of green turtles (*Chelonia mydas*) worldwide (Seminoff, 2004) revealed that the nesting colony in Florida, although small, is increasing in size and importance in the Western Atlantic.

There are nine subspecies of turtles that are found only within the borders of the state of Florida. They can be considered endemic. These include the Florida snapping turtle (*Chelydra serpentina osceola*), the Florida mud turtle (*Kinosternon subrubrum steindachneri*), the peninsula cooter

Table 3. Subspecies that occur in Florida as used in this volume.

Species	Subspecies
Chelydra serpentina	*Chelydra s. serpentina* *Chelydra s. osceola*
Apalone mutica	*Apalone m. calvata*
Apalone spinifera	*Apalone s. aspera*
Kinosternon subrubrum	*Kinosternon s. subrubrum* *Kinosternon s. hippocrepis* *Kinosternon s. steindachneri*
Terrapene carolina	*Terrapene c. carolina* *Terrapene c. bauri* *Terrapene c. major* *Terrapene c. triunguis*
Trachemys scripta	*Trachemys s. scripta* *Trachemys s. elegans*
Malaclemys terrapin	*Malaclemys t. centrata* *Malaclemys t. tequesta* *Malaclemys t. rhizophorarum* *Malaclemys t. macrospilota* *Malaclemys t. pileata*
Deirochelys reticularia	*Deirochelys r. reticularia* *Deirochelys r. chrysea*
Pseudemys floridana	*Pseudemys f. floridana* *Pseudemys f. peninsularis*
Pseudemys concinna	*Pseudemys c. concinna* *Pseudemys c. suwanniensis*

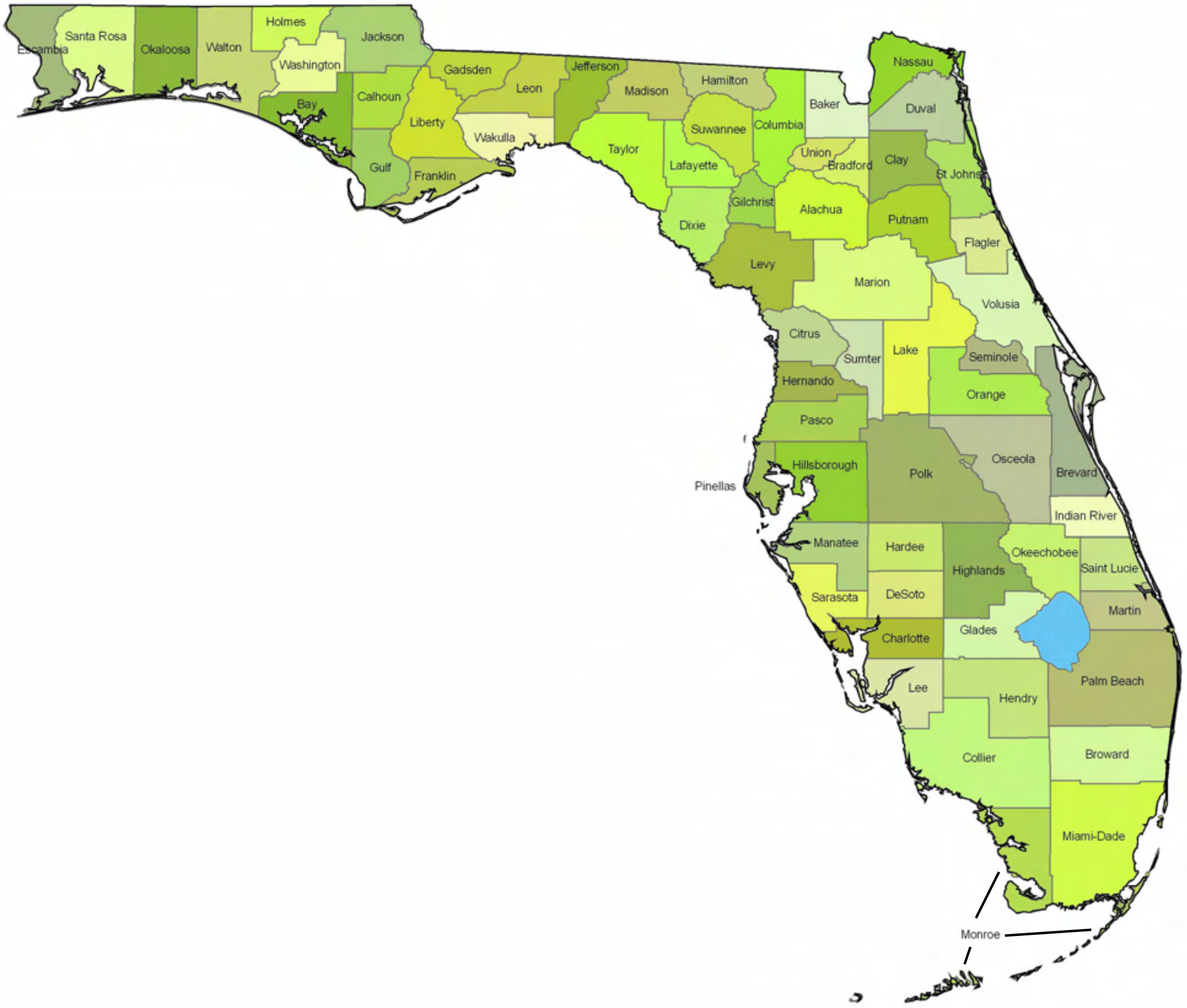

Figure 2. Map of Florida counties.

(*Pseudemys floridana peninsularis*), the Florida chicken turtle (*Deirochelys reticularia chrysea*), two kinds of box turtles, the Florida box turtle (*Terrapene carolina bauri*) and the Gulf Coast box turtle (*Terrapene carolina major*), and three kinds of diamondback terrapins, the Florida east coast terrapin (*Malaclemys terrapin tequesta),* the mangrove terrapin *(Malaclemys terrapin rhizophorarum),* and the ornate terrapin *(Malaclemys terrapin macrospilota*). A tenth subspecies, the Suwannee cooter (*Pseudemys concinna suwanniensis*) is nearly endemic but occurs in a few drainages in southwestern Georgia. The subspecies that occur in Florida are listed in Table 3.

There is one species that may have made its way to Florida naturally but is not included in this volume. The olive ridley (*Lepidochelys olivacea*) is now known from strandings in the Florida Keys. At least three have stranded in recent years (Foley et al., 2003). They are well known in the southern Caribbean where they nest on the coast of Suriname, Guyana, and French Guiana (Pritchard and Trebbau, 1984). They forage in the waters off the north coast of South America, Trinidad, Tobago, and the Windward Islands regularly and on occasion reach as far north as Puerto Rico. Thus, it should not be surprising that a carefully run stranding program would eventually detect this species as a waif on the coast of Florida.

Scientific and Common Names for Florida Turtles. — There is no universal agreement about the common and scientific names of the 25 species of turtles living in Florida. Generally the taxonomy used in the accounts in this book is that used in the current scientific literature (Crother et al., 2000, 2003) but there are exceptions. The authors of each account comment briefly on the longevity and stability of the scientific name by which each Florida turtle is currently known. The only controversy serious enough to require comment in the introduction is the use of the names *Pseudemys concinna* and *Pseudemys floridana* for turtles that go by the common name of river cooters and Florida cooters. In this book we use the nomenclature that was in common use about 10 years ago (Ernst et al, 1994). *Pseudemys concinna concinna* is used for river cooters from the Apalachicola River westward through the panhandle of Florida and *Pseudemys concinna suwanniensis* is used for the river cooters, commonly called Suwannee cooters, from east of the Apalachicola River in Gulf drainages to Tampa Bay. For

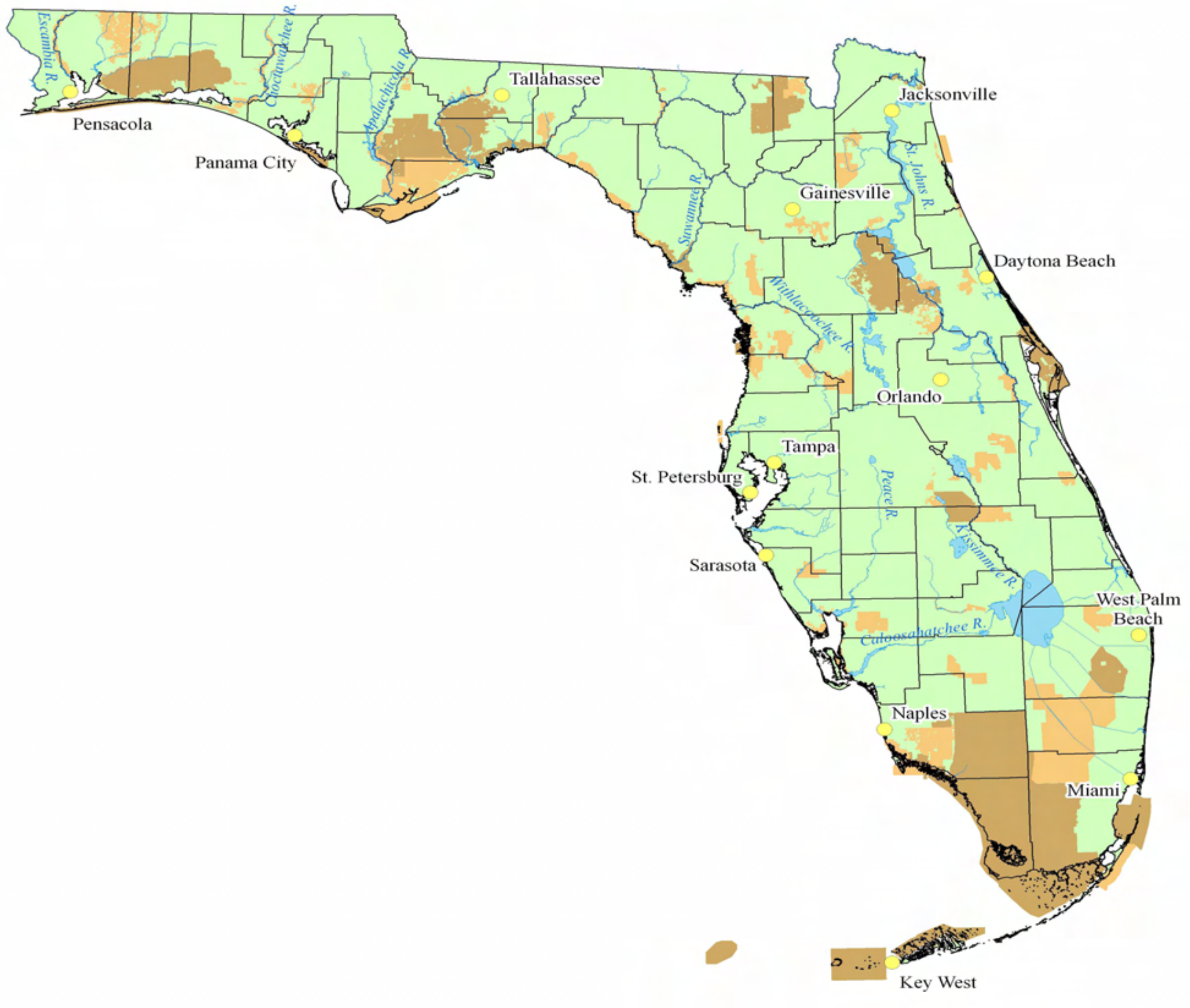

Figure 2. Map of major protected areas (dark brown = Federal, light brown = State) in Florida, as well as major cities and rivers.

Florida cooters in the panhandle, we use the name *Pseudemys floridana floridana* rather than the proposed name, *Pseudemys concinna floridana* (Seidel, 1994). We do so because *P. concinna concinna* and *P. floridana floridana* occur in the same rivers in western Florida (Jensen and Birkhead, 2003; Ewert, Pritchard and Wallace, this volume; D. Jackson, *pers. comm.*; Fig. 24-3). When two closely related forms like these occur together and do not interbreed they should be recognized as separate species. Furthermore, *Pseudemys floridana floridana* has a wide area over which it intergrades with *Pseudemys floridana peninsularis* between Ocala and Tallahassee. These forms do appear to be exchanging genes throughout this area and are thus acting as a single species, suggesting that the use of the name *Pseudemys peninsularis* (Seidel, 1994) for the peninsular form should not be followed, because it implies that the peninsular form is isolated from the mainland form. While it may be true that outside of their Florida range *Pseudemys floridana* and *Pseudemys concinna* exchange genes and do not act like good species, as far as can be determined in Florida, they do act like two separate species and thus, they are treated as such in this volume. More detail on this taxonomic issue is found in the accounts of these two species.

A related naming issue is the use of subspecies. Subspecies are problematic because they are hard to define and they do not fit well into modern systematic philosophy. Subspecies are usually recognized as distinct morphotypes of a given species with a prescribed distribution. For example, box turtles in peninsular Florida have a distinctive carapacial pattern of bright yellow, narrow, radiating lines on a black shell (Fig. 16-1) that is quite different from the patterns of adjacent forms of box turtles in which the lines are broader, usually smudged and darker in color. Because of this unique coloration, the box turtles in peninsular Florida are known as a subspecies, *Terrapene carolina bauri*. They are not treated as a full species because where they meet other subspecies of box turtles intergrades are found which implies that genes are exchanged and these taxa are not acting as separate species.

Based on this example, it would seem that subspecies are a useful and simple concept. However, subspecies have fallen into disuse because it is difficult to show that they are natural or monophyletic groups (a single common ancestor and all descendants in the group) and there is a very useful and pervasive trend in systematics to recognize only monophyletic groups. In fairness to the subspecies concept, it seems clear that subspecies were not originally construed as phylogenetic entities (monophyletic groups), but simply as "unique morphotypes." In the interest of uniformity, bringing subspecies into line with the rest of modern systematic philosophy is the right thing to do. However, for the purposes of summarizing the biology and assessing the status of turtles in Florida at the beginning of the 21st century, continued consideration of subspecies is useful. It provides the option of considering the biology and status of widespread species on a more localized scale rather than treating each only at the species level. The decision to consider subspecies has been left up to the account authors. In some cases (*Chelydra serpentina, Kinosternon subrubrum*), the validity of Florida subspecies has been re-examined; for others (*Malaclemys, Terrapene*), such a re-examination is beyond the scope of this volume.

About this Book. — The authors of this volume have worked hard to understand the biology of Florida turtles and have compiled their work in the hope that it will improve the outlook for turtle populations of all species across the entire state and beyond. It is only by understanding the biology of our fauna and flora, and knowing what each species requires to survive and flourish, that we can take the steps necessary to keep more species off of endangered and threatened species lists.

This book is not meant to serve as a field guide to Florida turtles. It is meant as a guide for current and future generations of biologists, conservationists, and land managers to make progress in the direction of keeping all 25 of the species of turtles that occur in Florida today in all of the regions of the state in which they now exist. Thus, the emphasis of the individual accounts is on those aspects of biology most closely related to the conservation of the species in question. In addition, the known and anticipated threats faced by each one as well as conservation solutions are included.

This introduction includes a county map (Fig. 2) to help the reader locate Florida counties that are mentioned in the text. A map that summarizes protected areas in Florida, and thus the best sites for long-term survival of certain turtle species, is also provided (Fig. 3).

It is a privilege for me to be able to bring together the efforts of nearly 40 biologists who are experts on the species about which they have written. Many have studied turtles for decades, others are rapidly rising students. The authors all share the qualification that they have extensive first-hand experience with the species they cover. They are therefore highly qualified to summarize the biology of these species and to describe the kinds of problems the 25 turtle species found in Florida are now facing, are likely to face in the near future, and more important, what we might do to alleviate these problems.

As Florida races towards complete development, we absolutely must face the challenge of conserving as much of our natural history as possible. The effects of all of the different types of human impacts must be more completely appreciated and then carefully weighed and mitigated so that survivorship of species can be promoted along the path of least human resistance. People like turtles. They will want to keep them around, even if they can't make a profit from them.

If we are not willing to increase our conservation efforts on behalf of turtles, then we are poor stewards of this planet. Turtles are among our favorite animals. They are for the most part innocuous. They are long-lived, patient, and peaceful. We are fascinated by their remarkable shell, their longevity, their truly ancient history, and certain aspects of their biology, such as the migratory capabilities of sea turtles. Furthermore, what is good for turtles is good for people. The more healthy wetlands we have in this state, the more recharge areas we have for our critical aquifers. Clean rivers, beaches without seawalls, oligotrophic spring runs without motor boats, and regularly burned forests suitable for walking and admiring wild flowers will all benefit humans and turtles alike.

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LITERATURE CITED

Aresco, M.J. 2003. Highway mortality of turtles and other herpetofauna at Lake Jackson, Florida, USA, and the efficacy of a temporary fence / culvert system to reduce roadkills. In: Irwin, C.L., Garrett, P., and McDermott, K.P. (Eds.). Proceedings of the International Conference on Ecology and Transportation, Raleigh, NC: Center for Transportation and the Environment, North Carolina State University, pp. 433-449.

Clausen, C.J., Cohen, A.D., Emiliani, C., Holman, J.A., and Stipp, J.J. 1979. Little Salt Spring, Florida: a unique underwater site. Science 203:609-614.

Crother, B.I., Boundy, J., Campbell, J.A., de Quieroz, K., Frost, D., Green, B.M., Highton, R., Iverson, J.B., McDiarmid, R.W., Meylan, P.A., Reeder, T.W., Seidel, M.E., Sites, J.W., Tilley, S.G., and Wake, D.B. 2000. Scientific and Standard English Names of Amphibians and Reptiles of North America North of Mexico, with Comments Regarding Confidence in our Understanding. Society for the Study of Amphibians and Reptiles, Herpetological Circular No. 29.

Crother, B.I., Boundy, J., Campbell, J.A., de Quieroz, K., Frost, D., Green, B.M., Highton, R., Iverson, J.B., McDiarmid, R.W., Meylan, P.A., Reeder, T.W., Seidel, M.E., Sites, J.W., Tilley, S.G., and Wake, D.B. 2003. Scientific and Standard English Names of Amphibians and Reptiles of North America North of Mexico: Update. Herpetological Review 34:196-203.

Ernst, C.H., Lovich, J.E., and Barbour, R.W. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington DC, 578 pp.

Foley, A.M, Dutton, P.H., Singel, K.E., Redlow, A.E., and Teas, W.G. 2003. The first records of olive ridleys in Florida, USA. Marine Turtle Newsletter 101:23-25.

Gaffney, E.S. and Wood, R.C. 2002. *Bairdemys*, a new side-necked turtle (Pelomedusoides, Podocnemididae) from the Miocene of the Caribbean. American Museum Novitates 3359:1-28.

Holman, J.A. 1978. The late Pleistocene herpetofauna of Devil's Den Sinkhole, Levy County, Florida. Herpetologica 34(2):228-237.

Iverson, J.B. 1992a. Global correlates of species richness in turtles. Herpetological Journal 2:77-81.

Iverson, J.B. 1992b. A revised checklist with distribution maps of the turtles of the world. Privately printed. Richmond, Indiana, 363 pp.

Iverson, J.B. 1992c. Species richness maps of the freshwater and terrestrial turtles of the world. Smithsonian Herpetological Information Service 88:1-18.

Jensen, J.B. and Birkhead, W.S. 2003. Distribution and status of the alligator snapping turtle (*Macrochelys temminckii*) in Georgia. Southeastern Naturalist 2:25-34.

Márquez-M., R., Burchfield, P.M., Díaz-F., J., Sánchez-P., M., Carrasco-A., M., Jiménez-Q., C., Leo-P., A., Bravo-G., R., and Peña-V., J., 2005. Status of the Kemp's ridley sea turtle, *Lepidochelys kempii*. Chelonian Conservation and Biology 4(4):761-766.

Meylan, A.B. and Donnelly, M. 1999. Status justification for listing the hawksbill turtle (*Eretmochelys imbricata*) as Critically Endangered on the 1996 IUCN Red List of Threatened Animals. Chelonian Conservation and Biology 3(2):200-224.

Milsap, B.A., Gore, J.A., Runde, D.E., and Cerulean, S.I. 1990. Setting priorities for the conservation of fish and wildlife species in Florida. Wildlife Monographs 111:1-57.

Pritchard, P.C.H., and Trebbau, P. 1984. The Turtles of Venezuela. Contributions to Herpetology, 2. Society for the study of Amphibians and Reptiles, 403 pp.

Seidel, M.E. 1994. Morphometric analysis and taxonomy of cooter and red-bellied turtles in the North American genus *Pseudemys* (Emydidae). Chelonian Conservation and Biology 1(2):117-130.

Seminoff, J.A. 2004. *Chelonia mydas*. In: IUCN. 2004 IUCN Red List of Threatened Species. www.redlist.org.

Spotila, J.R., Dunham, A.E., Leslie, A.J., Steyermark A.C., Plotkin, P.T., and Paladino, F.V. 1996. Worldwide population decline of *Dermochelys coriacea*: are leatherback turtles going extinct? Chelonian Conservation and Biology 2(2):209-222.

Spotila, J.R., Reina, R.D., Steyermark, A.C., Plotkin, P.T., and Paladino, F.V. 2000. Pacific leatherbacks face extinction. Nature 405:529-530.

U.S. Census Bureau. 2004. Florida Quick Facts. http://quickfacts.census. gov/qfd/states/12000.

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Habitats and Ecosystems Utilized by Florida Turtles

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Conservation of any species requires protection of suitable resources. Thus, it is important that the resources used by turtles in Florida are identified so that the users of this volume are able to recognize them. This chapter provides an introduction to the habitats and ecosystems utilized by turtles in Florida and provides some guidelines for their recognition.

The habitats available to turtles everywhere include the natural ecosystems that existed historically before humans arrived, plus those altered habitats produced by humans, such as drainage canals, retention ponds, and agricultural fields. Natural or native ecosystems are disappearing, some in Florida are already very rare, and human-derived and altered habitats are becoming more common. Thus, the future for many species depends in part on their ability to utilize these human-derived or human-modified habitats. In this chapter I explore the classically recognized native ecosystems and habitats and also categorize those human-produced habitats that may be important to the long-term survival of turtles in Florida.

Numerous authors have discussed the native ecosystems of Florida at length (Table 1). Most recently, Myers and Ewel (1990) edited a volume on this subject and it is an excellent reference to supplement the information provided in this chapter. The general outline used by Myers and Ewel is followed here. Native ecosystems are divided into upland habitats, freshwater wetlands and aquatic ecosystems, and coastal ecosystems. In addition, a series of human-altered habitats that provide habitat for certain turtle species are listed and defined.

While I have relied heavily on Myers and Ewel (1990) and FNAI (1990) to prepare this chapter, I have also referenced a number of other works, particularly those by herpetologists or accompanying herpetological treatises. These include Carr (1940), Laessle (1942), Auffenberg (1981), Ashton and Ashton (1981), and Hartman (1992). Table 1 lists the corrsponding names that these authors have used for the various habitats discussed below.

Upland Habitats

Scrub. — The most xeric of the upland habitats; scrub occurs in excessively well-drained, nutrient-deficient sandy areas. It has an understory of evergreen shrubs, including myrtle oak, Chapman's oak, sand live oak, rusty lyonia, rosemary, and saw palmetto, and is usually dominated by an overstory of sand pine. In typical mature sand pine scrub, the pines often form a fairly closed canopy, but there may be gaps and areas of open sand. The oaks can form a solid subcanopy under the dense pine canopy. Originally, gaps would have been the result of fire. More commonly they are now caused by human disturbance such as roads, fire lanes, and logging. *Gopherus polyphemus* occurs in gaps in this habitat and Carr (1940) considered it to be frequent in this ecosystem. However, scrub supports only a low density of tortoises when hot fires produce large areas of even-aged pine stands with very few gaps .

High Pine. — This xeric ecosystem, also known as sandhill, is characterized historically by widely spaced longleaf pines and turkey oaks or other small oaks such as bluejack oak or sand live oak, with a ground cover of wiregrass. Timber harvest and winter burning in this habitat typically results in an ecosystem dominated by turkey oaks. In replanted areas, the dominant pine may be an alternate pine species such as slash or sand pine. Fire is an important element; if it occurs every year or two this habitat becomes open and park-like; ground cover does not become thick enough to support a fire that will damage the dominant trees. If unburned, this habitat will become dominated by hardwoods and succeed to xeric hammock. *Gopherus polyphemus* has its greatest abundance in high pine (= sandhill); *Terrapene carolina* occurs occasionally (Carr, 1940).

Xeric Hammock. — This habitat is dominated by evergreen oaks, usually live oak, that are often large in size. These oaks are interspersed with cabbage palm, laurel oaks, hickories, and occasionally longleaf pine. The understory consists of smaller trees and shrubs such as dogwood, beauty berry, sparkleberry, dwarf sumac, staggerbush, and saw palmetto. The canopy is open and soil usually well-drained making this a dry habitat. Where the soil is less well drained and/or succession has proceeded toward a mesic hammock ecosystem, water oaks, bay trees, magnolias, hackberries, sweet gum, and other species more typical of mesic hammock may be present. *Gopherus polyphemus* will occur in this habitat where the canopy is open. Carr (1940) considered *T. carolina* to be a frequent element of the herpetofauna of this ecosystem.

Mesic Hammock. — This habitat has a more complete canopy than xeric hammock. The canopy is also comprised of a larger set of deciduous trees than is found in xeric hammock. Some of these are evergreen—including magnolias and other bay trees, laurel oak, and water oak—and some are not, including sweetgum, beech, hackberry, elms, and hickories. Because the canopy is more complete, this habitat is often open below. Ferns, vines, and epiphytes may be abundant. Understory species include hollies, dogwood, and cherry laurel. In southern Florida tropical hardwood hammocks replace mesic hammock. They are dominated by tropical hardwood species including gumbo-limbo, Jamaica

Table 1. Alternative names for habitats and ecosystems utilized by Florida turtles. The names for ecosystems used in this chapter are given in the first column. Authors of individual chapters in this volume may use the terminology of other references listed above. Myers and Ewel (1990) includes authors therein, FNAI = Florida Natural Areas Inventory.

This chapter	Myers & Ewel 1990	FNAI 1990	Carr 1940	Laessle 1942	Auffenberg 1981	Ashton & Ashton 1981	Hartman 1992
scrub	scrub	scrub	rosemary scrub	scrub	sand pine–dwarf evergreen oak scrub	sand pine & rosemary scrub	sand pine scrub
high pine	high pine	sandhill	high-pine	sandhills	longleaf pine–deciduous oak	longleaf pine–turkey oak sandhills	sandhills, or longleaf pine–xerophytic oak woodlands
xeric hammock	xeric hammock	xeric hammock	upland hammock	xeric hammock	xeric hammock	xeric oak hammock	hardwood hammocks (part)
mesic hammock	mesic hammock	upland hardwood forest	mesophytic hammock	mesic hammock	mesic hammock	mesic hammock	hardwood hammocks (part)
dry flatwoods	scrubby flatwoods	scrubby flatwoods	palmetto flatwoods	longleaf pine flatwoods	flatwoods (part)	pine flatwoods (part)	longleaf pine flatwoods
wet flatwoods	mesic flatwoods	mesic flatwoods	wiregrass flatwoods	slash pine flatwoods	flatwoods (part)	pine flatwoods (part)	slash pine flatwoods
dry prairie	dry prairie	dry prairie	—	—	—	—	dry prairie
hydric hammock	hydric hammock	hydric hammock	low hammock	hydric hammock	—	hydric hammock	hardwood hammocks (part)
river swamps	river swamps	floodplain swamp	fluvial swamp	river swamp	—	gum swamps & river swamps	hardwood swamps
bay swamps	bay swamps	basin swamp	bayheads	bayheads	bay head	—	—
cypress swamps & cypress domes	cypress swamps	strand swamp & dome swamp	—	—	cypress & gum pond	cypress swamps & domes	cypress swamps
freshwater marshes	freshwater marshes	basin marsh	freshwater marshes	—	freshwater marshes	freshwater marshes	freshwater marshes & wet prairies
lakes	—	clastic upland lakes	lakes & sinkhole ponds	—	lakes & ponds	permanent ponds & lakes	—
rivers & streams	—	alluvial & blackwater streams	larger streams & spring runs	—	springs, alluvial rivers & non-alluvial rivers	rivers	—
small streams	—	seepage stream	—	—	—	small streams & creeks	—
temporary ponds	—	depression marsh	fluctuating ponds & flatwoods ponds	—	—	temporary ponds & roadside ditches	—
dunes & beaches	—	beach dune/ coastal strand	—	—	coastal dune environment	coastal beaches & dunes	coastal strand
salt marshes	—	tidal marsh	salt marsh	—	salt marsh	salt marsh	coastal marsh
mangroves	—	tidal swamp	mangrove swamps	—	mangrove	mangrove swamps	mangrove swamps
coral reefs/ live-bottom	coral reefs	coral reef, octocoral reef	—	—	—	—	—
sea grass beds	sea grass beds	seagrass beds	—	—	—	—	—
shears & fronts	—	—	—	—	—	—	—

dogwood, poisonwood, and lignum vitae, as well as live oak, sabal palms, and strangler figs (Carr, 1940; Snyder et al., 1990). Carr (1940) considered *T. carolina* to be an occasional element of the herpetofauna of this ecosystem.

Dry Flatwoods. — The dominant pine tree may be slash, long leaf, or Cuban pine, and the understory is dominated by saw palmetto that produces a dense, sometimes impenetrable understory. Other understory species include gall-berry, fetterbush, staggerbush, and dwarf live oak. Auffenberg (1981) did not distinguish wet from dry flatwoods but pointed out that slash pine is dominant in seasonally flooded flatwoods while longleaf is dominant on well-drained sites. Abrahamson and Harnet (1990) used the term scrubby flatwoods for flatwoods in which the upper meter or so of soil is always well-drained and the water table is rarely near the surface. Carr (1940) considered *T. carolina* to be a frequent element of the herpetofauna of this ecosystem. *Gopherus polyphemus* can also be abundant.

Wet Flatwoods. — The dominant pine tree may be slash, long leaf, or pond pine, and grasses, particularly wiregrass, dominate the understory. The water table lies close to the surface, which results in seasonal flooding of the habitat. Exclusion of saw palmetto by flooding combined with fire result in an open understory and more open ground than in dry flatwoods. Abrahamson and Harnet (1990) used the term mesic flatwoods for this type of flatwoods that is briefly inundated during periods of high rainfall. South Florida rockland pine forests (= limestone flatwoods of Carr, 1940) appear to represent a related ecosystem that is also regularly inundated and has an open, grass-dominated understory (Snyder et al., 1990). Carr (1940) considered *T. carolina* to be characteristic of limestone flatwoods and frequent in wet flatwoods. He considered *G. polyphemus* to be an occasional element of the herpetofauna of wet flatwoods.

Dry Prairie. — Abrahamson and Harnet (1990) and Hartman (1992) described this as pine flatwoods minus the overstory of pine trees. It is an open treeless plain dominated by grasses such as broomsedge and wiregrass, but often including shrubby vegetation such as palmetto, fetterbush, staggerbush, and dwarf blueberry. It has a limited distribution in Florida but does provide suitable habitat for *G. polyphemus* (Mushinsky et al., this volume).

Freshwater Wetlands and Aquatic Ecosystems

Hydric Hammock. — This habitat occurs in poorly drained, often saturated soils, which are not generally subjected to seasonal flooding, drying, or fire (Laessle, 1942). It is dominated by swamp laurel oak, red maple, sweet gum, water oak, sabal palms, or sometimes ironwood. Wax myrtle and various hollies are frequently common in the understory. Carr (1940) considered *T. carolina* to be an occasional element of the herpetofauna of this ecosystem. Both *Kinosternon baurii* and *K. subrubrum* are encountered in this ecosystem.

River Swamps. — These are the seasonally flooded forests of major stream and river flood plains. They are frequently dominated by cypress, gum, or tupelo, but may also contain species typical of mesic hammock such as red maple and sweetbay magnolia. A fairly complete canopy and seasonal flooding usually produce an open understory. Carr (1940) considered *Sternotherus minor* to be a frequent element of the herpetofauna of this ecosystem; he considered *K. baurii*, *Chelydra serpentina*, *Pseudemys nelsoni*, *P. floridana*, *P. concinna*, *Trachemys scripta*, and *Apalone ferox* to be occasional.

Bay Swamps. — These are non-fluvial swamps with saturated, acidic soils that are high in organic matter and not normally subject to drying. They are dominated by evergreen trees such as loblolly bay, sweetbay, and swampbay, often with some black gum and pond cypress. They often have a thick understory of willow, wax myrtle, smilax, fetterbush, and gallberry. Sphagnum moss is often present on the ground. Carr (1940) suggested that *T. carolina* and *Kinosternon* occasional occur in this ecosystem.

Cypress Swamps and Cypress Domes. — Auffenberg (1981) described these as cypress-dominated depressions with varying numbers of black gum, sweet gum, and slash pine. Ewel (1990) indicated that fire is an important element in maintaining cypress swamps. In the absence of periodic fire, cypress swamps can become hardwood-dominated. Auffenberg (1981) considered *K. baurii* and *Deirochelys reticularia* to be typical faunal elements of cypress ponds.

Marshes. — Marshes are shallow bodies of freshwater that dry out rarely. They are populated by a variety of species of emergent vegetation depending on the depth of the water. These emergents may include sawgrass, cattail, pickerel weed, water lilies, and bull rushes; trees are usually few in number and limited to water tolerant forms such as cypress and willows. Fire appears to play an important role in limiting the extent to which woody plants invade marshes (Kushlan, 1990). Carr (1940) considered *P. nelsoni* and *K. subrubrum* to be characteristic of this ecosystem; *Sternotherus odoratus*, *C. serpentina*, *P. floridana*, *T. scripta*, *D. reticularia* and *A. ferox* to be frequent; and *K. baurii* and *T. carolina* to be occasional. Auffenberg (1981) considered the following turtles typical: *K. baurii*, *K. subrubrum*, *P. nelsoni*, *C. serpentina*, and *D. reticularia*. Kushlan (1990) indicated that *K. baurii*, *K. subrubrum*, *S. odoratus*, *P. floridana*, and *P. nelsoni* occur in deeper marshes while *D. reticularia* is restricted to shallow marsh.

Lakes. — These are permanent or nearly permanent freshwater bodies of various sizes that may be surrounded by cypress trees (e.g., Newnan's Lake, Alachua Co.), marsh (e.g., Lake Okeechobee), or upland ecosystems (e.g., Cowpen Lake, Putnam Co.). These water bodies may have emergent vegetation at their margins and may have floating vegetation (hyacinths, water lettuce, or water lilies) at the surface. Auffenberg (1981) suggested that shoreline vegetation is an important determinant of herpetofaunal content. Carr (1940) considered *P. floridana* and *A. ferox* to be characteristic of this ecosystem; *K. subrubrum*, *K. baurii*, *C. serpentina*, *P. nelsoni*, *T. scripta*, and *D. reticularia* to be frequent; and *S. minor* and *Clemmys guttata* to be occasional. Auffenberg (1981) considered nearly all of the species listed by Carr (1940) to be typical elements of the lake herpetofauna, but pointed out that *K. baurii* and *D. reticularia* are common only in lakes with marshy borders.

Rivers and Streams. — These are the permanent watercourses that drain Florida. They are combined here since they support the same basic suite of "riverine" turtle species. They are far more numerous in the panhandle and northern peninsula than in the southern peninsula. They include alluvial rivers (those with heavy sediment loads), blackwater rivers (those with lighter sediment loads that are colored by organic acids), and spring runs, rivers in which the majority of flow is produced by a spring (e.g., Silver River and Rainbow River, Marion Co.). Alluvial rivers are restricted to the panhandle and often drain adjacent states (e.g., Apalachicola and Escambia rivers). Blackwater rivers are clear to tea-colored with a lower inorganic sediment load. Examples would include the Suwannee, Sante Fe, and St. John's rivers. Auffenberg (1981) pointed out that while spring heads or spring boils are poorly vegetated, spring runs are very productive due to deep light penetration and may have lush beds of the grasses *Vallisneria* and *Sagittaria*. Marchand (1942) provided a detailed description of the vegetation of Rainbow Run, a typical Florida spring run, in conjunction with his study of the turtles there. Carr (1940) considered *Macrochelys temminckii, S. minor, S. odoratus*, and *P. concinna* to be characteristic of these types of habitats; *C. serpentina, P. nelsoni, P. floridana* and *A. ferox* to be frequent; and *T. scripta* to be occasional. Auffenberg (1981) added *Graptemys* species and *Apalone spinifera*, which he specified as typical of panhandle alluvial rivers.

Small Streams. — These smaller streams vary from dark swamp streams to clear forest brooks but are typically under a closed canopy. Carr (1940) suggested that *K. subrubrum* and *K. baurii* are characteristic of this habitat and that *S. minor, S. odoratus, C. serpentina, T. carolina, P. nelsoni, P. floridana, T. scripta, D. reticularia,* and *A. ferox* are occasional.

Temporary Ponds. — These are ponds that normally fill and dry on an annual basis. Auffenberg (1981) included temporary ponds in his treatment of lakes and ponds but suggested that "small temporary ponds are a special category", and defended this on the basis of their importance as amphibian breeding sites. *Kinosternon baurii* and *D. reticularia* are frequent in these habitats; and *K. subrubrum, C. serpentina, P. nelsoni, P. floridana, T. scripta,* and *A. ferox* are occasional (Carr, 1940).

Coastal Ecosystems

Dunes and Beaches. — Beaches and dunes are the product of sorting and stacking of sediments along shorelines by water and wind. Sandy beaches and dunes stretch for over 800 miles along the coast of Florida (Clark, 1992) although most dunes have been lost to human development. Few stretches of Florida coastline are submerged. Those that are support mangroves or salt marshes (see below). Auffenberg (1981) considered the dune and beach ecosystem seaward of coastal hammock (a type of xeric hammock) to consist of a dune meadow and a shrub-dune zone. The former is a canopy-less, shrub-free zone closest to the beach and dominated by pioneer species such as sea oats, bitter panicum, sandspur, railroad vine, and penny-wort. The latter is a very dense, even impenetrable tangle of such well-defended plants as prickly-pear cactus, Spanish bayonet, and saw palmetto, as well as sea grape. The former provides nesting habitat for marine turtles, especially *Caretta, Chelonia,* and *Dermochelys*, the latter provides habitat for *G. polyphemus* (Auffenberg, 1981).

Salt Marshes. — Salt marshes consist of grasslands formed by a few salt tolerant grasses along low energy coastlines that are subjected to tidal and seasonal flooding. The dominant grasses are cord grass (*Spartina*) and salt grass (*Distichlis*) closer to the salt water, with needle rushes (*Juncus*) in the slightly higher areas. Salt marshes frequently contain islands or hammocks dominated by sabal palms. Carr (1940), Auffenberg (1981), and Ashton and Ashton (1981) considered *Malaclemys terrapin* characteristic of this habitat.

Mangroves. — These are coastal forests limited to the southern half of the peninsula, south of Crystal River on the west coast, and south of Merritt Island on the east coast. From seaward to landward, the dominant trees are usually red mangrove, black mangrove, white mangrove, and buttonwood. In many areas the entire progression is not seen and one or two species dominate. In many places where it occurs, this ecosystem provides important habitat for *M. terrapin.*

Coral Reefs and Live-Bottom Communities. — In addition to coral reefs that exist from the Dry Tortugas to Palm Beach Co., there are several other hard-bottom or live-bottom habitats along the coasts of Florida that are thought to provide important sea turtle habitat. These include exposed limestone ledges on the Florida Middle Ground off the Gulf coast, worm reefs along the east coast from Biscayne Bay to Merritt Island, and reefs produced by vermetid mollusks in the region of the Ten Thousand Islands (Jaap and Hallock, 1990). These habitats are characterized by colonial invertebrates, especially hard and soft corals, sponges, and bryozoa, which along with marine algae, produce a complex physical environment. These hard-bottom ecosystems provide foraging habitat and resting sites for sea turtles, including *Eretmochelys, Chelonia,* and *Caretta*.

Sea Grass Beds. — Shallow flats in low energy areas along the Florida coastline have historically been dominated by a series of marine flowering plants collectively known as sea grasses. The dominant forms include turtle grass, manatee grass, and shoal grass. Sea grasses support a diverse assemblage of other species of marine organisms including certain sea turtles. *Chelonia mydas* is typical of this ecosystem where it forages on the sea grasses. *Lepidochelys* and *Caretta* are also found in this habitat and on adjacent mud flats where they feed on macroinvertebrates.

Oceanic Shears and Fronts. — These are oceanographic features that provide important habitat for hatchling sea turtles. Shears and fronts occur at convergence zones where two opposing currents meet head on and cause a down-welling, or pass by each other in opposite directions setting up a system of eddies (Carr, 1987). These physical phenomena act to align otherwise dispersed floating matter on the ocean surface, including seaweed, especially the brown algae, *Sargassum*, floating terrestrial and marine debris, and hatchling sea turtles. The resulting weed lines or strand lines apparently provide both food and shelter for post-hatchling sea turtles. The length of time that young sea turtles spend in these habitats remains to be determined for each species. But it is clear from the work of Witherington (2002) that this habitat is critical to loggerheads (*Caretta*) and other sea turtles along the east coast of Florida during what has previously been called the "lost-year". Because it is no longer lost and is very likely longer than one year, the “lost-year” may better be termed the “pelagic phase”. All sea turtles found in Florida waters enter this phase just after hatching.

Human-Produced Habitats

Canals and Drainage Ditches. —Ditches and canals are the usually permanent, linear bodies of water that are found throughout the state but are particularly abundant in south Florida. They do not usually dry out and are frequently covered with floating vegetation such as water lettuce or water hyacinth. Some roadside ditches, especially those in flatwoods, are seasonally flooded and may contain some flatwoods pond vegetation. Because they dry seasonally they provide an alternative breeding site for some frog species that normally breed in temporary ponds. Thus, Ashton and Ashton (1981) classified these with temporary ponds. Where permanent, canals and ditches are similar to sloughs—natural, linear water bodies with minimal flow. Carr (1940) classified sloughs with drainage ditches and canals, and considered *K. subrubrum*, *P. nelsoni*, and *D. reticularia* to be characteristic of this habitat; *P. floridana*, *S. odoratus*, *K. baurii*, and *A. ferox* to be frequent; and *C. serpentina* and *T. scripta* to be occasional.

Retention Ponds and Borrow Pits. — These are human-made ponds of varying size. Retention ponds have the primary purpose of receiving run-off, borrow pits remain after substrate has been removed to be used as fill elsewhere. In many cases these excavations serve both purposes. They may or may not be created on the site of an existing wetland or pond and typically do not have associated native upland habitat. They are known to support both native and non-native turtle species. Our understanding of which turtle species use this habitat and the degree to which turtle populations prosper in these man-made ponds is meager.

City Park Ponds. — These are natural ponds and lakes that have become completely surrounded by development. That is, there is no associated native upland. Examples would be Crescent Lake near downtown St. Petersburg, the Duck Pond near downtown Gainesville, and the ponds on the old Crandon Park Zoo grounds on Key Biscayne. It is important to distinguish these isolated ponds and lakes from more natural lakes and ponds (Lakes ecosystem above) because the former will gradually replace the latter as Florida continues to develop.

Old Fields. — These are agricultural fields or orchards that have been abandoned for a sufficiently long period of time that weeds and other non-agricultural species make up the understory. Old fields can provide habitat for *G. polyphemus* and *T. carolina*, at least at certain stages during their succession.

Agricultural Fields. — These are agricultural fields or orchards that are still in active production and in which the intended agricultural species makes up the understory. Although agricultural fields may not provide habitat for any turtle species, they do provide nest sites for aquatic species in some cases. When forest canopies adjacent to aquatic systems become closed due to lack of fire, agricultural fields may be an important alternate site for placement of nests.

Silviculture. — Monoculture plantations of pine trees, especially slash pine and sand pine, are common throughout Florida. During the early years of growth, when the canopy is open, pine plantations can provide some habitat for *G. polyphemus* if on sufficiently drained soil. They may also serve in the same capacity as other agricultural fields in providing open ground for turtle nests. However, as the trees grow and the canopy closes, the herbaceous ground cover required by *G. polyphemus* is lost and the shading makes more mature plantations far less suitable as nest sites.

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LITERATURE CITED

Abrahamson, W.G. and Harnet, D.C. 1990. Pine flatwoods and dry prairies. In: Myers, R.L. and Ewel, J.J. Ecosystems of Florida. University of Central Florida Press, pp. 103-149.

Ashton, R.E. and Ashton, P.S. 1981. Handbook of reptiles and amphibians of Florida, part one, the snakes. Windward Publishing, Miami, 176 pp.

Auffenberg, W. 1981. Florida environments and their herpetofaunas, Part 1, Environmental characteristics. Florida Herpetologist 2:1-36.

Carr, A. F. 1940. A contribution to the herpetology of Florida. University of Florida Publication, Biological Science Series 3:1-118.

Carr, A.F. 1987. New perspectives on the pelagic stage of sea turtle development. Conservation Biology 1:103-121.

Clark, R.R. 1992. Beach Conditions in Florida: A Statewide Inventory and Identification of the Beach Erosion Problem Areas in Florida. Beaches and Shores Technical Memorandum 89-1. Fourth Edition. Florida Department of Natural Resources, 208 pp.

Ewel, K.C. 1990. Swamps. In: Myers, R.L. and Ewel, J.J. Ecosystems of Florida. University of Central Florida Press, pp. 281-323.

Florida Natural Areas Inventory and Florida Department of Natural resources. 1990. Guide to the natural communities of Florida. Florida Natural Areas Inventory, Tallahassee, Florida.

Hartman, B. 1992. Major terrestrial and wetland habitats. In: Moler, P.E. (Ed.). Rare and Endangered Biota of Florida, Volume III. Amphibians and Reptiles. University Press of Florida, Gainesville, pp. xvii-xxviii.

Jaap W.C. and Hallock, P. 1990. Coral reefs. In: Myers, R.L. and Ewel, J.J. Ecosystems of Florida. University of Central Florida Press, pp. 574-616.

Kushlan, J.A. 1990. Freshwater marshes. In: Myers, R.L. and Ewel, J.J. Ecosystems of Florida. University of Central Florida Press, pp. 324-363.

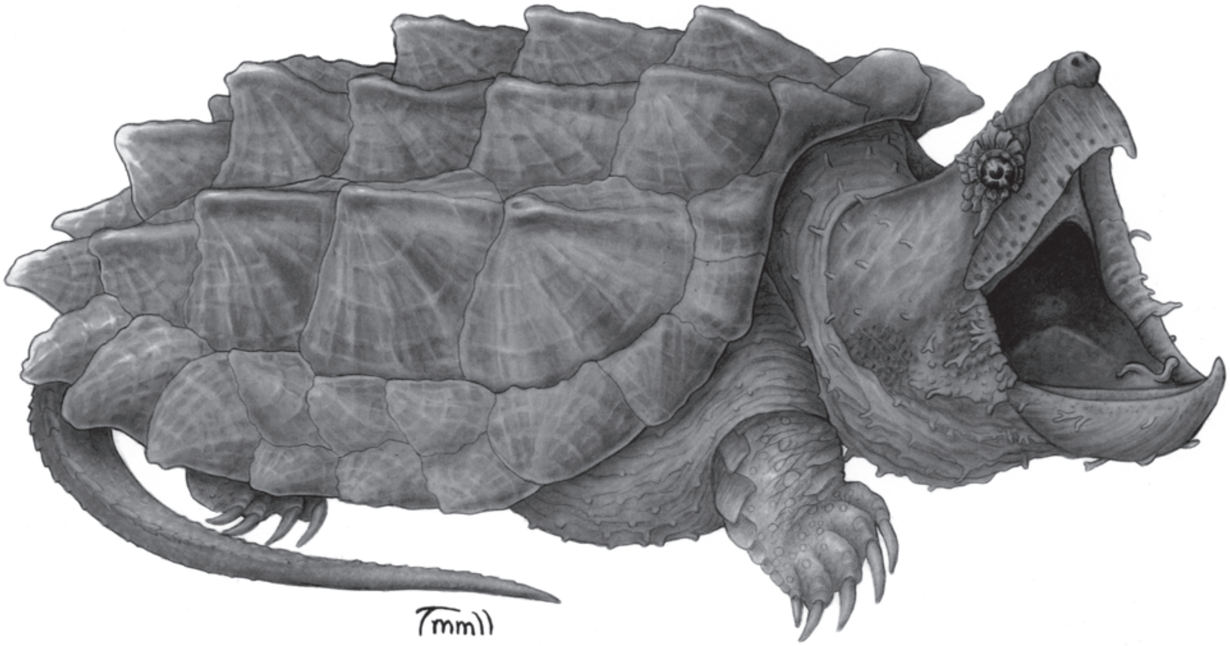
Laessle, A.M. 1942. The plant communities of the Welaka area. University of Florida Publication, Biological Science Series 4:1-143.

Marchand, L.J. 1942. A contribution to a knowledge of the natural history of certain freshwater turtles. Master’s Thesis, University of Florida.

Myers, R.L. and Ewel, J.J. 1990. Ecosystems of Florida. University of Central Florida Press, 765 pp.

Snyder, J.R., Herndon, A., and Robertson, W.B. 1990. South Florida rocklands. In: Myers, R.L. and Ewel, J.J. Ecosystems of Florida. University of Central Florida Press, pp. 230-277.

Witherington, B.E. 2002. Ecology of neonate loggerhead turtles inhabiting lines of downwelling near a Gulf Stream front. Marine Biology 140:843-853.



Alligator Snapping Turtle, *Macrochelys temminckii* (Chelydridae).
Drawing by Susan Trammell.

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Introduction to the Snapping Turtles: Family Chelydridae

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This family is represented in Florida by two species, the snapping turtle (*Chelydra serpentina*) and the alligator snapping turtle (*Macrochelys temminckii*). The former is found throughout the state except for the Florida Keys. The latter is restricted to the major river systems from the Suwannee River westward. Snapping turtles are easily recognized by their relatively large size, long tails, large heads, and defensive attitudes.

Content. — Some authors include only the two snapping turtles mentioned above in the family Chelydridae. Others argue that the big-headed turtle (*Platysternon*) from Asia should also be included (Gaffney, 1975; Gaffney and Meylan, 1988; Shaffer et al., 1997). The remarkable anatomy of the tail vertebrae of *Platysternon*, *Macrochelys*, and *Chelydra* has been the primary reason for uniting them in a single family. However, it is possible that this tail morphology may be primitive for living cryptodires (the Polycryptodira of Gaffney, 1984).

Relationships. — Morphological data suggest that snapping turtles are likely to be the most primitive group of living cryptodiran turtles. That is, snapping turtles branched off of other hidden-necked turtles before any of the other living branches. Their long, armored tail is reminiscent of the tails of several early groups of turtles that are now extinct. There are also morphological similarities between primitive sea turtles and snapping turtles. Recent molecular studies have recovered evidence from both mitochondrial and nuclear genes that suggest that *Platysternon* is more closely related to the Testudinoidea than to *Chelydra* (Near et al., 2005).

Geologic Distribution. — The early fossil record of this family consists of isolated elements from the late Cretaceous of western North America (Hutchison and Archibald, 1986; Brinkman, 2003). The earliest relatively complete fossil of this family is *Protochelydra zangerli* from the Paleocene of North Dakota (Erickson, 1973). The family was represented in Eurasia from the Eocene to the Pliocene by the genus *Chelydropsis* (Lapparent de Broin, 2001).

Geographic Distribution. — If limited to the genera *Chelydra* and *Macrochelys*, the modern distribution of this family is restricted to the New World. However, *Chelydra* has one of the largest distributions of any turtle in the New World, being found all across the eastern two-thirds of North America from Nova Scotia to Florida and Manitoba to New Mexico and Texas. It is also found from southern Mexico, south throughout Central America to the Pacific coast of Colombia and Ecuador. The range of *Macrochelys* lies completely within that of *Chelydra* in the south-central U.S.

Status. — While *Chelydra* was until recently generally considered to be a common species, it is now threatened by widespread decline and the possibility of local extinctions (Aresco et al., this volume). The survival status of *Macrochelys* has been of serious concern for the last 30 years (Pritchard, 1989; Ewert and Jackson, 1994). The state of Florida granted this species full protection from commercial use in 1972. This large riverine species was heavily harvested for food and it is likely that many populations were depleted. The degree of recovery of populations in the states in which this species occurs is a subject of ongoing research.

LITERATURE CITED

Brinkman, D.B. 2003. A review of nonmarine turtles from the Late Cretaceous of Alberta. Canadian Journal of Earth Sciences 40:557-571.

Erickson, B.R. 1973. A new chelydrid turtle *Protochelydra zangerli* from the Late Palaeocene of North America. Scientific Publications of the Science Museum of Minnesota 2:1-16.

Ewert, M.A. and Jackson, D.R. 1994. Nesting ecology of the alligator snapping turtle (*Macroclemys temminckii*) along the lower Apalachicola River, Florida. Florida Game and Fresh Water Fish Commission, Nongame Wildlife Program Report NC89- 020, Tallahassee, Florida, 45 pp.

Gaffney, E.S. 1975. Phylogeny of the chelydrid turtles: A study of shared derived characters in the skull. Fieldiana Geology 33-157-178.

Gaffney, E.S. 1984. Historical analysis of theories of chelonian relationship. Systematic Zoology 33:283-301.

Gaffney, E.S., and Meylan, P.A. 1988. A phylogeny of turtles. Pages 157-219 In: Benton, M.J. Ed. The phylogeny and classification of tetrapods. Clarendon Press, Oxford, England.

Hutchison, J.H. and Archibald, J.D. 1986. Diversity of turtles across the Cretaceous/Tertiary Boundary in northeastern Montana. Palaeogeography, Palaeoclimatology, Palaeoecology 55:1-22.

Lapparent de Broin, F. de. 2001. The European turtle fauna from the Triassic to the present. Dumerilia 4: 155-217.

Near, T.J., P.A. Meylan, and H.B. Shaffer. 2005. Assessing concordance of fossil calibration points in molecular clock studies: an example using turtles. American Naturalist 165:137-146.

Pritchard, P.C.H. 1989. The alligator snapping turtle, biology and conservation. Milwaukee Public Museum.

Shaffer, H.B., Meylan, P.A., and McKnight, M. 1997. Tests of turtle phylogeny: molecular, morphological and combined approaches. Systematic Biology 46: 235-268.

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Chelydra serpentina – Snapping Turtle

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SUMMARY. – The snapping turtle, *Chelydra serpentina*, is a large and familiar freshwater species that is easily recognized by its large head, long tail, large claws, serrated rear carapace, and reduced plastron. It is a widely distributed species that represents an ancient lineage of turtles. We follow the current taxonomy in recognizing two subspecies in Florida: *C. s. serpentina* and *C. s. osceola*. We found intergrades of *C. s. serpentina* and *C. s. osceola* in northwestern Florida that showed considerable overlap in shape of neck tubercles and ratio of the width of the third vertebral scute to the height of the second pleural scute. We did not find evidence of intergradation in northeastern Florida, thus the intergrade zone between *C. s. osceola* and *C. s. serpentina* appears to extend from coastal southeast Georgia and the Okeefenokee Swamp to the Apalachicola River and northward into southwest Georgia. Although not abundant in Florida, *C. serpentina* is found throughout the state with the exception of the Florida Keys. In Florida, *C. serpentina* is most abundant in small creeks, spring fed streams, small ponds (< 5 ha), floodplain swamps, borrow pits, drainage ditches, and other small fresh waters with soft bottoms and aquatic vegetation. They are also regularly found in cypress dome ponds and strand swamps in wet pine flatwoods of the Florida panhandle. Overland movements of *C. serpentina* are common in Florida and are associated with dispersal, nesting, and migrations from wetlands during drying or refilling. There are few data on growth of *C. serpentina* in Florida, but growth rates may be higher than in northern populations because of a longer growing season. In a population from Leon County in northwestern Florida, early growth (1–6 yrs) was variable among individuals and ranged from 10–30 mm/year; females matured at about 22 cm CL (6–8 yrs) and males at 18–19 cm CL (4–6 yrs). In central and south Florida, the nesting season begins as early as February–March and continues until late June, whereas nesting occurs from mid-April through June in northern Florida. Aquatic plants and macroinvertebrates are major components of the diet of *C. serpentina* in Florida. This species is not currently considered rare or endangered in Florida, however, it suffers from several threats and populations should be monitored. Habitat loss and fragmentation are significant threats as Federal and State regulations are insufficient to protect many of the wetland habitats (e.g., small, isolated, and seasonal wetlands) that support *C. serpentina* populations in Florida. Mechanical removal of organic sediment ("muck") from lakes and ponds is an established wetland management technique in Florida and is a type of habitat alteration that is a serious threat to *C. serpentina* populations. There are currently no regulations in Florida that protect *C. serpentina* from excessive harvest and we lack adequate baseline data on the level of harvest of this species to properly assess population viability and set sustainable limits on use.

CONSERVATION STATUS. – FNAI Global - G5 (Demonstrably Secure), State - S5 (Demonstrably Secure); ESA Federal - Not Listed; State - Not Listed; CITES - Not Listed; IUCN Red List - Not Listed (LC-Least Concern).

Species Recognition. — This large species (maximum size in Florida 42.4 cm carapace length (CL); FLMNH 66157) is recognized by a long tail with a dorsal ridge of large tuberculate scales (Figs. 1-1, 1-2). Average mass of adults in a northern Florida (Leon Co.) population was 5.5 kg (n = 43) with the largest individuals weighing 8–11 kg (Aresco and Gunzburger, unpubl. data). *Chelydra serpentina* has large claws, a small plastron, and large head. The neck is long and can be extended rapidly. The carapace is brown to black, relatively flattened and serrated in the rear, with three parallel rows of low ridges that become less pronounced with age. The carapace of large and presumably old adults is nearly smooth. The carapace of hatchlings and juveniles is darker and more rugose than those of adults (Fig. 1-2).

Figure 1-1. Adult male snapping turtle, *Chelydra serpentina,* from Leon Co., Florida. Photo by Matt Aresco.

The small, hingeless plastron is loosely attached by ligaments to the carapace at a narrow bridge (Fig. 1-3). It is cruciform-shaped, resulting in extensive areas of exposed skin with all four muscular limbs clearly visible. Skin on the undersides of the legs has many small tubercles. The plastron of hatchlings is black, often with light flecks (Fig. 1-4), but the black fades and the entire plastron becomes light brown, yellow-brown, or gray in adults (Fig. 1-3).

Chelydra serpentina is frequently mistaken for the alligator snapping turtle, *Macrochelys temminckii*. In contrast to *C. serpentina*, *M. temminckii* grows to a much larger size, has a larger head and more pointed snout with eyes facing laterally rather than dorsolaterally, a strongly hooked beak, a carapace with three rows of very well-developed longitudinal keels throughout life, and an extra row of scutes on the carapace between the marginals and costals (Figs. 1-1, 1-2).

Taxonomic History. — *Chelydra serpentina* was first described by Linnaeus (1758) as *Testudo serpentina*, and placed in the genus *Chelydra* by Schweigger (1812). Until recently the common name used for this turtle was the Common Snapping Turtle. Crother et al. (2000) recommended a change in the name to the Eastern Snapping Turtle because the term "common" might be misinterpreted to imply abundance.

Stejneger (1918) described the Florida snapping turtle, *Chelydra osceola*, as a separate species from peninsular Florida. He differentiated this species from *C. serpentina* based on much wider vertebral scutes (width of the third vertebral equal to or greater than one third of the length of all five vertebrals combined), knobs on dorsal keels of scutes located closer to the centers (rather than rear of scutes in *C. serpentina*), two pairs of small chin barbels (rather than only one pair in *C. serpentina*), and pronounced lateral scales on the tail. Stejneger (1918) also reported that the more anterior location of the dorsal keel knobs is most visible on the fifth vertebral and arises near the middle of that scute in *C. osceola*, instead of at the posterior edge in *C. serpentina*.

Subsequent to its description, *Chelydra osceola* was treated as a subspecies, *C. serpentina osceola* (Babcock, 1932; Carr, 1952; Feuer, 1971; Gibbons et al., 1988; Ernst et

Figure 1-2. Hatchling snapping turtle, *Chelydra serpentina,* from Pinellas Co., Florida. Photo by Dick Bartlett.

Figure 1-3. Adult female snapping turtle, *Chelydra serpentina,* from Leon Co., Florida. Photo by Matt Aresco.

Figure 1-4. Hatchling snapping turtle, *Chelydra serpentina,* from Pinellas Co., Florida in ventral view. Photo by Dick Bartlett.

al., 1994). However, Richmond (1958) considered *Chelydra osceola* a full species based on an analysis of 20 morphological and osteological characters from a sample of several dozen specimens from peninsular Florida that he compared to a large sample from elsewhere in the USA. The primary characters that distinguished the two taxa were the shape of neck tubercles (pointed, papillate tubercles in *C. osceola* and flattened, rounded tubercles in *C. serpentina*) (Fig. 1-5), width of the third vertebral equal to or greater than 33% of the total length of the five vertebrals in *C. osceola*, and length of plastral forelobe < 40% of carapace length in *C. osceola*. Generally, in young turtles, the carapace of *C. s. osceola* is more rugose than that of *C. s. serpentina*.

Walker et al. (1998) and Walker and Avise (1998) examined geographic variation in mitochondrial DNA (control region) in 66 snapping turtles from across the southeastern USA. This sample demonstrated virtually no variation within or among populations in the portion of the genome that they studied. Furthermore, they found no evidence to support any distinction between *C. s. serpentina* and *C. s. osceola*. They proposed that *C. serpentina* had greater terrestrial dispersal capability across historical biogeographic barriers that limit gene flow in other freshwater turtles. Thus, moderate to high rates of gene flow among populations of *C. serpentina* probably reduced phylogeographic structure in the southeastern USA. However, because several morphological characters clearly support the current subspecies designations, we recommend that the current taxonomy recognizing *C. s. serpentina* and *C. s. osceola* be retained until additional portions of the genome are studied**.**

Figure 1-5. Adult Florida snapping turtle, *Chelydra serpentina osceola*, from Marion Co., Florida showing the distribution and length of tubercles on the neck of this subspecies. Photo by Steve Johnson.

DISTRIBUTION

Geographic Distribution.—*Chelydra serpentina* ranges across southern Canada from Nova Scotia to Saskatchewan and throughout the eastern and central United States, south to the Gulf of Mexico and west to the Rocky Mountains, including most of Texas. Populations of *Chelydra* in Central America and northwestern South America previously referred to the subspecies *C. s. rossignonii* and *C. s. acutirostris* are now considered to be full species distinct from *C. serpentina* (Gibbons et al., 1988; Phillips et al., 1996).

Chelydra serpentina is found throughout Florida with the exception of the Florida Keys. Gaps in the distribution of *C. serpentina* in Florida probably reflect incomplete collecting rather than the absence of this species (Fig. 1-6). Richmond (1958) found no intergrades in the area between north-central Florida and southeastern South Carolina and recommended that *C. s. osceola* be recognized as a full species unless it could be demonstrated that it interbreeds with *C. s. serpentina*. However, Feuer (1971) reported intergradation of *C. s. serpentina* and *C. s. osceola* in the vicinity of the Okeefenokee Swamp in southern Georgia and northeastern Florida and, thus, argued for subspecific status for the Florida snapping turtle. He also found that variation in neck tubercles was the best means of distinguishing the two subspecies and that the ratio of the width of the third vertebral scute to the height of the second pleural scute was significantly greater in *C. s. osceola* (mean = 0.973, n = 113) than in *C. s. serpentina* (mean = 0.838, n = 1097). Four of seven specimens from the Okeefenokee Swamp had neck tubercles that were intermediate between the long, pointed tubercles of *C. s. osceola*, and the rounded, wart-like tubercles of *C. s. serpentina*, and the average width of the third vertebral scute/height of the second pleural scute was intermediate between that in each subspecies (mean = 0.855, n = 7). Feuer (1971) proposed that the morphological variation between the subspecies likely occurred as a result of inundation of the northern peninsula of Florida during a Pleistocene interglacial period that isolated peninsular Florida and mainland populations.

Our examination of specimens in the Florida Museum of Natural History (FLMNH) collections (n = 70,

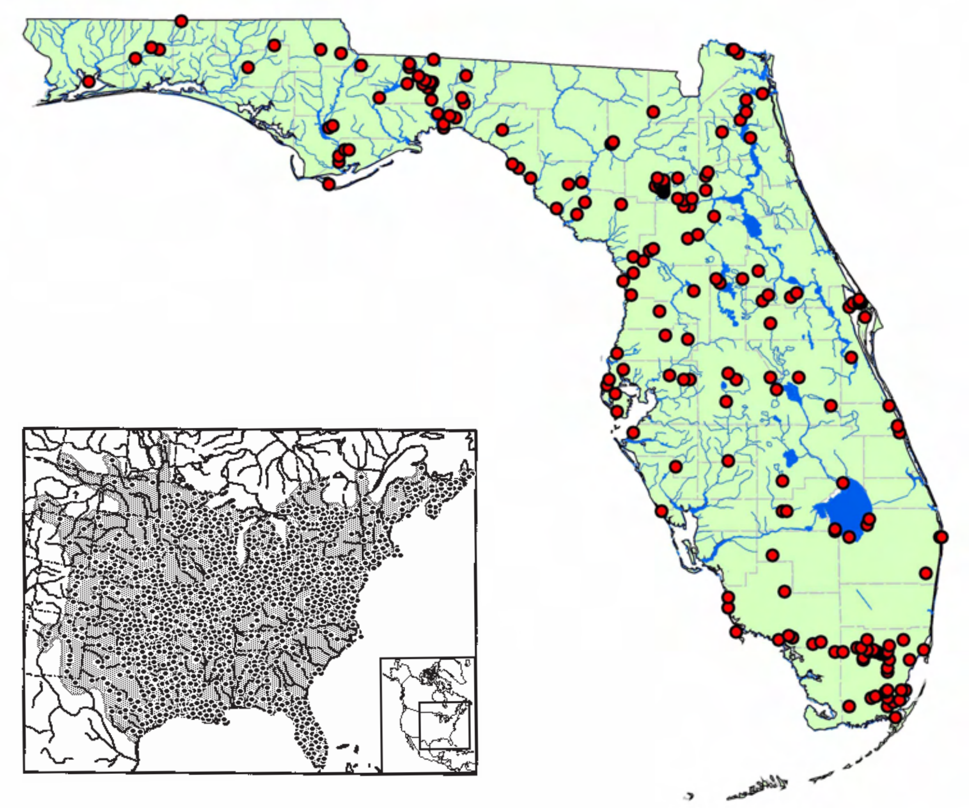

Figure 1-6. Available locality records for the snapping turtle, *Chelydra serpentina*, in Florida. Inset: distribution records from entire range of *C. serpentina* (adapted from Iverson, 1992; distribution in inset map not current for Florida as presented here).

all >10 cm SCL) has uncovered possible intergrades from Leon Co. (FLMNH 67790), Gadsden Co. (FLMNH 66141), Jefferson Co. (FLMNH 65107), and Bibb Co., GA (FLMNH 4167). A specimen from Grady Co., GA, also appeared to be an intergrade (Aresco, unpubl. data). Specimens from west of the Apalachicola River in the Florida Panhandle (Jackson Co., FLMNH 6523; Okaloosa Co., FLMNH 64730; and Santa Rosa Co., FLMNH 65106) all have short, rounded tubercles and appear to be *C. s. serpentina*. At a pond in Tallahassee, Leon Co., a sample of 35 *C. serpentina* shared characteristics of both subspecies suggesting that the population consisted of intergrades of *C. s. serpentina* and *C. s. osceola* (Table 1-1, Aresco and Gunzburger, unpubl. data). For example, the average ratio of the width of the third vertebral scute to the height of the second pleural scute was intermediate between that reported for *C. s. serpentina* and *C. s. osceola* (mean = 0.876, SD = 0.057, range 0.78–1.07, *n* = 35). In the lower Apalachicola River (Liberty and Franklin Co.), *C. serpentina* also shows the influence of *C. s. osceola* with pointed neck tubercles (although less pronounced than those in southern Florida) and moderately prominent lateral scale ridges on the tail (Ewert, unpubl. data); except for one individual from Liberty Co., FLMNH 10189, that exhibited features of *C. s. serpentina*. We did not find evidence of intergradation in northeast Florida, thus the intergrade zone between *C. s. osceola* and *C. s. serpentina* appears to extend from coastal SE Georgia and the Okeefenokee Swamp to the Apalachicola River and northward into southwest Georgia. An examination of variation in plastral forelobe length/carapace length to third vertebral width/second pleural height showed considerable overlap in these characters between *C. s. serpentina* and intergrades from Leon Co., Florida, but little overlap with *C. s. osceola* (Fig. 1-7).

Ecological Distribution. — In Florida, *C. serpentina* is most abundant in small creeks, spring fed streams, small ponds (< 5 ha), floodplain swamps, borrow pits, drainage ditches, and other small fresh waters with soft bottoms. They are also regularly found in cypress dome ponds and strand swamps in wet pine flatwoods of the Florida Panhandle (authors, unpubl.). Given that females have frequently nested on Forbes Island and elsewhere along the west bank of the lower Apalachicola River, the species appears to be widespread in waters of the large, wooded floodplain (Ewert and Jackson, 1994 and unpubl.). In eastern Sarasota Co., Punzo (1975) found *C. s. osceola* in swamps, woodland ponds, and streams. In the eastern Everglades (Dade Co.), *C. s. osceola* occurs at least locally in small ditches with clear water and abundant vegetation (Ewert, unpubl.). In a survey of turtle populations in Leon Co., *C. serpentina* was most abundant in small, eutrophic ponds (0.5–1.5 ha) with relatively shallow water, thick muck bottoms (muck depth of 0.5–1.5 m), and an abundance of duckweed (*Spirodela* sp.) and emergent macrophytes (Aresco and James, 2005).

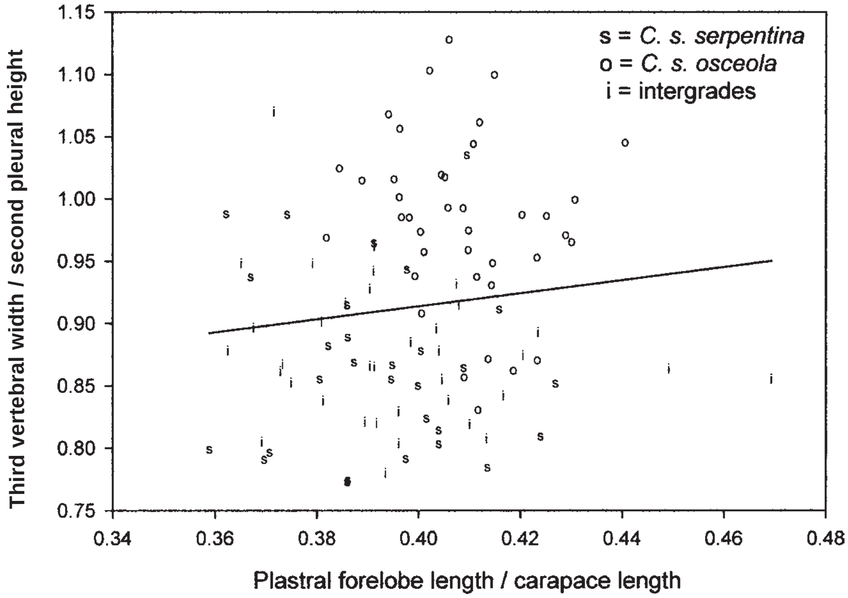

Figure 1-7. Variation in plastral forelobe length/carapace length versus third vertebral width/second pleural height among *C. s. serpentina* (including individuals from northwestern Florida, Georgia, Tennessee, Arkansas, and the Carolinas) (n = 29), *C. s. osceola* (peninsular Florida) (n = 39), and intergrades from Leon County, Florida (n = 35). Subspecies and intergrades are assigned based on length and shape of neck tubercles.

In Florida, *C. serpentina* appears to occur at lower densities in large lakes than in small ponds and creeks. For example, only 9 *C. serpentina* were found among 4896 turtles at Lake Jackson, a 1620 ha sinkhole lake in Leon Co., during a natural dry-down event (Aresco, 2005). Similarly, at Lake Conway in central Florida, only 21 snapping turtles were among 4817 turtles captured during a three-year study (Bancroft et al., 1983). Recapture of six of these snapping turtles suggested that the population was small. Within Lake Conway, *C. serpentina* was associated with shallow water with an abundance of aquatic vegetation and a mud substrate. The physiology of *C. serpentina* includes apparent adaptations for burying in mud and muck and surviving under low oxygen conditions (Jackson et al., 1984). *Chelydra serpentina* is also tolerant of brackish water and inhabits coastal estuaries (Dunson, 1986).

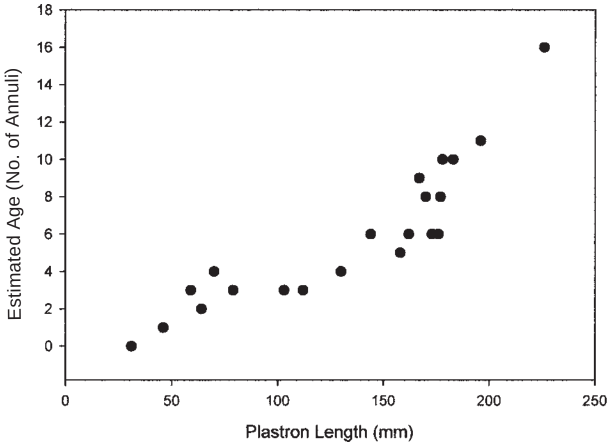

Figure 1-8. Relationship of size and age of *Chelydra serpentina* (n = 22) in Leon County, Florida. Age was estimated using counts of growth annuli on the 2nd pleural scute and included only those turtles with complete sets of clearly visible annuli.

HABITAT RELATIONS

Activity. — This species is a "bottom-walker" and prefers shallow water where it can breathe by extending its long neck to the surface. When active, individuals typically move slowly along the bottom or remain hidden in dense aquatic vegetation. In Florida, when *C. serpentina* is inactive during hot summer days or winter months, it may hide under submerged logs or bury into deep mud, muck, or leaf litter (Aresco, *pers. obs.*).

Chelydra serpentina may be active during day or night (Aresco, unpubl. data). In Tallahassee, Leon Co., a 34.7 cm CL male was observed foraging at the edge of a pond in 20 cm of water in mid-morning, an 8.3 cm CL juvenile active in shallow water at night (2345 hrs), and a large adult in shallow water with neck fully extended at night (2230 hrs), possibly foraging on crayfish (Gunzburger and Aresco, unpubl. data). Individuals were observed both basking and crawling slowly through submergent aquatic vegetation during mid-day on the Wacissa River, Jefferson Co. (Aresco and Gunzburger, unpubl. data). At Rainbow Run, Marion Co., this species is infrequently encountered during daytime surveys (1 of 2500 turtle captures) but is more abundant according to data from overnight trapping (Meylan, unpubl. data). Adults have been encountered moving during the morning and after sundown in ditches in Dade Co. in March (Ewert, unpubl. data). *Chelydra serpentina* has often been seen moving on land during the day (Aresco, unpubl. data). At an ephemeral cypress dome pond in Liberty Co., both juveniles and adults were typically captured at drift fences in the morning following moderate to heavy rain during the night (Palis, Aresco, and Kilpatrick, unpubl. data). Individuals were observed moving overland into a cypress dome pond when it refilled, remaining

Table 1-1. Variation in morphological features of *Chelydra serpentina serpentina* x *Chelydra serpentina osceola* (*n* = 35) from a population at McCord Pond, Tallahassee, Leon County, Florida.

Character	Mean (SD, Range)	% with *osceola* trait
vertebral 3 width/ total length of vertebrals	0.32 (0.02, 0.30-0.37)	12%
plastral forelobe length/ carapace length	0.40 (0.02, 0.36-0.47)	66%
vertebral 3 width/ pleural 2 height	0.88 (0.06, 0.78-1.07)	31%
no. pairs chin barbels	9% two pairs (*osceola*)	
lateral tail scales	11% moderately prominent ridges (*osceola*)	
dorsal keel knobs	100% at rear of scute (*serpentina*)	
neck tubercles	100% moderately pointed (intermediate)	

in the pond for relatively short time periods, and leaving when the pond dried (3–4 wks).

Seasonality. — From November to early March, individuals in a Leon Co. pond were inactive and buried in a deep muck bottom under shallow water (< 0.5 m) (Aresco and Gunzburger, 2004). *Chelydra serpentina* was captured in baited hoop traps as late as October in Leon Co. (Aresco, unpubl. data). At Lake Jackson in Leon Co., individuals were found moving overland as early as 15 March and as late as 15 September (Aresco, unpubl. data). Individuals were found migrating into or out of an ephemeral cypress dome pond located in pine flatwoods of the Apalachicola National Forest in Liberty Co. on 2 November (male), 3 March (male), 20 March (adult female), 4 April (subadult female), 10 April (male), 15 April (2 juveniles), and 25 April (juvenile) (Palis, Aresco, and Kilpatrick, unpubl. data). Seasonal variation in activity of *C. s. osceola* was not apparent at Lake Conway in central Florida (Bancroft et al., 1983).

Movements and Terrestrial Activity. — Overland movements of *C. serpentina* are common in Florida and are associated with dispersal, nesting, and migrations from wetlands during drying or refilling. Carr (1952) reported that both sexes may move overland between water bodies after emerging from hibernation and cover distances of > 0.5 km. In northwestern Florida, subadult and adult males and females (independent of nesting movements) are frequently observed moving overland in pine flatwoods between permanent water in swamps and ephemeral cypress dome ponds (with and without water) (Palis, Aresco, and Kilpatrick, unpubl. data). Males, females, and immatures are often found attempting to cross roads 0.5 km or more from the nearest wetland. During the dry-down of Lake Jackson, Leon Co., two juveniles (4.0 cm CL) were found at a drift fence moving directly towards nearby permanent water after apparently migrating at least 0.5 km from the nearest remaining pool on the lake bottom during the final days of drying (Aresco, unpubl. data). A large male (34.6 cm CL) migrated from a drying pool at Lake Jackson on 20 April 2000 to Little Lake Jackson on the opposite side of U.S. Highway 27 and was captured migrating back to Lake Jackson on 15 March 2001 as the lake refilled. These observations suggest that *C. serpentina* has the ability to detect water from relatively long distances and may prefer moving to new water rather than attempting to burrow and aestivate in a dry lake bottom. Several juveniles apparently moved overland and quickly re-colonized a portion of Lake Jackson, which had recently refilled with shallow water after being completely dry for 5–6 months.

Home Range. —Home range size has not been determined in Florida. In more northern populations, home range size may be highly variable among individuals of the same sex in adjacent lakes, even when those lakes have similar densities and biomass of snapping turtles (Obbard and Brooks, 1981; Galbraith et al., 1987).

Temperature Relationships. —Aerial basking by adult *C. serpentina* was observed in April on the Wacissa River in Jefferson Co. and in September on the Sante Fe River in Columbia Co. (Ewert, 1976; Gunzburger and Aresco, unpubl. data).

GROWTH AND REPRODUCTION

Growth. —There are few data on growth of *C. serpentina* in Florida, but growth rates may be greater than in northern populations because of a longer growing season, depending on habitat productivity. In a population from Leon County in northwestern Florida, early growth (1–6 yrs) was variable among individuals and ranged from 10–30 mm/year (Fig. 1-8) (Aresco, unpubl. data). In contrast, a juvenile from Lake Conway in central Florida grew only 4.3 mm/year (Bancroft et al., 1983). Jackson and Ewert (1997) suggested that female *C. s. osceola* have the potential to grow to large sizes based on a series of large specimens (e.g., 36.8, 35.2, 34.8 cm CL) collected from Lake Apopka, Orange County, in 1928–29.

Christiansen and Burken (1979) used growth rings to calculate annual growth increments and found that *C. serpentina* in Iowa grew 25–35 mm/yr for the first 3 or 4 years. Female *C. serpentina* in Ontario grew 15–20 mm/yr for the first 11 years of life (Galbraith et al., 1989). In all populations studied, growth of *C. serpentina* began to slow when individuals approached size at sexual maturity and most individuals stopped growing once they had attained maturity. For example, a radio-tracked adult male (32.7 cm CL) from Lake Conway in central Florida grew only 1 mm in 15 months and most large adults (> 30 cm CL) from Leon County in northwestern Florida showed no evidence of recent growth (Aresco, unpubl. data).

Sexual Dimorphism. —In a population of *C. serpentina* in Leon Co., carapace length of males (mean = 29.6 cm, range = 18.4–37.0, *n* = 28) was significantly larger than that of females (mean = 26.8 cm, range = 22.0–33.0, *n* = 25) (Aresco and Gunzburger, unpubl. data). The sexual dimorphism index (SDI) in this population is 1.11. A similar pattern of sexual size dimorphism was reported in populations outside of Florida, where males typically also grow to larger sizes than females (reviewed in Gibbons and Lovich, 1990). In individuals > 20 cm CL, the distance from the plastron to the cloaca is relatively longer in males than in females.

Size and Age at Sexual Maturity. — Size and age at sexual maturity of *C. serpentina* has not been well studied in Florida. In a sample of *C. serpentina* from Leon County, females matured at about 22 cm CL (6–8 yrs) and males at 18–19 cm CL (4–6 yrs) (Aresco and Gunzburger, unpubl. data). For example, a road-killed gravid female *C. serpentina* from Leon Co. measured 22.5 cm CL and 16.2 cm PL with 6 growth rings (Aresco, unpubl. data). In a sample from Dade Co., the smallest gravid female was 18.5 cm CL, 13.8 cm PL, 1.4 kg, and had 4 large growth rings. Other gravid females in the population had 4 large rings plus a few much smaller ones. This suggests achievement of sexual maturity in less than 6 yrs (Ewert, unpubl. data). In contrast, a dissected female from the Wacissa River in Jefferson Co. was 24.6 cm CL, 17.3 cm PL, and 3.3 kg but had tiny, immature gonads and 10 growth rings (Ewert, unpubl. data).

Longevity. — In the north, at least, *C. serpentina* has the potential for long life, as some individuals probably exceed 50 yrs in age (Congdon et al., 1987; Congdon and Gibbons, 1989).

Male Reproductive Cycle. — The male reproductive cycle has not been studied in Florida. In Tennessee and Wisconsin, *C. serpentina* has a post-mating or dissociated spermatic cycle in which sperm are produced primarily during summer and stored until mating in the following spring (White and Murphy, 1973; Mahmoud and Cyrus, 1992). In Tennessee, sperm is produced from late June to November with a peak in mid-September, whereas epididymides are largest from November to May (White and Murphy, 1973).

Female Reproductive Cycle. — The reproductive cycle of female *C. serpentina* has not been studied in Florida. In Tennessee, this species has a pronounced ovarian cycle with follicles growing in summer and fall and reaching maximum size in May and June of the following year just before ovulation (White and Murphy, 1973). In Iowa, Christiansen and Burken (1979) found that subadult females had enlarged follicles which they did not ovulate during the two years prior to reaching maturity, thus suggesting that the criterion for maturity in *C. serpentina* should be either the presence of eggs in the oviducts or corpora lutea in the ovaries.

Courtship and Mating. — Mating and copulation may occur throughout the year in southern Florida. In northern Florida, mating has a late fall to early spring hiatus (Ernst et al., 1994). In indoor captivity, one male *C. s. osceola* (Highlands Co.) mounted introduced females during all months. Females attempted to escape by snapping or "butting" with nearly closed mouths. The mounted male rubbed female heads with its chin and a closed mouth (Ewert, unpubl. data). Female *C. serpentina* are known to store sperm in storage tubules in the posterior albumen region of the oviduct (Gist and Jones, 1989).

Nesting Season. — Nesting begins earlier in Florida than in states further north, resulting in a longer nesting season (reviewed in Iverson et al., 1997). In central and south Florida, the nesting season may begin as early as February–March and continues until late June. For example, *C. serpentina* was observed nesting on 7 February at Lake Maggiore in Pinellas Co. (Heinrich, unpubl. data). Nesting probably commences in February in Dade Co., based on the presence of fresh corpora lutea, shelled oviductal eggs, or both (Ewert, 1976, 2000). Near Gainesville in north-central Florida, nests were observed on 18 May, 3 June, and 9 June (Iverson, 1977). At Lake Jackson in Leon County, nesting occurs from April–June and nesting females were observed on 4 April, 28 April, and 14 June (Aresco, unpubl. data). Also, nesting along the lower Apalachicola River has occurred mainly from mid-April to May but extending to mid-May during several years (Ewert, unpubl. data).

Nest Sites and Nesting Behavior. — Range-wide, nest sites for *C. serpentina* vary from open, sunny sites to shaded sites (Ewert, 1976; Ewert et al., 1994; Ernst et al., 1994). Along the lower Apalachicola River, only three of 91 nests were fully open to sunlight and 75 nests were mostly shaded (Ewert, unpubl. data). *Chelydra serpentina* may prefer more shaded nest sites with a decrease in latitude. Selected sites are often in broad-leaved forest or under bushes (Ewert, 1976; Ewert et al., 1994; unpubl. data). In Sarasota Co., however, *C. s. osceola* nests were somewhat less shaded (Punzo, 1975).

In Florida, nests are constructed moderately close to water in some habitats (e.g., lakes, rivers). Along the lower Apalachicola River, most females nested < 10 m from water in a high water year (Ewert, 1976) but averaged about 19 m (range 1.5–50 m, *n* = 12 nests) from water in more normal years (Ewert, unpubl. data). In Sarasota Co. seven nests ranged from 38–141 m from water with an average of 94 m (Punzo, 1975). These females nested between 0600 and 0800 hrs. Further north, in Leon and Franklin Co., females were found nesting in the mid-morning (1000–1200 hrs) (Aresco and Ewert, unpubl. data).

Nest depth to top and bottom eggs in 17 nests along the lower Apalachicola River averaged 9.5 and 20.3 cm, respectively, with an overall range of 5–25 cm. In horizontal aspect, seven egg cavities were approximately round and 11.5–16 cm across (Ewert, unpubl. data).

Clutch Size. — Clutch sizes in peninsular Florida are rather small for the species (2–28 eggs, Dade Co., Ewert, 2000; 6–21 eggs, Sarasota Co., Punzo, 1975; 14–20 eggs, Alachua Co., Iverson, 1977). Jackson and Ewert (1997) reported "large" clutches for *C. s. osceola* at 30 and 31 eggs in Dixie County and 23 eggs in Seminole County. The current maximum clutch size in Florida is 54 eggs from a female found nesting near Goose Pond in Tallahassee, Leon County (Jackson and Ewert, 1997). A radiographed 36.7 cm CL *C. s. osceola* x *serpentina* from the same locality contained 49 eggs (Aresco, unpubl. data). In Leon Co., a radiographed 28.5 cm CL female *C. s. osceola* x *serpentina* contained 34 shelled eggs and a fresh road-killed 22.5 cm CL female *C. s. serpentina* at the outset of nesting season in early April contained only 5 shelled eggs, suggesting that this was a full clutch for this small individual (Aresco, unpubl. data). Along the lower Apalachicola River in Franklin Co., the average size of 46 clutches of *C. s. serpentina* x *osceola* was 33.2 eggs (range 17–52; Ewert and Jackson, 1994). Clutch sizes in northern Florida are similar in size to those northward along the Atlantic Coastal Plain into Nova Scotia, but smaller than those in the upper Midwest and northern Plains (reviewed in Iverson et al., 1997).

Reproductive Potential. — This species produces only one clutch per year in the northern portion of its range and females may not reproduce every year (Congdon et al., 1987). Iverson (1977) suggested that *C. serpentina* in the Gainesville area produced only a single clutch per year, and certain individuals may follow this pattern. However, combined counts of multiple sets of corpora lutea and enlarged follicles indicate that females in Dade Co. can produce two to three, and possibly four clutches per season (Ewert, 2000). The estimated annual output was 27.6 eggs (range 19–36) per female**.** Females in this population tended to be quite small in size for adult *C. serpentina* (Ewert, 2000, unpubl. data). Some of the south Florida females retained in a heated laboratory produced clutches in the fall as well as two or more in the winter and spring. This observation begs the question of whether the reproductive cycle in *C. s. osceola* is entrained differently to the annual seasonal cycle than that of *C. s. serpentina*. There are only indirect data to suggest multiple clutching in central and northern Florida. In these samples, a proportion of dissected gravid females had many enlarged, perhaps pre-ovulatory, ovarian follicles (Dixie and Franklin Co.). Additionally, the broad range in dates of nesting in northern Florida allows that an early nesting female might also produce a late season clutch (Ewert, 2000, unpubl. data).

Eggs. — Eggs of *C. serpentina* in Florida and elsewhere are approximately spherical and have pliable to rigid eggshells that become turgid during early incubation (Ewert, 1979, unpubl. data). A sample of 490 normal eggs from 34 clutches from along the lower Apalachicola River averaged 14.1 ± 2.6 g (range 10.1–17.5 g). Smaller normal eggs (to 7.2 g) have come from Dade County. Linear measurements of eggs have ranged from 23.4 x 23.0 mm to 31.8 x 30.1 mm (Ewert, unpubl.). Egg masses from Sarasota Co. ranged from 5–13 g (Punzo, 1975). Egg diameters from Alachua Co. ranged from 24.9 to 30.8 mm (Iverson, 1977).

Incubation and Hatching. — Under identical laboratory conditions for incubation, the eggs of *C. serpentina* from Florida (Dade, Dixie, Franklin and Seminole Cos.) take longer to develop and hatch than similar sized eggs from northern populations (Ewert, 1979, 1985, unpubl. data). Mean incubation periods of Florida eggs range from 74–78 days at 30°C to 145 days at 21.5°C. Probable incubation times in natural nests would be intermediate, ca. 80 to 102 days. *Chelydra serpentina* exhibits a pattern of environmental sex determination where eggs incubated at very warm or very cool temperatures produce mostly females, while those at moderate temperatures produce mostly males (Yntema, 1976; Wilhoft et al., 1983). This also holds true for the subspecies *C. s. osceola* (Ewert, unpubl. data). There is no evidence that hatchling *C. serpentina* overwinter on land in Florida.

Hatchlings. — Hatchlings of *C. serpentina* from the Gainesville area ranged from 24–30 mm CL (Iverson, 1977), but have frequently measured 35 mm CL from along the lower Apalachicola River and elsewhere in Florida (Ewert, unpubl. data). The fresh mass of a hatchling developed in a damp substrate averages near or slightly over 75 % of the mass of its original egg. There is no indication that hatchlings of *C. s. serpentina* and *C. s. osceola* differ from each other in size. However, hatchlings of *C. s. osceola* from the eastern Everglades differ by having neutral gray coloration dominating the carapace, with a few mid-dorsal black marks. The plastron is black with white flecks. From Dixie Co. northward, hatchlings of both *C. s. serpentina* and *C. s. osceola* are uniformly black except for some white dots on the plastron (Ewert, unpubl. data).

POPULATION BIOLOGY

Density and Biomass. — Data on population density and biomass of this species in Florida are only available from four populations in Leon County in the panhandle. They demonstrate considerable variation in density among sites (Aresco, unpubl. data; Table 1-2). In northern populations, this species also shows significant variation in density (0–66 adults/ha) and biomass (9–340 kg/ha) (Froese and Burghardt, 1975; Major, 1975; Iverson, 1982; Iverson et al., 2000; Galbraith et al., 1988; Congdon and Gibbons, 1989).

From available accounts of commercial harvest of *C. serpentina* in the Midwest, this species must have occurred at very high densities in Midwestern rivers in the early 1900s (Clark and Southall, 1920). For example, a single fish company at La Crosse, Wisconsin, handled almost 30,000 snapping turtles between November 1917 and May 1918.

Population Dynamics. — Survivorship schedules of adult snapping turtles in Florida are unknown.

Population and Community Structure. — Sex ratio of adult males: adult females was not significantly different from 1:1 at McCord Pond, a natural suburban pond/marsh in Tallahassee, Leon Co. (25 females, 30 males) (Aresco and Gunzburger, unpubl. data). Similarly, sex ratios were 1:1 in some northern populations (Lagler and Applegate, 1943; Mosimann and Bider, 1960; Major, 1975).

In a determination of absolute abundance at McCord Pond, turtles were initially trapped with aquatic hoop traps prior to a mechanical muck removal project. Then all remaining turtles were hand-collected while heavy machinery was removing muck (Aug 1999–March 2000) (Aresco and Gunzburger, 2004). The size distribution was dominated by large adults, but with sufficient numbers of juveniles and subadults to indicate low levels of recruitment (Fig. 1-9). In Leon County, *C. serpentina* represented only 0.18% of the

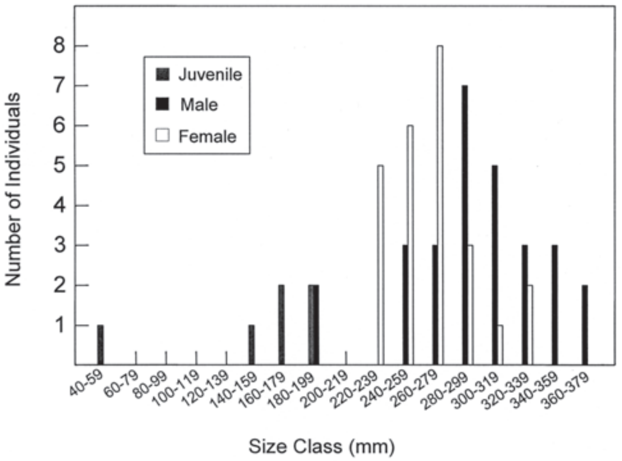

Figure 1-9. Size distribution of *Chelydra serpentina* at McCord Pond, Tallahassee, Leon Co., Florida.

turtle community at Lake Jackson, whereas it represented 18% of the turtle community at the 1.5 ha muck-bottomed McCord Pond (Table 1-2) (Aresco and Gunzburger, 2004; Aresco, unpubl. data).

INTERSPECIFIC INTERACTIONS

Diet. — *Chelydra serpentina* is omnivorous and is known to feed on a wide variety of aquatic invertebrates, fish, amphibians, and plants. This species can complete a feeding strike in 78 milliseconds and has the ability to capture fast-moving prey items such as fish, crayfish, and amphibians (Lauder and Prendergast, 1992). There is only one quantitative diet study of this species in Florida. Punzo (1975) examined the digestive tracts of 59 *C. s. osceola* from several habitats in west-central Florida and found that earthworms, insects, isopods, and plant material were present in all individuals. The remains of amphibians were present in 95% of tracts, amphipods in 92% (probably eaten incidentally with plants), and crayfish in 83%. Bone fragments were present in 100% of individuals but most were not identified, thus the relative importance of fish, birds, and mammals in the diet of snapping turtles could not be evaluated in that study. At McCord Pond in Tallahassee, Leon Co. with a high density of *C. serpentina*, 5.1% of adult yellow-bellied sliders (*Trachemys scripta*) and Florida cooters (*Pseudemys floridana*) were missing one or more limbs, possibly the result of attacks by snapping turtles (Aresco and Gunzburger, unpubl. data).

Aquatic plants are a major component of the diet of snapping turtles. Three adult *C. serpentina* collected in Leon Co. contained plant material. A fecal sample of an adult male (31 cm CL) captured in July contained 95% duckweed (*Spirodela polyrhiza*) and 5% stems of American lotus (*Nelumbo lutea*), the stomach of a 37 cm CL male found in August contained 100% wild taro (*Colocasia esculenta*), an exotic emergent plant, and the stomach of a 28.2 cm CL female found in July contained 100% bladderwort (*Utricularia* sp.) (Aresco, unpubl. data). Other studies have reported herbivory by snapping turtles throughout their range. In Illinois, Budhabhatti and Moll (1990) observed the same 33 cm adult grazing on duckweed (*Lemna minor*) on 10 occasions between late May and early August.

Table 1-2. Variation in density, biomass, and percent composition in the turtle community of *Chelydra serpentina* among four sites in Leon County, Florida.

Site (ha)	*n*	Density (turtles/ha)	Biomass (kg/ha)	% composition
McCord Pond (1.5)	64	43.0	201.0	18.0
Harriman Pond (0.5)	11	22.0	69.5	10.0
Chapman Pond (1.0)	3	3.0	10.6	3.5
NW Lake Jackson (405)	17	0.04	0.1	0.2

Predation. — Depredation of nests of *C. serpentina* can be significant, especially by mammalian predators such as raccoons and foxes, but also by fish crows. Rates of nest depredation appear to be > 90% along the lower Apalachicola River. When nesting was simultaneous with *Macrochelys temminckii*, nests of *C. serpentina* have been depredated within a day, whereas nests of *M. temminckii* have lasted 1–2 days (Ewert and Jackson, 1994; Ewert, unpubl. data). In the northern part of the range, nests are often destroyed within a few days of oviposition but after two or three weeks nest survivorship increases to almost 100% (Robinson and Bider, 1988). Rates of nest depredation may vary among years at the same site (Hammer, 1969; Congdon et al., 1987) suggesting variation in predator abundance or environmental conditions (e.g., nesting during rain).

During the dry-down of Lake Jackson, Leon Co., under severe drought conditions, two *C. serpentina* were found dead on the dry lake bottom, a 14.0 cm CL juvenile and 26.8 cm CL adult, both probably killed by raccoons (Aresco, unpubl. data). Despite speculation that alligators cause the low densities of *C. serpentina* in Florida lakes, *C. serpentina* was not reported in a diet study of alligators in north-central Florida although Florida red-bellied turtles (*Pseudemys nelsoni*), peninsula cooters (*Pseudemys floridana*), striped mud turtles (*Kinosternon baurii*), and common musk turtles (*Sternotherus odoratus*) were present in alligator stomachs in this study (Delany and Abercrombie, 1986).

Parasites and Disease. — Leeches (*Placobdella parasitica*) are commonly found on the soft parts of *C. serpentina* (Brooks et al., 1990, Aresco and Gunzburger, unpubl. data). Plastral shell lesions (shell rot) infected several adult *C. serpentina* from a suburban pond in Tallahassee, Leon Co. (Aresco and Gunzburger, unpubl. data).

THREATS

Documented Threats. — Habitat loss and fragmentation are significant threats to snapping turtle populations in Florida. Many small, isolated wetlands that support populations of *C. serpentina* are destroyed or altered because they receive little or no legal protection in Florida. Terrestrial habitats associated with wetlands that are vital to *C. serpentina* for nesting and linkage to other wetlands are afforded no protection as they are outside of the wetland delineation boundaries (Gibbons, 2003). Direct loss of natural wetlands as a result of residential and commercial development and conversion of natural wetlands to stormwater retention ponds associated with urbanization can eliminate snapping turtle populations (Aresco, unpubl. data).

Even without commercial land development, diversions of natural water flows appear to have adversely affected *C. s. osceola* populations in dedicated natural areas, such as the eastern part of Everglades National Park. Water diversion has aggravated drought conditions leading to deaths following complete drying (Koschman, 1966).

Mechanical removal of organic sediment ("muck") from lakes and ponds is an established wetland management technique in Florida and is a type of habitat alteration that is a serious threat to *C. serpentina* populations (Aresco and Gunzburger, 2004). Mechanical muck removal is conducted by the Florida Fish and Wildlife Conservation Commission (FFWCC) in attempts to enhance sport fisheries and improve boater access, and by local municipalities to increase stormwater capacity of wetlands that serve as stormwater retention ponds in suburban areas. In most cases, the ponds are pumped dry and heavy machinery (large backhoes and bulldozers) remove all organic sediment to a depth at which sand or clay is reached, or much deeper in the case of the stormwater ponds. Organic sediment is either piled on the shore and allowed to dry before transport to off-site landfills or immediately loaded onto trucks as it is removed. In the process, *C. serpentina* are either killed by suffocation in excavated piles of sediment or crushed by heavy machinery, with virtually no chance to escape (Aresco and Gunzburger, 2004). In some cases, turtles found by workers during pumping or excavating are taken for human consumption (Mitchell Brothers Construction Co., Tallahassee, *pers. comm.*). During cold weather, turtles are inactive and often buried in organic sediment and are incapable of escaping mechanical excavation or digging themselves out from muck piles. For example, at McCord and Harriman Ponds in Tallahassee, Leon Co., populations of 64 and 11 individuals, respectively, were completely eliminated from these ponds and many additional sediment removal projects are planned in the next few years throughout Florida (Aresco and Gunzburger, 2004). In cases where entire wetlands are drained and dredged, local extinction of *C. serpentina* populations is likely with no foreseeable recovery. In suburban landscapes, the probability of successful recolonization by *C. serpentina* of stormwater ponds is greatly reduced by a road-fragmented landscape (Aresco, 2005). Large-scale sediment removal operations leave lakes and ponds with a hard, graded sand or clay substrate devoid of any organic material and aquatic plants. Therefore, habitat alteration resulting from sediment removal reduces the likelihood of population recovery of species such as *C. serpentina* that are primarily associated with habitats of thick organic sediment and dense macrophytes.

Roads built through or near wetlands are significant sources of mortality of turtle populations in Florida (Aresco, 2005). *Chelydra serpentina* is frequently observed attempting to cross roads when females emerge from water to nest or when adults or juveniles move overland between aquatic habitats. During drought conditions in Florida, lakes, ponds, and swamps may dry completely, causing *C. serpentina* to migrate in search of water (Aresco, 2005). Thus, roads are barriers to both normal seasonal movements and mass migrations during periodic drought conditions. Highway roadsides also create artificial disturbed and open habitats that may be attractive to nesting females but may cause significant annual road mortality. In central Ontario, a 3-yr study found 86 *C. serpentina* killed on roads during the nesting season, of which 24% were mature females (Haxton, 2000). In a 4-yr survey on the 3.6 km Long Point Causeway at Lake Erie, Ontario, 272 *C. serpentina* were found road-killed (Ashley and Robinson, 1996). Unfortunately, there are few quantitative data on road mortality of *C. serpentina* in Florida. Smith and Dodd (2003) reported 8 *C. serpentina* killed in one year on a 3.2 km section of U. S. Highway 441 at Paynes Prairie. Although *C. serpentina* was at low density (0.04 turtles/ha) at Lake Jackson, Leon Co., it had the greatest level of road mortality relative to abundance compared to other turtle species (11 road-killed individuals on 1.2 km of U.S. Highway 27 in four years) (Aresco, 2005). Without careful monitoring of turtle populations, the effects of road mortality on *C. serpentina* populations might not be detected until after population declines have occurred.

Potential Threats. — Historically, snapping turtles were harvested for their meat throughout their range (Clark and Southall, 1920; Harding and Holman, 1987). In colder climates, much of the commercial collecting of this species was done with long, recurved hooks that were used to probe muddy bottoms and undercut riverbanks at resting and/or hibernation sites (Clark and Southall, 1920). During World War II Americans were encouraged to consider snapping turtles as an alternative meat supply (Lagler, 1943). In the early 1970s, commercial harvest of *C. serpentina* in New York resulted in an average take of 2.4 adults/ha/year, a level of harvest that was not sustainable and a fourth-year yield that was half of that in the first year (Kiviat, 1980).

Commercial exploitation of snapping turtles has recently increased in many states because of a new demand from Asian markets (both in the U. S. and in China) for turtle meat, organs, and bones for food and traditional medicines. The wholesale value of hatchling *C. serpentina* increased to $6 each in 2002–03. Photographs accompanying Internet sales clearly show offerings of hatchling *C. s. osceola* from south Florida (Ewert, *pers. obs.*). Although turtle farms in China are attempting to produce their own *C. serpentina* (P. Moler, FFWCC, *pers. comm.*), China continues to import them from North America. A turtle trapper in Maine reported an Asian buyer who had solicited 5,000 pounds of small female snapping turtles. In North Carolina, 23,000 turtles were harvested in 2002, many of which were snapping turtles that were shipped to China or U. S. Asian markets (North Carolina Division of Wildlife Management, *pers. comm.*). The Maine Department of Inland Fisheries and Wildlife banned commercial harvest of snapping turtles in 2002 because of decades of overexploitation and the potential increase in harvest from Asian buyers offering high prices. In Florida the level of harvest of *C. serpentina* is unknown as the FFWCC does not require permits or reporting for turtles harvested for personal consumption and most commercial turtle harvest (65-85%) goes unreported (Enge, 1993). Enge (1993) reported that 83 lb (37 kg) of dressed snapping turtle meat was sold to one fish market in the Lake Okeechobee area from 1990–92, prior to the considerable increase in Asian demand for U.S. turtles in the last several years. Conversations with local turtle trappers in north Florida indicate that *C. serpentina* are often captured on trotlines, set lines, and bush hooks, both intentionally and as bycatch while trapping Florida softshells (*Apalone ferox*). According to trappers, snapping turtle meat is kept for personal consumption or sold locally. In the 1980s–1990s, baited trotlines set to catch Florida softshells were prevalent on Lake Jackson, Leon Co. (M. Hill, FFWCC, *pers. comm.*). Although *C. serpentina* may naturally be less abundant in large lakes, long-term exploitation of *C. serpentina* both directly or as bycatch to Florida softshell harvest may at least partially explain the very low density of this species at Lake Jackson compared to nearby ponds, which have relatively high densities of *C. serpentina* but no harvest pressure. A series of very large *C. s. osceola* collected in the 1920s from Lake Apopka, Orange Co. (FLMNH 53698, 66157, 66158; CL's 40.5, 42.5, and 39.9 cm) suggests the historic presence of large individuals in lake populations that are rarely observed today. Therefore, although levels of unreported harvest for personal consumption or local sales may be relatively low, some *C. serpentina* populations may be adversely affected if population densities are naturally low and the same populations are exploited over time.

Population viability models derived for northern populations demonstrate that low levels of harvest (less than 10%) of adult *C. serpentina* can lead to rapid depletion of populations (Galbraith and Brooks, 1987; Congdon et al., 1994), and even light conventional harvest is not sustainable **(**Galbraith et al., 1997)**.** Without close monitoring of the population status of this species, the effects of overharvesting may not be recognized until they become severe. Consumption of this species by humans might be tempered by the observation that it is high on the food chain, long lived, and has been shown to concentrate organochlorine toxicants (e.g., from pesticides in agricultural areas) to a degree considered unsafe for humans under USDA standards (Stone et al., 1980; Golet and Haines, 2001).

Incidental killing of all species of turtles, including *C. serpentina*, by bank fishermen continues in north Florida and is especially problematic during drought conditions when turtles become concentrated in relatively small areas (Aresco, unpubl. data). Turtles are killed due to a misconception that they compete with humans for fish and because they may take bait (e.g., worms, chicken parts) or tackle that fishermen retrieve by destroying the turtle (Aresco, *pers. obs.*). Juvenile snapping turtles are more vulnerable to this threat than adults. Some government and private managers of fisheries ponds, sport fish stocks, and waterfowl at both private and public water bodies continue to employ lethal methods of predator control on perceived fish and waterfowl predators such as turtles. Although there is no scientific evidence that *C. serpentina* reduces populations of fish or waterfowl, this species is often trapped and killed for this reason throughout its range (J. Birdsley, *pers. comm.*, Aresco, *pers. obs.*).

Despite Federal regulations that prohibit sale of turtles less than four inches in length, hatchling and small juvenile *C. serpentina* are commonly sold in pet stores (e.g., at three pet stores in Tallahassee in 2003) (Aresco, *pers. obs.*). From 1990–92, 262 *C. serpentina* taken from the wild were sold in pet stores, but clearly the actual numbers collected were far greater than reported (Enge, 1993).

STATUS

The status of *C. serpentina* is unknown in most of Florida, but is generally considered secure. The species is not currently listed by CITES, USFWS, FCREPA, or FFWCC.

CONSERVATION OPTIONS AND SOLUTIONS

Chelydra serpentina is not State or Federally listed as threatened or endangered. However, Federal and state regulations are insufficient to protect many of the wetland habitats (e.g., small, isolated, and seasonal wetlands) that support snapping turtle populations in Florida. Therefore, state legislative regulations should be passed to protect these wetlands (not connected with U.S. navigable waters) that are no longer protected due to a recent Supreme Court decision (Gibbons, 2003). Additional regulations should extend wetland conservation boundaries to include the terrestrial periphery and terrestrial corridors between isolated wetlands (Buhlmann and Gibbons, 2001).

The negative effects of sediment removal on populations of *C. serpentina* and other herpetofauna should be carefully considered prior to the permitting of future projects by regulatory agencies and, if possible, mitigation efforts such as capturing and relocating turtles to nearby ponds prior to and during these projects should be undertaken.

Reducing or eliminating road mortality of *C. serpentina* can be accomplished by constructing diversion fencing or barriers along the road in combination with under-highway culverts at key crossing locations (Dodd et al., 2004; Aresco, 2005; M. Papin, NYDOT, *pers. comm.*). Areas where road-kills are concentrated along defined stretches of road, such as where highways bisect wetlands or at important nesting sites, should be identified for mitigation (Aresco, 2005). In Florida, such projects typically originate at the county level (e.g., Metropolitan Planning Organization) and involve cooperation with the Florida Department of Transportation (FDOT), with potential funding sources such as Federal transportation enhancement funds under TEA-21 (Transportation Equity Act for the 21st Century) or FDOT environmental mitigation funds (Transportation Research Board, 2002). New road projects should be carefully evaluated for their environmental impacts during the PD&E phase (Project Development and Environmental) and wildlife crossing and diversion structures designed into such projects beforehand. For *C. serpentina* and other turtles with good climbing ability, diversion structures should be at least 1 m tall, have an inward facing lip, and buried to at least 30 cm. Wire exclusion fencing typically installed along major highways in Florida to prevent wildlife-vehicle collisions does not work for all size classes of turtles. There are numerous large gaps under fencing, especially at watercourses and wetlands, and standard wire size only excludes larger turtles (greater than $4^{1}/_{2}$ inches shell width, Aresco, *pers. obs.*).

There are currently no regulations in Florida that protect *C. serpentina* from excessive harvest and we lack adequate baseline data on the level of harvest of this species to properly assess population viability and set sustainable limits on use. We recommend that the Florida Fish and Wildlife Conservation Commission consider a moratorium on harvest of *C. serpentina* until baseline data are collected. If other states follow North Carolina and ban commercial turtle harvest, commercial turtle trapping will probably increase in Florida over the next several years. At a minimum, all turtle harvest (personal and commercial) should require a specific trapping permit and mandatory reporting of size, sex, and number of harvested turtles. This strategy should be implemented immediately in order to closely track the status of harvested populations and the activities of turtle trappers throughout the state.

Fishermen and fisheries and waterfowl managers should be educated that *C. serpentina* does not significantly affect fish and waterfowl populations, but in fact, provide important ecological functions as scavengers and herbivores. Needless eradication of *C. serpentina* from public and private ponds and lakes should be specifically prohibited by the FFWCC. In areas where bank fishermen continually kill turtles that are incidentally caught on fishing lines, those individuals should be prosecuted under the FFWCC general regulation prohibiting “wanton and willful destruction of wildlife.” Trotlines, setlines, and bush hooks should be prohibited in Florida as they indiscriminately capture non-target species and incidental mortality of turtles can occur from abandoned bush hooks in Panhandle rivers (e.g., Ochlockonee River, Apalachicola River, and Wacissa River).

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LITERATURE CITED

Aresco, M. J. 2005. Mitigation measures to reduce highway mortality of turtles and other herpetofauna at a north Florida lake. Journal of Wildlife Management 69:549-560.

Aresco, M. J., and Gunzburger, M. S. 2004. Effects of large-scale sediment removal on herpetofauna in Florida wetlands. Journal of Herpetology 38:275-279.

Aresco, M. J., and F. C. James. 2005. Ecological relationships and abundance of turtles in north Florida lakes: a study of omnivory and an analysis of the trophic structure of a whole lake food web. Final Report. Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida, 66 pp.

Ashley, E. P. and Robinson, J. T. 1996. Road mortality of amphibians, reptiles and other wildlife on the Long Point causeway, Lake Erie, Ontario. Canadian Field Naturalist 110, 403-412.

Babcock, H. L. 1932. The American snapping turtles of the genus *Chelydra* in the collection of the Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A. Proceedings of the Zoological Society of London 4:873-874.

Bancroft, G. T., Godley, J. S., Gross, D. T., Rojas, N. N., Sutphen, D. A., and McDiarmid, R. W. 1983. Large-scale operations management test of use of the white amur for control of problem aquatic plants. The herpetofauna of Lake Conway: Species accounts. Misc. Paper A-83-5. U. S. Army Engineer Waterways Experiment Station, CE, Vicksburg, Mississippi.

Brooks, R. J., Galbraith, D. A., and Layfield, J. A. 1990. Occurrence of *Placobdella parasitica* (Hirudinea) on snapping turtles, *Chelydra serpentina*, in southeastern Ontario. Journal of Parasitology 76:190-195.

Budhabhatti, J., and Moll, E. O. 1990. *Chelydra serpentina* (common snapping turtle). Feeding behavior. Herpetological Review 21:19.

Buhlmann, K. A., and Gibbons, J. W. 2001. Terrestrial habitat use by aquatic turtles from a seasonally fluctuating wetland: implications for wetland conservation boundaries. Chelonian Conservation and Biology 4:115-127.

Carr, A. F., Jr. 1952. Handbook of turtles. The turtles of the United States, Canada, and Baja California. Comstock Publ. Co., Cornell University Press, Ithaca, New York.

Christianson, J. L., and Burken, R. R. 1979. Growth and maturity of the snapping turtle *Chelydra serpentina* in Iowa. Herpetologica 35:261-266.

Clark, H. W., and Southall, J. R. 1920. Fresh water turtles: A source of meat supply. U.S. Bulletin Fish Doc. 889:3-20.

Congdon, J.D., and Gibbons, J.W. 1989. Biomass productivity of turtles in freshwater wetlands: A geographic comparison. In: Sharitz, R. R., and Gibbons, J. W. (Eds.). Freshwater wetlands and wildlife, pp. 583-592. DOE Symposium Series No. 61.

Congdon, J. D., Breitenbach, G. L., Van Loben Sels, R. C., and Tinkle, D. W. 1987. Reproduction and nesting ecology of snapping turtles (*Chelydra serpentina*) in southeastern Michigan. Herpetologica 43:39-54.

Congdon, J. D., Dunham, A. E., and Van Loben Sels, R. C. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. American Zoologist 34:397-408.

Crother, B. L., Boundy, J., Campbell, J. A., De Quieroz, K., Frost, D., Green, D. M., Highton, R., Iverson, J. B., McDiarmid, R.W., Meylan, P. A., Reeder, T. W., Seidel, M. E., Sites, J. W., Tilly, S. G., and Wake, D. B. 2000. Scientific and standard English names of amphibians and reptiles of North America north of Mexico, with comments regarding confidence in our understanding. Society for the Study of Amphibians and Reptiles Herpetological Circular No. 29.

Delany, M. F., and Abercrombie, C. L. 1986. American alligator food habits in north-central Florida. Journal of Wildlife Management 50:348-353.

Dodd, C. K., Jr., W. J. Barichivich, and L. L. Smith. 2004. Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily traveled highway in Florida. Biological Conservation 118:619-631.

Dunson, W. A. 1986. Estuarine populations of the snapping turtle (*Chelydra*) as a model for the evolution of marine adaptations in reptiles. Copeia 1986:741-756.

Enge, K. M. 1993. Herptile use and trade in Florida. Final Performance Report, Nongame Wildlife Program, Florida Game and Fresh Water Fish Commission.

Ernst, C. H., Lovich, J. E., and Barbour, R. W. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington, D. C.

Ewert, M. A. 1976. Nests, nesting and aerial basking of *Macroclemys* under natural conditions, and comparisons with *Chelydra* (Testudines: Chelydridae). Herpetologica 32:150-156.

Ewert, M. A. 1979. The embryo and its egg: development and natural history. In: Harless, M., and Morlock, H. (Eds.). Turtles: Perspectives and Research. John Wiley & Sons, New York, pp. 333-413.

Ewert, M. A. 1985. Embryology of Turtles. In: C. Gans, F. Billett, and P.F.A. Maderson (Eds.). Biology of the Reptilia 14, Wiley-Interscience, New York, pp. 73-267.

Ewert, M. A. 2000. *Chelydra serpentina osceola* (Florida snapping turtle). Reproduction. Herpetological Review 31:172

Ewert, M. A., and Jackson, D. R. 1994. Nesting ecology of the alligator snapping turtle (*Macroclemys temminckii*) along the lower Apalachicola River, Florida. Florida Game and Fresh Water Fish Commission, Nongame Wildlife Program Report NC89-020, Tallahassee, Florida, 45 pp.

Ewert, M. A., Jackson, D. R., and Nelson, C. E. 1994. Patterns of temperature-dependent sex determination in turtles. Journal of Experimental Zoology 270:3-15.

Feuer, R. C. 1971. Intergradation of the snapping turtles *Chelydra serpentina serpentina serpentina* (Linnaeus, 1758) and *Chelydra serpentina osceola.* Herpetologica 27:379-384

Froese, A. D., and Burghardt, G. M. 1975. A dense natural population of the common snapping turtle (*Chelydra s. serpentina).* Herpetologica 31:204-208

Galbraith, D. A., and Brooks, R. J. 1987. Survivorship of adult females in a northern population of common snapping turtles, *Chelydra serpentina.* Canadian Journal of Zoology 65:1581-1586.

Galbraith, D. A., Chander, M. W., and Brooks, R. J. 1987. The fine structure of home ranges of male *Chelydra serpentina:* are snapping turtles territorial? Canadian Journal of Zoology 65:2623-2629.

Galbraith, D. A, Bishop, C. A., Brooks, R. J., Simser, W. L., and Lampman, K. P. 1988. Factors affecting the density of common snapping turtles (*Chelydra serpentina serpentina*). Canadian Journal of Zoology 66:1233-1240.

Galbraith, D. A., Brooks, R. J., and Obbard, M. E. 1989. The influence of growth rate on age and body size at maturity in female snapping turtles (*Chelydra serpentina*). Copeia 1989:896-904.

Galbraith, D. A., Brooks, R. J., and Brown, G. P. 1997. Can management intervention achieve sustainable exploitation of turtles? In: Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles, pp. 186-194. New York Turtle and Tortoise Society.

Gibbons, J. W. 2003. Terrestrial habitat: a vital component for herpetofauna of isolated wetlands. Wetlands 23: 630-635.

Gibbons, J. W., and Lovich, J. E. 1990. Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). Herpetological Monographs 4:1-29.

Gibbons, J. W., Novak, S. S., and Ernst, C. H. 1988. *Chelydra serpentina.* Catalogue of American Amphibians and Reptiles 420:1-4.

Gist, D. H., and Jones, J. M. 1989. Sperm storage within the oviduct of turtles. Journal of Morphology 199:379-384.

Golet, W. J., and Haines, T. A. 2001. Snapping turtles (*Chelydra serpentina*) as monitors for mercury contamination of aquatic environments. Environmental Monitoring and Assessment 71:211-220.

Hammer, D. 1969. Parameters of a marsh snapping turtle population, Lacreek Refuge, South Dakota. Journal of Wildlife Management 33:995-1005.

Harding, J. H., and Holman, J. A. 1987. The paleohistory of turtles: a brief history. Bulletin Chicago Herpetology Society 22:109-116.

Haxon, T. 2000. Road mortality of snapping turtles, *Chelydra serpentina*, in central Ontario during their nesting period. Canadian Field Naturalist 114:106-110.

Iverson, J. B. 1977. Reproduction in freshwater and terrestrial turtles of north Florida. Herpetologica 33:205-212.

Iverson, J. B. 1982. Biomass in turtle populations: A neglected subject. Oecologia 55:69-76.

Iverson, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately printed, 363 pp.

Iverson, J. B., Higgins, H., Sirulnik, A., and Griffiths, C. 1997. Local and geographic variation in the reproductive biology of the snapping turtle (*Chelydra serpentina*). Herpetologica 53:96-117.

Iverson, J. B., Hearne, D., Watters, J., Croshaw, D., and Larson, J. 2000. *Chelydra serpentina* (common snapping turtle). Density and biomass. Herpetological Review 31:238.

Jackson, D. C., Herbert, C. V., and Ultsch, G. R. 1984. The comparative physiology of diving in North American freshwater turtles. II. Plasma ion balance during prolonged anoxia. Physiological Zoology 57:632-640.

Jackson, D. R., and Ewert, M. E. 1997. *Chelydra serpentina* (snapping turtle). Reproduction. Herpetological Review 28:87.

Kiviat, E. 1980. A Hudson River tidemarsh snapping turtle population. Transactions of the Northeast Section of the Wildlife Society 37:158-168.

Koschman, G. 1966. Turtles and the Everglades water problem. International Turtle and Tortoise Society Journal 1:21-22, 36, 47.

Lagler, K. F. 1943. Turtle: an unrationed ration. Michigan Conservation 12:6-7.

Lagler, K. F, and Applegate, V. C. 1943. Relationship between the length and the weight in the snapping turtle *Chelydra serpentina.* American Naturalist 77:476-478.

Lauder, G. V., and Prendergast, T. 1992. Kinematics of aquatic prey capture in the snapping turtle *Chelydra serpentina.* Journal of Experimental Biology 164:55-78.

Linnaeus, C. 1758. Systema Naturae. 10th ed. Holmiae, Sweden. 1:1-824.

Mahmoud, I. Y., and Cyrus, R. V. 1992. The testicular cycle of the common snapping turtle, *Chelydra serpentina,* in Wisconsin. Herpetologica 48:193-201.

Major, P. D. 1975. Density of snapping turtles, *Chelydra serpentina,* in western West Virginia. Herpetologica 31:332-335.

Mosimann, J. E., and Bider, J. R. 1960. Variation, sexual dimorphism, and maturity in a Quebec population of the common snapping turtle, *Chelydra serpentina.* Canadian Journal of Zoology 38:19-38.

Obbard, M. E., and Brooks, R. J. 1981. A radio-telemetry and mark-recapture study of activity in the common snapping turtle, *Chelydra serpentina*. Copeia 1981:630-637.

Phillips, C. A., Dimmick, W. W., and Carr, J. L. 1996. Conservation genetics of the common snapping turtle (*Chelydra serpentina*). Conservation Biology 10:397-405.

Punzo, F. 1975. Studies on the feeding behavior, diet, nesting habits and temperature relationships of *Chelydra serpentina osceola* (Chelonia: Chelydridae). Journal of Herpetology 9:207-210.

Richmond, N. D. 1958. The status of the Florida snapping turtle *Chelydra osceola* Stejneger. Copeia 1958:41-43.

Robinson, C., and Bider, J. R. 1988. Nesting synchrony – a strategy to decrease predation of snapping turtle (*Chelydra serpentina*) nests. Journal of Herpetology 22:470-473.

Schweigger, A. F. 1812. Monographiae Cheloniorum. Königsberg. Arch. Naturwiss. Math. 1:271-368, 406-458.

Smith, L. L., and Dodd, Jr., C. K. 2003. Wildlife mortality on U.S. Highway 441 across Paynes Prairie, Alachua County, Florida. Florida Scientist 66:128-140.

Stejneger, L. 1918. Description of a new snapping turtle and a new lizard from Florida. Proc. Biol. Soc. Washington 31:89-92.

Stone, W. B., Kiviat, E., and Butkas, S. A. 1980. Toxicants in snapping turtles. New York Fish and Game Journal 27:39-50.

Transportation Research Board. 2002. Interaction between roadways and wildlife ecology: A synthesis of highway practice. National Cooperative Highway Research Program, Synthesis 305, Transportation Research Board of the National Academies, Washington, D.C.

Walker, D. and Avise, J. C. 1998. Principles of phylogeography as illustrated by freshwater and terrestrial turtles in the southeastern United States. Annual Review of Ecology and Systematics 29:23-58.

Walker, D., Moler, P. E., Buhlmann, K. A., and Avise, J. C. 1998. Phylogeographic uniformity in mitochondrial DNA of the snapping turtle (*Chelydra serpentina*). Animal Conservation 1:55-60.

White, J. B., and Murphy, G. G. 1973. The reproductive cycle and sexual dimorphism of the common snapping turtle, *Chelydra serpentina serpentina*. Herpetologica 29:240-246.

Wilhoft, D. C., Hotaling, E., and Franks, P. 1983. Effects of temperature on sex determination in embryos of the snapping turtle, *Chelydra serpentina*. Journal of Herpetology 17:38-42.

Yntema, C. L. 1976. Effects of incubation temperatures on sex differentiation in the turtle, *Chelydra serpentina*. Journal of Morphology 150:453-462.

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Macrochelys temminckii – Alligator Snapping Turtle

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Summary. – The alligator snapping turtle, *Macrochelys temminckii*, is the largest freshwater turtle in Florida. Males grow much larger than females; females rarely exceed 25 kg, whereas males may grow to 75 kg or more. The carapace has three prominent longitudinal ridges, the head is massive, and the mouth, often held wide open, has a darkly camouflaged soft lining and a strongly hooked beak. This highly aquatic species inhabits rivers that drain into the Gulf of Mexico from the Suwannee River westward across northern Florida. The fairly brief nesting season extends from late April through most of May. Females lay only one clutch of 17–52 moderately large eggs in a season. Incubation requires about 15–18 weeks, and the sex of hatchlings is strongly influenced by incubation temperature. The young are inclined toward piscivory, whereas adults consume a variety of items. Despite a history of take for human consumption, field surveys show that the species remains widespread and fairly numerous across its known Florida range. Although there is appreciable nest depredation, this may still occur within natural limits. Engineering modifications to rivers, while tolerated by this species, probably degrade habitat and lower carrying capacity. Reservoirs have reduced abundance of favored swamp forest habitat, whereas silt deprivation below dams, as in the Apalachicola and Ochlockonee rivers, lowers the main channel and deprives connecting swamp forest channels. Because alligator snapping turtles rarely leave the water except to nest, little or no movement occurs between rivers. This has led to differentiation of Florida populations into three major genetic units: Suwannee, Ochlockonee/Apalachicola/Choctawhatchee, and Pensacola Bay drainages. The population in the Suwannee River drainage is the most genetically divergent; conservation planning should consider this population difference.

Conservation Status. – FNAI Global - G3G4 (Rare, Local, or Vulnerable / Apparently Secure), State - S3 (Rare, Local, or Vulnerable); ESA Federal - Not Listed; State - SSC (Species of Special Concern); CITES - Appendix III (USA); IUCN Red List - VU (Vulnerable).

Species Recognition. — The most obvious features of the alligator snapping turtle are its very large overall size, massively tricarinate (three-ridged) carapace, and huge head (Figs. 2-1, 2-2). Three other characters of the carapace and mouth are unique among living turtles. Midway along each side of the carapace is an extra row of typically two to four small scutes (Fig. 2-2). These supramarginal scutes lie between the typical perimeter of marginal scutes and the large costal scutes. Except for rare abnormalities, only certain long-extinct species of turtles also have supramarginal scutes. Two other unique characters are evident within the gaping mouth, which individuals larger than hatchlings readily present to the viewer when aggravated. Particularly in subadult *Macrochelys,* the interior lining of the mouth is not pink, as in most turtles, but gray brown with black speckles, approximating the color of the rest of the turtle (Fig. 2-3). No other turtles have "camouflaged" mouths. On the floor of the mouth, a mobile, worm-like structure extends from the tongue. Young turtles, especially, use this appendage as a lure. No other turtle species has such an appendage (detailed by Spindel et al., 1987) or attempts to lure prey into an open mouth.

The tricarinate carapace is very rugose in juveniles but becomes smooth with age while still retaining the three ridges. The carapace is posteriorly serrated throughout life. The plastron is narrow and cruciform, which leaves much skin exposed ventrally; the turtle can retract its limbs under its carapace but they remain exposed below.

The head is large to massive and cannot be fully retracted. The jaws are tapered anteriorly, and both are strongly hooked. The tail is large and includes a mid-dorsal row and two dorsolateral rows of scales elevated like dull saw teeth. These scales are less prominent than in *Chelydra*. The skin on young individuals appears rough and includes many cornified ridges, small flaps, bumps, and papillae. The skin of old adults takes on a wrinkled appearance.

The generally dark brown hatchlings, although rough on the carapace, are soft, almost velvety elsewhere. The softness arises from a minute fringe on the tips of the carapacial marginals, from numerous soft bumps, flaps, and papillae on the skin, and from a soft, slightly spongy texture on the plastron. Larger juvenile turtles are also brown but may show faint striping on the sides of the head. Old adults

Figure 2-1. Old adult male alligator snapping turtle, *Macrochelys temminckii*, from Washington Co., Florida. Photo by Barry Mansell.

tend to be dark brown to dark gray-brown above and lighter brown, grayish tan, or ivory colored on the skin and underneath. The heads of some old males may become partially yellow.

The appearance of *Macrochelys*, especially that of small individuals, can lead to confusion with its smaller relative, *Chelydra serpentina*, the snapping turtle. However, the shell of *Chelydra* is only slightly if at all tricarinate. The mouth of *Chelydra*, as in most turtles, is pink to almost white, rather than camouflage brown as in *Macrochelys*. As viewed from below the head, the eyes of *Macrochelys* tend to protrude to the sides, whereas those of *Chelydra* are barely if at all evident (but readily visible from above, in contrast to *Macrochelys*).

Taxonomic History. — As a distinct genus with only one living species, the alligator snapping turtle has a relatively simple taxonomic history, but one with its own measure of confusion. The first description of this species should be attributed to Harlan (1835; see below), who used the name *Chelonura temminckii* (Pritchard, 1989). Since *Chelonura* is a synonym of *Chelydra*, Gray replaced this name with a new genus name. The principal controversy in the taxonomy of this species surrounds which of two names, *Macrochelys* or *Macroclemys*, is now the correct name for the genus. In an apparent mental lapse, Gray (1856a, b), in two separate publications both dated 1855 but printed in 1856, gave the alligator snapping turtle the two different generic names. Standard scientific protocol recognizes the first validly printed and distributed name for an animal as its official name (senior synonym). The correct name for the alligator snapping turtle rests on which of Gray's two publications in 1856 was actually printed first. For the current decision, Webb (1995) determined that *Macrochelys* was the first printed name (in Gray 1856a) and, therefore, merits recog-

Figure 2-2. Adult alligator snapping turtle, *Macrochelys temminckii*, from Alachua Co., Florida. Note the 3 supramarginal scutes. Photo by Peter Meylan.

nition as the valid name for the genus. This name is the one most often used for this turtle prior to about 1953. The conclusion of Webb (1995) supersedes that of Smith (1955), who had concluded that *Macroclemys* (occasionally misspelled as *Macroclemmys*) was the earlier of the two names. *Macrochelys* is currently the accepted scientific name (Crother et al., 2000).

The specific name *temminckii* (sometimes misspelled *temmincki*), in honor of Coenraad Jacob Temminck, Director of the Leiden (Netherlands) Museum, was first proposed in 1834 by the Dutchman Gerard Troost (as *Chelonura temminckii*), but he did not publish. Then, Harlan (1835), giving full credit to Troost, published both names and a formal description of the turtle, and by the rules of nomenclature inadvertently took authorship of the name.

Although recent genetic studies (Walker and Avise, 1998; Roman et al., 1999) identified a major phylogeographic division within the total distribution of *M. temminckii*, no subspecies have been named. However, two other specific names are assigned to fossils in the genus. *Macrochelys schmidti* is known from the Miocene of Nebraska (Whetstone, 1978), and *M. auffenbergi* from what is now considered the late Miocene of Florida (Dobie, 1968). Both are distinguished from *M. temminckii* by only minor differences, some of which may be due to geologic crushing of the fossils (Pritchard, 1989). We suspect that a thorough review of osteological variation within the modern species may cast doubt upon the supposed distinctness of these fossil species, especially *M. auffenbergi*. Florida Pleistocene fossils once assigned to *M. floridana* already have been reassigned to *M. temminckii* (Auffenberg, 1957).

Figure 2-3. Juvenile alligator snapping turtle, *Macrochelys temminckii*, from Calhoun Co., Florida, showing dark interior lining of mouth and lure. Photo by Dick Bartlett.

DISTRIBUTION

Geographic Distribution. — *Macrochelys* is strictly North American in fossil and current distribution. Currently, the species is restricted to Gulf Coast drainages, of which about 15 independent, moderate to large drainages may have recent records. There is, however, some doubt whether *Macrochelys* occurs naturally in the three westernmost drainages (San Antonio, Colorado, and Brazos rivers in Texas). The 12 remaining drainages, from the Trinity River in Texas to the Suwannee River in Florida and Georgia each include two or more locality records (Pritchard, 1989; Dixon, 2000).

Macrochelys occurs in many and perhaps all of the larger drainages from the Panhandle and into the Big Bend region of Florida (Fig. 2-4). Every county in this region includes a locality (Iverson and Etchberger, 1989; Pritchard, 1989; Lane and Mitchell, 1997). Recent sampling has largely filled a gap in distribution between the Apalachicola River drainage and the Pensacola Bay drainages by establishing presence in the Choctawhatchee River drainage and in Econfina Creek (Washington Co.) (Moler, 1996a). Between the Ochlockonee River and the Suwannee River, just two records, from the Aucilla drainage (Pritchard, 1989; Anonymous, 2000), are known. Lack of records from several small rivers in Taylor Co. (Econfina, Fenholloway, and Steinhatchee rivers) appears to represent a genuine gap in distribution between the Suwannee drainage and the rivers to the west.

Currently *Macrochelys* does not range south of the Suwannee River. However, fossils have been found south on the peninsula into the Tampa Bay area, and *Macrochelys* is represented during several eras of the fossil record (Late Blancan to Rancholabrean; 2.3 to 0.1 million years before present, MYBP). It occurred in the upper Peace River during the Hemphillian era (ca. 5 MYBP). An additional extension beyond the current distribution placed the species in an Atlantic drainage at three sites that currently drain into the St. Johns River as recently as 0.1 MYBP (Rancholabrean of the Pleistocene era). Evidently, elevated sea levels between 0.1 MYBP and the present eliminated *Macrochelys* from this extensive peninsular distribution (Meylan, 1995, *pers. comm.*; Hulbert, 2001).

Across the 12 Gulf drainages in which the species presently occurs are three genetic assemblages or "evolutionary units" that represent clusters of adjacent drainages (Roman et al., 1999). All three genetic assemblages are represented in Florida. Most populations fall into one large genetic assemblage that extends eastward from Texas to the rivers of the Pensacola Bay area of Florida. A second genetic assemblage extends east from the Choctawhatchee River

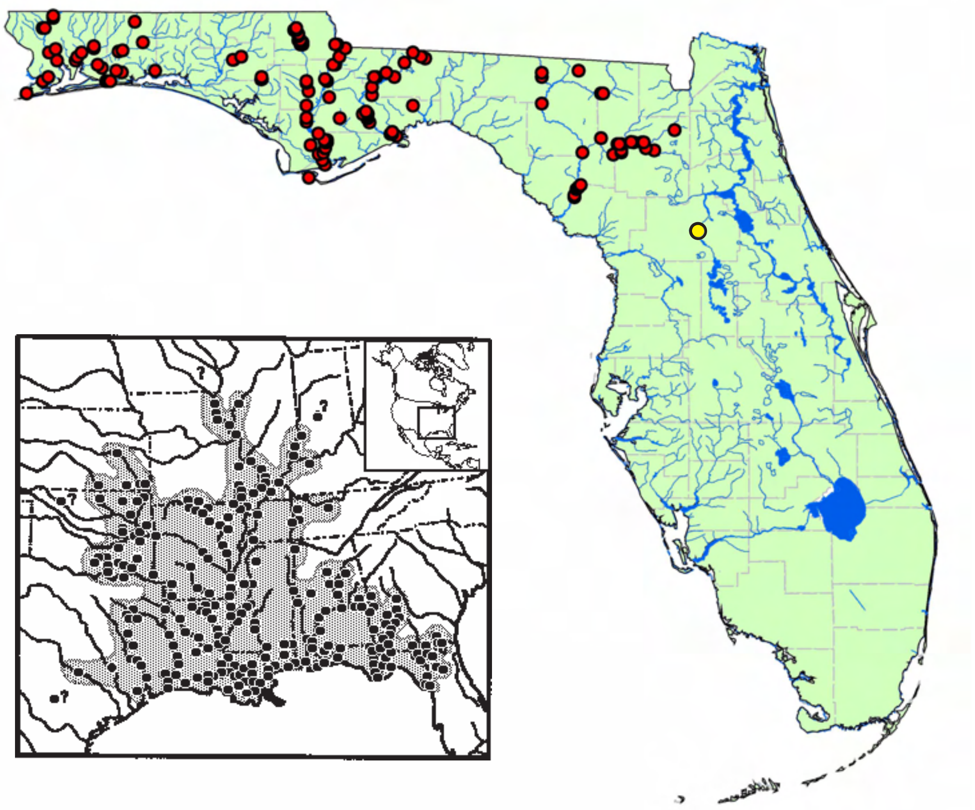

Figure 2-4. Known records for the alligator snapping turtle, *Macrochelys temminckii,* in Florida. Inset: distribution records from entire range of *M. temminckii* (adapted from Iverson, 1992; distribution in inset map not current for Florida as presented here). The southeastern-most record (yellow dot), in Marion Co., is considered to be an escapee, probably from Ross Allen's Reptile Institute (see text).

drainage to the Ochlockonee River. The third and most genetically distinct population occurs only in the Suwannee River drainage. This suggests that the Suwannee River population has evolved in isolation and that the apparent gap in current distribution between the Aucilla River and the Suwannee River is real and not an artifact of inadequate sampling. Given that *Macrochelys* is somewhat tolerant of salt water (see below), the apparent restriction of dispersal along Santa Rosa Sound between Choctawhatchee and Escambia bays seems odd.

Ecological Distribution. — Rivers comprise the most favored habitat. However, the fundamental ecological requirement probably is permanent fresh water or easy access to it. Floodplain swamp forest with bald cypress and tupelo in close association with numerous flooded channels can be considered optimum habitat (Ewert and Jackson, 1994). Such channels often contain deep holes in association with logs or tight passages between trees. In Florida, tannins often darken the water, or as in the Apalachicola River, suspended silt renders the water turbid. The only impounded sections of large rivers within the Florida range (Lake Seminole on the Apalachicola, Lake Talquin on the Ochlockonee) both support *Macrochelys* (Pritchard, 1989).

Although documentation of overland movement, as might occur during droughts, is extremely rare, there is one unverified instance near Sopchoppy, Wakulla Co. (Pritchard, 1989). The species does occasionally occupy aquatic habitats that become dry, or nearly so. A third-year juvenile (in 1970) and a fresh nest (in 1976) were associated with a section of the New River (Liberty Co.), a blackwater, swamp forest stream that occasionally dries down to small pools between long stretches of dry river bed. During the late 1990s to early 2000s, Lake Iamonia (Leon Co.), the site of a known nest (Ewert, 1976), became mostly dry, including all of it within 3 km of the nest site. This shallow lake has a high-water connection with the Ochlockonee River, which presumably provides occasional entry for *Macrochelys*. A small seepage-fed stream (Indigo Creek, Santa Rosa Co.) with a few deeper (ca.1 m) holes contained a small adult.

The species resides in brackish water in some locations, including Ochlockonee Bay (Franklin Co.; Pritchard, 1989) and the waters near Tyndall Air Force Base (Bay Co.; Lane and Mitchell, 1997). Also, an adult was able to cross brackish water to St. Vincent Island, Franklin Co., where it was found dead next to a freshwater pond on the island (Lewis and Irwin, 2001). However, the evidence for genetic isolation (Roman et al., 1999) indirectly indicates that movements at sea, such as between the mouths of rivers, must be extremely rare if they occur at all. In 1990, a nest near the mouth of the Apalachicola River (Gulf Co.) occurred adjacent to water sufficiently brackish to support fiddler crabs (*Uca* sp.; Ewert and Jackson, 1994). The location of this nest suggests either hatchling tolerance for brackish water or lack of adaptation to avoid nesting adjacent to brackish water. An adult turtle taken close to Mobile Bay (Alabama) supported barnacles thought to be several weeks old, indicating that this turtle had occupied brackish water long enough for the barnacles to grow (Jackson and Ross, 1971).

HABITAT RELATIONS

Aquatic Activity. — Apparently, much aquatic movement occurs at night. Spotting with a lamp in sufficiently clear water by Allen and Neill (1950), probably in the Suwannee River, revealed turtles coming to underwater baited lines. During the late afternoon, turtles assumed resting positions near shore, under large structures such as logs, in holes in banks, or buried in mud. During trapping surveys in Florida (Moler, 1996a) and Georgia (Johnson, 1989; Jensen and Birkhead, 2003), it was productive to set baited traps during the late afternoon and to inspect them the following morning. This procedure, however, does not differentiate crepuscular from nocturnal activity. Allen and Neill (1950) observed a juvenile luring for food in a small stream in Mississippi at night, and Moler (unpubl. data) has observed several adult *Macrochelys* actively foraging at night in Florida. As the latter turtles moved along the bottom, they periodically stopped, extended the neck, and pressed the snout to the substrate, presumably smelling for food.

Some daylight activity does occur, as evidenced by a juvenile seen floating about midday in the New River (Liberty Co.). A single observation of aerial basking over water (in Texas) also took place during the afternoon (Ewert, 1976; unpubl. data). Also, traps set in deep water during daylight hours captured several turtles (R. Evans, *pers comm*.).

In captivity in Florida, aggression between males has occurred soon after one has been placed with another (Allen and Neill, 1950). In Louisiana, captive males housed together and observed both day and night showed aggressive activity during both periods (Harrel et al., 1996).

Terrestrial Activity. — Hatchlings must travel overland from their nests to water. Aside from observations of females on nesting forays, the literature lacks documentation of other adults or juveniles on land, at least by choice. One apparently natural occurrence is a road-killed juvenile (ca. 25 cm CL) at the Santa Fe River in March, 1999 (Alachua Co.; P.A. Meylan, *pers. comm*.). Another road recovery involved a 29.5 kg adult, probably a male.

Macrochelys of many sizes are quite competent at walking on land. Average-sized adult females that have completed nesting, as well as subadult males placed on land, walk with their plastrons high off the ground, much like *Chelydra*. Very large females (> 50 cm CL) seem less able to do this, at least after extended periods of nesting. One very large female was able only to drag her body across a surface of firm sand.

Home Range. — Although mark-recapture data have been collected in Florida, there has not been intensive study of local movements. Radio-tracking data are available for populations in Louisiana. It appears that subadult and adult males on average have larger home ranges than subadult or adult females. By area, male adult home ranges tend to average half again as large as those of females (Sloan and Taylor, 1987). Linear home ranges of subadults vary from 0.12 to 1.2 km, with ranges of males averaging more than twice as long as those of females. Movements appear to peak in the spring (Harrel et al., 1996). These studies also indicated that individuals have “core” areas within their home ranges and that such areas, while diverse, include logs in the water more than other types of structure. Movement data from recaptures in Arkansas are compatible with the radio-tracking data in Louisiana, in that only one individual in 11 moved over 1 km during three months of study (Trauth et al., 1998). The studies in Louisiana and Arkansas pertained to permanent water. It is obvious from the presence of *Macrochelys* in temporary water in Florida (New River, Franklin Co.; Lake Iamonia, Leon Co.) that individuals must occasionally move from a few hundred meters to more than a kilometer.

Temperature Relations. — *Macrochelys* occurs geographically where water temperatures are often mild (25–28°C) for half of the year. There is little evidence that it is a heat-seeking species, given its preference for nocturnal activity and the single reported instance of aerial basking. The critical thermal maximum (temperature inducing spasms) ranged from 38.4 to 40.2°C for two juveniles from central Louisiana (Hutchison et al., 1966). This thermal range is cooler than for most other turtles tested in the same study, but similar to that of *Chelydra*.

Embryos in nests along the lower Apalachicola River can sustain brief exposure to 36.5°C and may endure longer periods as cool as 19.5°C in freshly constructed nests (Ewert and Jackson, 1994). At laboratory constant temperature, embryos from this locality appear just slightly stunted at 30°C; warmer incubation temperatures have not been applied. Embryos can develop a long way at constant 21.5°C but then fail after reaching half to two thirds of term embryo size. A constant incubation temperature of 22.5°C permits most embryos to hatch (Ewert and Jackson, 1994; unpubl. data).

GROWTH AND REPRODUCTION

Growth. — Growth rates in natural habitats in Florida have not been studied. In Louisiana, 12 large juveniles that averaged close to 25 cm CL grew an average of 13.3 mm in CL in about one year. Males and females in this small sample showed no consistent difference in growth (Harrel et al., 1997). According to growth ring widths from Louisiana turtles, average growth rate declined by about half at ages of 11–15 yrs from the rate during the first 5 yrs, and by about two-thirds at ages of 16–35 yrs (Dobie, 1971).

Sexual Dimorphism. — Males attain much larger sizes than females. Young of both sexes have open carapacial fontanelles. In females these gaps in the bone close or nearly close at a much smaller size than in males. Photographs of the scuteless shells of two similarly sized individuals (male at 48 cm CL, female at 44.5 cm CL) from the Flint River drainage, Georgia, illustrate this condition (Pritchard, 1989).

Although there are several records of very large individuals (Pritchard, 1989), published data for estimating average adult size dimorphism (as computed according to Gibbons and Lovich, 1990; Lovich and Gibbons, 1992) are available only for Louisiana (Dobie, 1971). Males average 46.3 cm CL, and females 40.2 cm CL, to yield a sexual size dimorphism index (SSDI) of -1.15 by length. If we assume that length-to-mass proportions are similar for Louisiana and Florida, unpublished data (mostly from Moler, 1996a), allow an SSDI estimate by mass of -1.46. However, male size in this computation appears to be underestimated substantially. For very large individuals, reliable data in Pritchard (1989) and unpublished data give an SSDI estimate by mass at -4 (114 kg male/28.2 kg female) and by maximum CL at -1.27 (72.4 cm CL male/57.0 cm CL female). Generally, however, the data of Moler (1996a), coupled with knowledge of the sizes of old females from the lower Apalachicola River, suggest more moderate SSDIs. Estimates are -1.8 by mass (36 kg male/20 kg female) and -1.2 by length (53.8 cm CL male/44.6 cm CL female). These values are substantial among SSDI values for turtles favoring males (Gibbons and Lovich, 1990).

In a comparison of Louisiana females and males of 37 cm CL or larger, the cloacal opening is located further posterior on the tail of males. This results in a greater “preanal” tail length for males than for females of similar size. The difference, however, can be as small as 8%, which can render sexual diagnosis in the field problematic (Dobie, 1971; Moler, 1996a).

Sexual Maturity. — No data are available for Florida. Data from Louisiana females with greatly enlarged ovarian follicles or oviductal eggs, and males with sperm, suggest that both sexes mature in 11–13 yrs and at minimum carapace lengths of 33 cm for females and 37 cm for males (Dobie, 1971). Secondary sexual characters sometimes allow identification to sex in Florida by about 22 cm CL (Allen and Neill, 1950).

Longevity. — Beyond counts of growth rings in Louisiana (Dobie, 1971; Harrel et al., 1997), nothing is known about survival of juveniles or longevity of adults in the wild. A male, captured as an adult, survived an additional 70 years in the safety of captivity at the Philadelphia Zoo (Snider and Bowler, 1992). Thus, this turtle was probably older than 80 years at death.

Male Reproductive Cycle. — In Louisiana, sperm are present in the vasa deferentia throughout the year (Dobie, 1971). Changes in testicular size or peaking in spermiogenesis have not been studied.

Female Reproductive Cycle. — In Louisiana, follicular enlargement commences in the fall, with some follicles reaching ovulatory size by December. On occasion, some enlarged follicles are not ovulated to form a clutch. These follicles evidently become atretic. Females never produce more than one clutch per year and appear on occasion to skip years without reproducing (Dobie, 1971). Females from the Suwannee and Apalachicola rivers also appear to produce only one clutch per year (Allen and Neill, 1950; Ewert and Jackson, 1994).

Courtship and Mating. — Turtles from the Suwannee River engaged in courtship during February, March, and April in captivity in north-central Florida. A male follows a female and attempts to mount her. After mounting, the male partially curves his tail about that of the female in order to achieve intromission. Contacts have lasted up to 25 min (Allen and Neill, 1950).

Observations on courtship and mating with appreciably more detail are available for turtles captured in northern Louisiana and observed in captivity. Although seemingly awkward because of disparity in size, functional matings are possible when the male has twice the mass of the female (e.g., SSDI of -2.28). There seems to be much sniffing and only occasional biting between unmounted courting pairs (Harrell et al., 1996).

Nesting Season / Nest Sites / Nesting Behavior. — The nesting season in western Florida extends from late April into the second half of May. The discovery of a developing clutch on 27 April suggests the nesting season begins 20–23 April during warm or wet years. Finds of fresh nests have extended through 18 May during cool years (Ewert, 1976; Ewert and Jackson, 1994; unpubl. data). Despite a high frequency of sunny, dry days and cool, dry nights during April and early May in northwestern Florida, *Macrochelys* appears to avoid this type of weather for nesting. Rather, females favor relatively warm and humid early mornings, particularly those that follow rains during the previous day or evening.

Figure 2-5. Track left by adult female alligator snapping turtle, *Macrochelys temminckii,* from Franklin Co., Florida. Photo by Mike Ewert.

Females emerge to nest before dawn but may not finish until mid-morning. It appears, however, that many females crawl onto land early enough to complete nesting near sunrise. Searches for the distinctive tracks (Fig. 2-5) and nests (Fig. 2-6) of this species conducted from 0700 to 1000 hrs along the lower Apalachicola River have yielded over 30 fresh nests, but females remained finishing only seven of them. One gravid individual, encountered on land in near full darkness, had not yet reached a location where females normally nest. Daylight encounters with females still digging or laying have included two females still digging or dropping eggs at 0750 and 0845 hrs, and five females filling or post-fill scraping at 0715–0845 and 1130 hrs. These females were nesting in damp sand. At another location (Lake Iamonia, Leon Co.), with compacted sandy loam, oviposition did not start until 0915 hrs, and the turtle remained at her nest until 1130 hrs (Ewert, 1976; unpubl. data).

Nests are usually within 20 m of water and less than 3 m above water level at the time of nesting. However, during dry years along the lower Apalachicola River, some nests have been up to 200 m from the nearest water. In one case, the shortest logical path to water exceeded 250 m. The nests closest to water have been on sloping banks only a meter distant. During dry years, occasional nests have been located next to the lower sides of protruding tree root mats along low eroding banks. These sites lie within wave wash zones and become flooded during wet years (Ewert, 1976; unpubl. data).

The most favored natural nesting habitat along the lower Apalachicola River appears to have been moderately high (2–3 m) natural berm. Man-made deposits of sandy dredged spoil have largely replaced these natural landforms. Dredge deposits form elevated mounds in floodplain forest or sandy places that superficially resemble riverside sandbars extending into the water. Nesting females seem to prefer these semi-open locations. Nest sites often have open sky directly above but receive some shading from trees or shrubs during the day. Such locations are distinctly more exposed than an average natural berm (Ewert and Jackson, 1994). Overall, however, nests can be in diverse locations that range from shady groves of native cane and cabbage palms to central locations on the barren portions of sandbars. Oddly, searches of two naturally elevated areas that immediately border the river have never yielded signs of nesting (Ewert, 1976; unpubl. data). Nest sites elsewhere than the Apalachicola River include two on a moderately high bank of the New River (Union Co., Suwannee River drainage). Five others have all been associated with man-made features, including a cornfield (Leon Co.), earthen bridge abutments (Liberty and Gulf cos.), an intersection between two sandy roads (Gulf Co.), and a sandy roadside (Union Co.). Along more swiftly flowing rivers, the high, partially shaded edges of sandbars may also be favored.

That some nests occur within the same small area every year suggests that there is nest site fidelity, if not philopatry, among certain females. One case in point is a small open area

Figure 2-6. Adult female alligator snapping turtle, *Macrochelys temminckii*, from Franklin Co., Florida, in the process of "covering" a recently completed nest. This behavior produces a long mound of sand as it does in some sea turtles. Photo by Mike Ewert.

that occupies less than a twentieth of the area of an old spoil mound along the lower Apalachicola River. This opening, far removed from the river, is all that remains open within a much larger, overgrown area. It has been the site of one or two nests during three consecutive years. At other sites, nesting occurred just once during four years. These instances could represent plasticity in nest site choice but do not exclude an alternative that females have nest site fidelity but do not always nest every year (this account; see Dobie, 1971).

Along the lower Apalachicola River, 69 nests constructed in the sandy spoil averaged 20.3 cm (range 13–30 cm) to the topmost egg and 32.6 cm (range 26–40 cm) to the bottom of the egg chamber. Similarly, 9 nests in the harder natural substrate averaged 19.4 cm (range 13–29 cm) to the topmost egg and 32.3 cm (range 28–39 cm) to the bottom of the egg chamber. The vertical distance through the mass of eggs averaged about 12.5 cm (range 7–22 cm; Ewert and Jackson, 1994, unpubl. data). Ewert (1976) gave other details of nests and nesting. One of these was the description of a very elongate area of disturbance that the female turtle makes in soft substrates after nesting. The female turtle constructs this entirely with her hind legs. She rotates her hind legs in a pattern associated with the filling process long after the nest has been filled. Without using her front legs, each rotation of the hind limbs advances her forward slightly until, in some cases, the path of churned earth has stretched for 5 m and resembles the product of a small rototiller (Fig. 2-6).

Nesting by captive females originally from the Suwannee River followed a slightly different schedule at a slightly more southerly location (Ross Allen's Reptile Institute, Silver Springs, Marion Co.). Here, nesting did not occur or was not noticed before dawn. Nesting dates varied from 21 April to 15 June (Allen and Neill, 1950) and, thus, appear less constrained than those observed along the lower Apalachicola River.

Clutch Size and Reproductive Potential. — Along the lower Apalachicola River, clutch sizes recorded from 1972 through 1991 varied from 17 to 52 eggs in 160 clutches, with a mean clutch size of 35.1 eggs (Ewert and Jackson, 1994). Statistics on 31 clutches examined from 1992 to 1996 are about the same (mean: 37.3 eggs, range: 21–50). Captive females from the Suwannee River drainage produced clutches of 16–44 eggs per clutch (*n* = 6; Allen and Neill, 1950). Additional records of clutches produced in other drainages are few (18, 38, 40 eggs; Ewert, 1976; unpubl. data).

Eggs, Incubation, Development, and Hatching. — Normal eggs in Florida are approximately round. Eggs from recently laid clutches from along the lower Apalachicola River weighed 26.47 ± 3.50 g (range 16.9-36.1 g; *n* = 466) and measured from 31.7 x 30.3 to 41.0 x 40.0 mm. As in *Chelydra* (Ewert, 1979), freshly laid eggs in some clutches can be moderately rigid to touch, whereas eggs in other clutches have pliable eggshells. All of the eggshells become turgid and flexible coincident with the normal uptake of water during development. The eggs succumb rapidly to dehydration if exposed to open air (Ewert, 1985; unpubl. data).

Embryonic development lacks periods of post-ovipositional arrest. However, development is also slower than in other North American turtles with similar eggs incubated under similar laboratory conditions (Ewert, 1985; see also Miller, 1985).

Nest temperature influences incubation time. As a general trend, temperatures in freshly laid nests along the lower Apalachicola River typically are cool (19.0–26.5°C) and become warmer (26.1–36.5°C) as the season progresses, which follows the general trend in soil temperatures. One nest laid in a warm location on 26 April 1990 contained hatchlings with reduced umbilical scars on 14 August, indicating that hatching had occurred several days previously. Other eggs laid in 1991 in cooler locations were still developing by 16 August. Laboratory incubation to complete development in these eggs provided estimated hatching dates up to 29 August (i.e., about the same as realized when incubating at 27°C in the laboratory). Thus, natural incubation lasted approximately 103–124 days. Most eggs probably hatch in 105–110 days. (Ewert and Jackson, 1994; unpubl. data).

Field and laboratory observations indicate that incubation temperature influences sex determination in *Macrochelys*. Constant incubation temperatures of 25–27°C produce mostly males, whereas 29° and 30°C yield only females. There are two pivotal temperatures (i.e., yielding nearly equal numbers of males and females) for the lower Apalachicola population, a warm one at 27.2°C and a cooler one at 24.6°C (Ewert et al., 1994). Temperature-dependent sex determination is also evident in the field. Nests giving warm readings when monitored for temperature yield all or nearly all females, whereas cool nests yield a few, to many males. Thus, temperatures fluctuating around the warm pivotal temperature probably exert the most influence on sex determination. Because some cool nests yield somewhat less masculinized sex ratios than slightly warmer ones, cool-temperature females probably occur naturally, though perhaps not often. Nests yielding all or nearly all females have had extensive exposure to direct sunlight, whereas nests favoring males have had much shading by trees and shrubs. In one case, a nest adjacent to the north side of a log received enough shading from the log to give a male-biased sex ratio (Ewert and Jackson, 1994; unpubl. data).

Hatchlings probably never overwinter in the nest. All of the older hatchlings (those with reduced umbilical scars) in nests fitted with retaining screens (*n* >15 nests), along the lower Apalachicola River (see Ewert and Jackson, 1994) had burrowed upward to the screens. In 1993, 137 of 139 hatchlings in five unprotected and non-depredated nests had emerged before 6 October. One hatchling had died in a nest and another was alive but entangled in a mass of roots.

Hatchling Size. — Linear measurements of hatchlings change rapidly and remain in flux after the turtles emerge from the eggs and unfold from their curled position. Growth along the seams of the scutes also commences almost immediately. The size range of 162 hatchlings from 15 clutches from Florida was approximately 34–45 mm in carapace length, 23–30 mm in plastron length, and 11.5–20.5 g in mass (mean about 18 g). Hatchling size varies with egg size and, as in *Chelydra*, almost certainly is reduced if the embryo experiences periods of dehydration (Ewert, 1976; unpubl. data).

POPULATION BIOLOGY

Population Density. — A trapping survey yielded *Macrochelys* at 20 of 26 trapping sites across its Florida range (Moler, 1996a). The traps caught 92 turtles in 367 overnight sets, or roughly one turtle per four trap nights (one baited trap set overnight, TTN). However, some sets caught more than one turtle per trap. All of the large to moderately large drainages yielded turtles, except the Aucilla River, for which one recent capture is reported (photograph in Woods 'n Water, December 2000). The upper Escambia, western Econfina (Washington Co.), upper Chipola, middle Apalachicola, and upper Ochlockonee rivers all had trap yields of better than 50%. However, interpretation of relative local abundance remains difficult. For instance, trap yields within the well-studied nesting area along the lower Apalachicola River (see below) ranked only 18th among the 20 sites that yielded turtles. However, trapping occurred during the fall, and spring-nesting turtles may have migrated from afar. On average, trapping in Florida yielded three times as many turtles per unit effort as similar trapping in the commercially depleted Flint River, Georgia, and large individuals formed a greater proportion of the Florida yield (Moler, 1996a).

As a general indication of relative abundance, results of the trapping survey in Florida compare well with similarly conducted surveys in states believed to have sustained moderate but not extreme harvest. Florida averaged 0.251 turtles per trap night across 367 trap nights. Similarly, a survey of all of Arkansas resulted in 0.234 TTN across 1905 trap nights (Wagner et al., 1996). Northeastern Arkansas, alone, yielded 0.273 TTN during 352 trap nights for three creeks previously known to contain *Macrochelys* (Trauth et al., 1998).

From counts of nests along the lower Apalachicola River in 1991, Ewert and Jackson (1994) estimated that a minimum of 150 adult turtles resided in the region (ca. 125 km^2 of floodplain forest and channels south from River Mile #22). As there was a good chance of overlooking many nests and an assumption of a 1M: 2F adult sex ratio (i.e., as with hatchlings from nests), the true adult population probably was much larger.

Nesting density has been somewhat higher along a smaller, 7.5 km reach of the river south of River Mile #22. This reach yielded 29 nests in 1976, 32 in 1990, 44 in 1991, 20 in 1992, and 30 in 1993. The search in 1976 was probably less intensive than in other years, and in 1992 the last part of the nesting season was probably missed. However, with these caveats, the data suggest population stability over the 18-year period (Ewert and Jackson, 1994; unpubl. data).

As detailed below (see predation), the only available estimate of annual recruitment is three hatchlings per nesting female along the lower Apalachicola River. This rate of recruitment could surpass rates of smaller local species (e.g., *Sternotherus*, *Terrapene*, *Trachemys*), which invest a smaller overall annual production in three to four clutches per female but which also have shorter maturation times for females.

INTERSPECIFIC INTERACTIONS

Community Structure. — In the lower Apalachicola River, *Sternotherus minor*, *S. odoratus*, *Graptemys barbouri*, *Pseudemys concinna*, and *Trachemys scripta* are common in the mainstem; *Apalone spinifera* is present but locally rare. All of these species, except *P. concinna* and *A. spinifera*, are known from local backwater areas, which additionally include *Chelydra serpentina*, *Kinosternon baurii*, and an occasional *Apalone ferox*. Although encounters with *Deirochelys reticularia* (seldom a visitor to flowing waters) are probably rare, *Macrochelys* likely encounters all of the freshwater turtles in the rivers of western Florida at least rarely. It is peculiar to *Macrochelys* that several of these members of the overall turtle community may constitute prey (see below).

Diet and Feeding. — Although natural diets in Florida have not been quantified, diets elsewhere suggest some staples along with much opportunism. Across its range, *Macrochelys* consumes a wide variety of food items including many faunal elements. These include fish, mollusks, crustaceans, large salamanders, water birds, small mammals, small alligators, and other turtles. *Macrochelys* also consumes plant material such as roots, grapes, acorns, and the fruits of palmetto and tupelo (reviewed in Ernst et al., 1994). In the digestive tracts of Louisiana individuals, fish were highest in abundance, followed by acorns, which constituted the greatest volume. A Florida specimen (UF/FLMNH collection) from the Santa Fe River also contained acorns. Mammals (including raccoons, *Procyon lotor*) represented appreciable volume (Sloan et al., 1996). The extent to which acorns provide nutrition invites further study. Fish remains (otoliths) defecated by Louisiana *Macrochelys* represented six species of carnivorous centrarchid fishes (Harrel and Stringer, 1997). In the Suwannee River drainage, bivalve as well as gastropod mollusks contribute to the diet (Allen and Neill, 1950). Wild *Macrochelys* from Louisiana had eaten slider turtles (*Trachemys scripta*; Sloan et al., 1996). Captive *Macrochelys* from Florida have attempted to lure musk turtles (*Sternotherus*; Allen and Neill, 1950).

The transition in diet from mainly piscivory to a more opportunistic composition may occur with growth and maturation. The high contrast of the lure, as a pink structure against a darkly grayish brown tongue and mouth, and the vermiform shape of the appendage decline as turtles age (Pritchard, 1989). The mouth may lose some of its dark, contrasting pigmentation (e.g., Scott, 1987), and the appendage may become proportionately shorter or otherwise lose some of its distinctness.

Predation and Nest Failure. — Ewert and Jackson (unpubl. data) quantified nest depredation along the lower Apalachicola River in 1993. Of 46 nests, 40 (87%) were depredated. Although 191 eggs escaped predation, only 138 eggs produced hatchlings that were able to exit the nests. However, this recruitment still averaged three hatchlings per nesting female in a single year.

The greatest number of failed eggs in the non-depredated group, an entire nest with 39 eggs, resided in soil that was slightly "oily" and slightly discolored. In this case and two others involving "oily" and discolored soil and recently laid eggs, the eggs did not develop, although none showed signs of penetration. Fire ants (*Solenopsis invicta*) were present in two of the nests, as if the eggs had been laid in a fire ant nest. However, whether fire ant activity can cause early embryonic death needs confirmation. When fire ants invade from afar, it appears as though they do not affect intact eggs but kill pipping or emerging hatchlings (Parris et al., 2002).

Raccoons appear to be the primary if not only vertebrate predators of nests along the lower Apalachicola River. Nine-banded armadillos (*Dasypus novemcinctus*) are locally common, and feral hogs are occasionally present, but neither species has left evidence of taking eggs from nests. There are only rare observations of tracks of canids in the area. Fish crows (*Corvus ossifragus*), which often depredate nests of small turtle species, seem unable to dig to the depths of *Macrochelys* clutches. The footprints of fish crows, however, are often abundant on the freshly churned bare ground associated with *Macrochelys* nests.

Hatchlings and small juveniles doubtlessly succumb to natural predation; however, there is no documentation of age-specific mortality rates in Florida or elsewhere. According to Dobie (1971), juveniles in Louisiana grow to about 20 cm carapace length in six growing seasons, which may afford them the same resistance to predation achieved by similar-sized adult turtles of other species.

THREATS

Documented Threats. — *Macrochelys* has a significant record of commercial and personal harvest for meat (Dobie, 1971; Pritchard, 1989; Sloan and Lovich, 1995). Harvest has reduced populations in Georgia (from the Flint River, in particular), as evident in low rates of trapping (0.08 TTN in Georgia [Johnson, 1989]; vs. 0.23–0.27 TTN in Arkansas and Florida [Moler, 1996; Wagner et al., 1996; Trauth et al., 1998]; and 0.28 TTN in Oklahoma [Riedle, 2000]). Although there are oral accounts of large trapping efforts in Florida (Pritchard, 1989), permanent impact of human take in Florida is less clear. Trapping for census still yields turtles throughout the historical range in Florida. In particular, census has indicated moderate abundance in the middle Suwannee River (Moler, 1996a) and a higher abundance in its main Florida tributary, the Santa Fe, (Moler, unpubl. data). Take from several rivers in northwestern Florida definitely has occurred. A photograph in Pritchard (1989:78) shows at least 16 carapaces, presumably of local origin, arranged as a garden wall in the town of Apalachicola. All of these shells seemed to be from recent butchering, as they lacked appreciable weathering. Also, numerous discarded shells were found at an illegal dump site in Liberty Co. (Neill Hunter, *pers. comm.*; Fig. 2-7).

Figure 2-7. Butchered remains of adult alligator snapping turtles, *Macrochelys temminckii*, from Liberty Co., Florida. This photo was taken in 1987. This level of harvest in Florida is no longer thought to occur. Photo by Neill Hunter.

Since measures restricting harvest in Florida went into effect in 1973, local news articles and law enforcement authorities have reported occasional illegal take. One incident involved 33 adults and large juvenile turtles that were confiscated during transport. The turtles, which apparently had originated from the Apalachicola River, were released there into the wild (Anonymous, 1992; Moler, 1996a).

Several methods enable the capture of *Macrochelys*. Professional turtle trappers commonly use large, generously baited traps. These consist of long cylinders of wide mesh netting supported by three to seven hoops (122 cm in

Figure 2-8. Dead adult alligator snapping turtle, *Macrochelys temminckii*, from Leon Co., Florida, entangled in a bush hook. These fishing lines are frequently set for other species. Their impact on *Macrochelys* remains unknown. Photo by Matt Aresco.

diameter) joined to the netting (Moler, 1996a; B. Harrel, *pers. comm.*; photos in Riedle, 2001). Currently, a permit is required for the use of such traps in Florida. Long lines of submerged baited hooks (trot lines) and single hooks suspended from tree branches (bush lines) also capture many turtles, usually unintentionally (Fig. 2-8; see also Pritchard, 1989). More direct methods include luring turtles after dark with bait set in clear water followed by spotlighting and gaffing the turtles that have come to the bait. Some people have also gone diving for turtles and muddling for them under overhanging banks and in knots of submerged debris (Allen and Neill, 1950). Occasional large turtles show evidence of having been shot (e.g., Anonymous, 2000; holes observed in the carapace of a nesting female).

Nest depredation by raccoons greatly reduces annual recruitment of hatchlings, although our single estimate of recruitment (see above) suggests that this could be normal. The seriousness of impacts from this unnaturally abundant, subsidized predator (see accounts of *Graptemys barbouri* and *Pseudemys concinna*) remains unknown across local populations of *Macrochelys*. Although the nests are quite easy to locate when abundant, humans do not appear to be interested in taking them. We have noticed an apparent association of failed or failing *Macrochelys* nest eggs with fire ant (*Solenopsis invicta*) activity (see above).

Potential Threats. — Turtles with populations primarily restricted to rivers always face a threat of decimation from a major chemical spill. However, with so many populated rivers, a spill in any one river would not endanger *Macrochelys* on a statewide level.

The long-term impact of impoundments along rivers on *Macrochelys* populations has not been studied. It seems that reduction in habitat structure (e.g., trees in water, undercut banks) in very large impoundments would lead to gradual reduction in *Macrochelys* populations relative to the original numbers in the pre-impounded lengths of the rivers. Recreational shoreline development only aggravates shoreline habitat loss. This concern applies to Lake Talquin (Ochlockonee River) and Lake Seminole (Apalachicola/ Chattahoochee/ Flint rivers), which have been in place for years but which still support *Macrochelys*.

Another problem that impoundments create is entrenchment of the main channel within the floodplain downstream from the dam. For example, Lake Seminole has reduced sediment transfer in the Apalachicola River downstream from Jim Woodruff Dam, resulting in a 1.5-meter drop of the channel near the dam. Entrenchment extends for a long distance downstream, such that a drop of 60 cm is present at Blountstown. Local removal of sand has aggravated this problem. The overall result is that annual low flows have caused longer periods of isolation of small channels in the floodplain. The floodplain in general has become relatively more elevated, with succession toward less-hydric communities (Light et al., 1998). For *Macrochelys*, which frequents the deeper sections of the channels in the floodplain, these changes result in greater seasonal fragmentation of its habitat and a net reduction in habitable area. The entrenchment below Lake Seminole will worsen with time and may eventually degrade more habitat than that flooded in forming the lake. A new impoundment has been proposed on the Yellow River to provide water in Okaloosa and Santa Rosa counties. This could negatively affect populations in this river.

Increases in recreational fishing may increase the incidental take of *Macrochelys*. If, however, sport fishing increasingly displaces the use of trot lines, the harm of additional fishing activity should be slight. We do not know what impact the use of small set lines or fishing with attended lines at night has on small (e.g., 1–5 yr-old) turtles.

STATUS

Macrochelys temminckii is listed by the Florida Fish and Wildlife Conservation Commission as a Species of Special Concern. It was first designated by FCREPA as "status undetermined" in 1978 and was elevated to FCREPA Species of Special Concern in 1986 (see also Pritchard, 1992). The current FNAI status is G3G4/S3, which means between globally vulnerable and secure/vulnerable in Florida. The species was recently listed on CITES Appendix III by the United States.

CONSERVATION OPTIONS AND SOLUTIONS

In Florida, substantial blocks of the riverine habitat of *Macrochelys* exist in a semi-natural condition as protected public lands managed by a multiplicity of state and federal agencies. These include water management district lands, wildlife management areas, state and national forests, and military bases (Jue et al., 2001). Some of the most comprehensive protection covers the Escambia, Choctawhatchee, lower Apalachicola, and lower Ochlockonee rivers. Several small state parks and conservation areas protect habitat within the Suwannee River drainage, the lowest portion of which lies within the Lower Suwannee National Wildlife Refuge. Given the unique genetic status of *Macrochelys* within the Suwannee River drainage, efforts toward additional habitat protection should focus there.

Macrochelys is legally protected from most commercial use in Florida. Rule 68A-25.002(9) provides that "No person shall buy, sell, or possess [the species] for sale. . ." The Florida Game and Fresh Water Fish Commission first prohibited commercial take in 1972, and then imposed a bag limit of one individual for personal use in 1974. Alabama and Georgia prohibit any take without special permits (Levell, 1997).

To assist enforcement of Florida's prohibition against commerce in *Macrochelys*, genetic techniques (using mitochondrial DNA) allow differentiation of meat from that of other turtles (Roman et al., 1999; Roman and Bowen, 2000). Sequencing a portion of the mitochondrial genome also permits distinguishing *Macrochelys* within Florida (but also in Georgia and adjacent Alabama) from another group that extends westward from Florida's western border (Moler, 1996b; Roman et al., 1999; see Distribution, above). Thus, analyses of haplotypes could facilitate prosecution of violations of the Federal Lacy Act if samples from Florida populations show up in Louisiana markets.

The Suwannee River population is the most genetically distinct as well as a much restricted "evolutionary unit" of *Macrochelys* (Roman et al., 1999). Although the population in the Santa Fe River (tributary to the Suwannee) seems robust, we recommend additional censuses in Florida and Georgia toward a comprehensive assessment of this "evolutionary unit" throughout the Suwannee drainage. The results of such survey could, for instance, influence decisions on take at the local level.

Because turtles of some species mature slowly but survive many years as breeding adults, population stability necessitates high adult survival (Congdon, et al., 1994). In a recent model on population growth for *Macrochelys*, Reed et al. (2002) suggested that populations depend on extremely high (98%) annual adult survival, despite a maximum longevity not known to exceed 70 yrs. Very high adult survival would essentially preclude harvest of adults, as allowed under current Florida regulations. However, the model of Reed et al. (2002) may demand too much of adult survival. Hypothetically, this model may preclude recovery from presettlement take by indigenous Americans or following natural disasters at intervals approaching thousands of years. The few estimates of population stability in freshwater turtles come from studies of populations probably near a natural carrying capacity for adults. Modeling for *Macrochelys* is based on one such population of *Chelydra* (see Congdon et al., 1994). This study and others may have assumed levels of density-dependent stress on juveniles that are higher than in populations below adult carrying capacity (see Congdon et al., 1994). The population model for *Macrochelys* begins with a projected 20% hatchling recruitment from nests, which is higher than our single observation of 10–13% recruitment (see Predation, above). The model then assumes an annual juvenile survival rate of only 68.7% for the next 12 yrs (vs. 98% annual survival for adults and juveniles more than 13 yrs old; Reed et al., 2002). Although first-year hatchling survival could be lower than 68.7%, survival likely increases dramatically during the next 5–6 yrs. By 6 yrs of age, juvenile *Macrochelys* will have grown as large as the adults of many smaller species. Hence, Reed et al. (2002) may have significantly underestimated net survival to adulthood. In brief, the population model for *Macrochelys* probably involves assumptions of annual juvenile survival that are too low, and hence, too limiting. If so, modeling for higher juvenile survival would show population stability with lower adult survival and would accommodate take at a very low level.

The biology of *Macrochelys* seems amenable to proactive measures that can prevent extinction. Although there is currently no apparent need for such measures in Florida, development of proactive measures seems appropriate in face of a mounting public concern for this large and unique species.

Captive propagation is the basis for some types of proactive measures, such as "hatch and release." Adult *Macrochelys* can survive on commercial "farms" in densities far in excess of estimated natural densities (Ewert, *pers. obs*.). These farms (e.g., Randleas Turtle Farm, Jackson, Arkansas) annually yield eggs and hatchlings in the thousands. It is most likely that export figures from Telecky (2001), which show "alarming" increases from 100s in the 1980s to 10,000s in the 1990s, reflect the export of farm-produced hatchlings. Telecky's figures suffer from failure to distinguish captive vs. wild origin, and hatchlings vs. adults. We hope that details of aquaculture will become available in the general literature. As for application in Florida, current rules on possession and sale prohibit commercial farming, and we do not endorse legalizing it.

On a small scale, nest protection in Florida would be feasible and would not need to be expensive. For instance, one could place predator-excluding screens over nests without otherwise disturbing the eggs. Limiting nest predators is potentially an important option. Unlimited raccoon removal is legal for anyone who holds the proper licenses and uses proper methods. Study has supported the efficacy of raccoon removal on enhancement of turtle nest survival (Christiansen and Gallaway, 1984), but removal might require extreme reductions in raccoon populations (Ratnaswamy and Warren, 1998). Currently, low pelt values discourage incentive for commercial raccoon harvest.

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LITERATURE CITED

ALLEN, E.R., AND NEILL, W.T. 1950. The alligator snapping turtle *Macrochelys temminckii* in Florida. Ross Allen's Reptile Institute Special Publication 4:1-15.

ANONYMOUS. 1992. Gulf County man arrested with 1,600 pounds of turtles. Calhoun-Liberty Journal 12(33).

ANONYMOUS. 2000. Woods 'n Water, Dec. 2000: p. 15.

AUFFENBERG, W. 1957. The status of the turtle *Macroclemys floridana* Hay. Herpetologica 13:123-126.

CHRISTIANSEN, J.L., AND GALLAWAY, B.J. 1984. Raccoon removal, nesting success, and hatchling emergence in Iowa turtles with special reference to *Kinosternon flavescens* (Kinosternidae). The Southwestern Naturalist 29:343-348.

CONGDON, J.D., DUNHAM, A.E., AND VAN LOBEN SELS, R.C. 1994.

Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation management of long-lived organisms. American Zoologist 34:397-408.

Crother, B.I., Boundy, J., Campbell, J.A., de Queiroz, K., Frost, D. R., Highton, R., Iverson, J.B., Meylan, P.A., Reeder, T.W., Seidel, M.E., Sites, JR., J.W., Taggart, T.W., Tilley, S.G., and Wake, D.B. 2000. Scientific and standard English names of amphibians and reptiles of North America north of Mexico, with comments regarding confidence in our understanding. Society for the Study of Amphibians and Reptiles, Herpetological Circular no. 29, 82 pp.

Dixon, J.R. 2000. Amphibians and reptiles of Texas, second edition. Texas A&M University Press, College Station, Texas.

Dobie, J. L. 1968. A new turtle species of the genus *Macroclemys* (Chelydridae) from the Florida Pliocene. Tulane Studies in Zoology 15:59-63.

Dobie, J.L. 1971. Reproduction and growth in the alligator snapping turtle *Macroclemys temminckii* (Troost). Copeia 1971:645-658.

Ernst, C.H., Lovich, J.E., and Barbour, R.W. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington, D.C., 578 pp.

Ewert, M.A. 1976. Nests, nesting and aerial basking of *Macroclemys* under natural conditions, and comparisons with *Chelydra* (Testudines: Chelydridae). Herpetologica 32:150-156.

Ewert, M.A. 1979. The embryo and its egg: Development and natural history. In: Harless, M., and Morlock, H. (Eds.). Turtles: Perspectives and research. John Wiley & Sons, New York, pp. 333-413.

Ewert, M.A. (1985). Embryology of Turtles. In: Gans, C., Billett, F., and Maderson, P.F.A. (Eds.). Biology of the Reptilia 14. Wiley-Interscience, New York, pp. 73-267.

Ewert, M.A., and Jackson, D.R. 1994. Nesting ecology of the alligator snapping turtle (*Macroclemys temminckii*) along the lower Apalachicola River, Florida. Florida Game and Fresh Water Fish Commission, Nongame Wildlife Program Report NC89-020, Tallahassee, Florida, 45 pp.

Ewert, M.A., Jackson, D.R., and Nelson, C.E. 1994. Patterns of temperature-dependent sex determination in turtles. Journal of Experimental Zoology 270:3-15

Gibbons, J.W., and Lovich, J.E. 1990. Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*) Herpetological Monographs 4:1-29.

Gray, J.E. 1856a. On some new species of freshwater tortoises from North America, Ceylon and Australia, in the collections of the British Museum. Proceedings of the Zoological Society of London 1855 (23):197-202.

Gray, J.E. 1856b. Catalogue of Shield Reptiles in the Collection of the British Museum. Part I. Testudinata (Tortoises). Taylor and Francis, London. 79 pp.

Harlan, R. 1835. Genera of North American Reptilia and a synopsis of the species. In: Medical and Physical Researches. Lydia R. Bailey, Philadelphia, Pennsylvania, pp. 84-160.

Harrel, J.B., and Stringer, G.L. 1997. Feeding habits of the alligator snapping turtle (*Macroclemys temminckii*) as indicated by teleostean otoliths. Herpetological Review 28:185-187.

Harrel, J.B., Allen, C.M., and Hebert, S.J. 1996. Movements and habitat use of subadult alligator snapping turtles (*Macroclemys temminckii*) in Louisiana. American Midland Naturalist 135:60-67.

Harrel, J.B., Allen, C.M., and Hebert, S.J. 1997. One year growth of subadult *Macroclemys temminckii* in a Louisiana bayou. Herpetological Review. 28(3):128-129.

Hulbert, R.C. 2001. Florida's fossil vertebrates, an overview. In: Hulbert, R.C. (Ed.), The Fossil Vertebrates of Florida. University Press of Florida, Gainesville, pp. 25-33.

Hutchinson, V.H., Vinegar, A., and Kosh, R. 1966. Critical thermal maxima in turtles. Herpetologica 22:32-41.

Iverson, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately printed, 363 pp.

Iverson, J.B., and Etchberger, C.R. 1989. The distributions of the turtles of Florida. Florida Scientist 52:119-144.

Jackson, C.G., Jr., and Ross, A. 1971. The occurrence of barnacles on the alligator snapping turtle, *Macroclemys temminckii* Troost. Journal of Herpetology 5:188-189.

Jensen, J.B., and Birkhead, W.S. 2003. Distribution and status of the alligator snapping turtle (*Macrochelys temminckii*) in Georgia. The Southeastern Naturalist 2:25-34.

Johnson, S. 1989. Population status of the alligator snapping turtle (*Macroclemys temmincki*) in the Flint River. Unpublished report to Georgia Dept. of Natural Resources, Forsyth, Georgia. 11 pp.

Jue, S., Kindell, C., AND Wojcik, J. 2001. Florida Conservation Lands 2001. Florida Natural Areas Inventory, Tallahassee, Florida. 316 pp.

Lane, J.J., and Mitchell, W.A. 1997. Species profile: alligator snapping turtle (*Macroclemys temminckii*) on military installations in the southeastern United States. U.S. Army Corps of Engineers Technical Report SERDP-97-9. 16 pp.

Levell, J.P. 1997. A Field Guide to Reptiles and the Law. Serpent's Tail Books. Lanesboro, MN.

Lewis, T.E., and Irwin, K.J. 2001. Geographic Distribution: *Macrochelys temminckii* (alligator snapping turtle). Herpetological Review 32:274.

Light, H.M., Darst, M.R., and Grubbs, J.W. 1998. Aquatic habitats in relation to river flow in the Apalachicola River floodplain, Florida: U.S. Geological Survey Professional Paper 1594, 78 pp.

Lovich, J.E., and Gibbons, J.W. 1992. A review of techniques for quantifying sexual size dimorphism. Growth, Development and Aging 56:269-281.

Meylan, P.A. 1995. Pleistocene amphibians and reptiles from the Leisey Shell Pit, Hillsborough County, Florida. Bulletin Florida Museum of Natural History 37:273-297.

Miller, J.D. 1985. Embryology of marine turtles. In: Gans, C., Billett, F., and Maderson, P.F.A. (Eds.). Biology of the Reptilia 14, 269-328. Wiley-Interscience, New York.

Moler, P.E. 1996a. Alligator snapping turtle distribution and relative abundance. Florida Game and Fresh Water Fish Commission, Final Report 7544, 13 pp.

Moler, P.E. 1996b. Forensic identification of alligator snapping turtle meat. Florida Game and Fresh Water Fish Commission, Final Report 7545, 6 pp.

Parris, L.B., Lamont, M.M., and Carthy, R.R. 2002. Increased incidence of red imported fire ant (Hymenoptera: Formicidae) presence in loggerhead sea turtle (Testudines: Cheloniidae) nests and observations on hatchling mortality. Florida Entomologist 85:514-517.

Pritchard, P.C.H. 1989. The alligator snapping turtle: biology and conservation. Milwaukee Public Museum, Milwaukee, Wisconsin. 104 pp.

Pritchard, P.C.H. 1992. Alligator snapping turtle, *Macroclemys temminckii* (Harlan), Family Chelydridae, Order Testudines. In: Moler, P.E. (Ed.). Rare and Endangered Biota of Florida, Vol. III. Amphibians and Reptiles. University Press of Florida, Gainesville, pp. 171-176.

Ratnaswamy, M.J., and Warren, R.J. 1998. Removing raccoons to protect sea turtle nests: are there implications for ecosystem management? Wildlife Society Bulletin 26:846-850.

Reed, R.N., Congdon, J.D., and Gibbons, J.W. 2002. The alligator snapping turtle [*Macroclemys (Macrochelys) temminckii*]: A review of ecology, life history, and conservation, with demographic analyses of the sustainability of take from wild populations. Report to: Division of Scientific Authority, United States Fish and Wildlife Service. [http://www.uga.edu/srelherp].

Riedle, J.D. 2000. The Ecology of the Alligator Snapping Turtle, *Macrochelys temminckii* in Oklahoma. Unpubl. M.S. Thesis, Oklahoma State University, Stillwater.

Riedle, J.D. 2001. La tortue alligator (*Macroclemys temminckii*) en Oklahoma. Manouria 4:23-32.

Roman, J., and Bowen, B. 2000. The mock turtle syndrome: genetic identification of turtle meat purchased in the south-eastern United States of America. Animal Conservation 3:61-65.

Roman, J., Santhuff, S.D., Moler, P.E., and Bowen, B.W. 1999. Population structure and cryptic evolutionary units in the alligator snapping turtle. Conservation Biology 13:135-142.

Scott, D. 1987. [cover photo]. BioScience 37.

Sloan, K., and Lovich, J. 1995. Exploitation of the alligator snapping turtle, *Macroclemys temminckii*, in Louisiana: a case study. Chelonian Conservation and Biology 1:221-222.

Sloan, K., and Taylor, D. 1987. Habitats and movements of adult alligator snapping turtles in northeast Louisiana. Proceedings of the Annual Conference of the Southeastern Association of Fish & Wildlife Agencies:343-348.

Sloan, K., Buhlman, K., and Lovich, J. 1996. Stomach contents of commercially harvested adult alligator snapping turtles, *Macroclemys temminckii*. Chelonian Conservation and Biology 2:96-99.

Smith, H.M. 1955. The generic name of the alligator snapping turtle. Herpetologica 11:16.

Snider, A.T., and Bowler, J.K. 1992. Longevity of reptiles and amphibians in North American collections, second edition. Society for the Study of Amphibians and Reptiles Herpetological Circular 21:1-40.

Spindel, E.L., Dobie, J.L., and Buxton, D.F. 1987. Functional mechanisms and histologic composition of the lingual appendage in the alligator snapping turtle, *Macroclemys temminckii* (Troost) (Testudines: Chelydridae). Journal of Morphology 194:287-301.

Telecky, T.M. 2001. United States import and export of live turtles and tortoises. Turtle and Tortoise Newsletter 4:8-14.

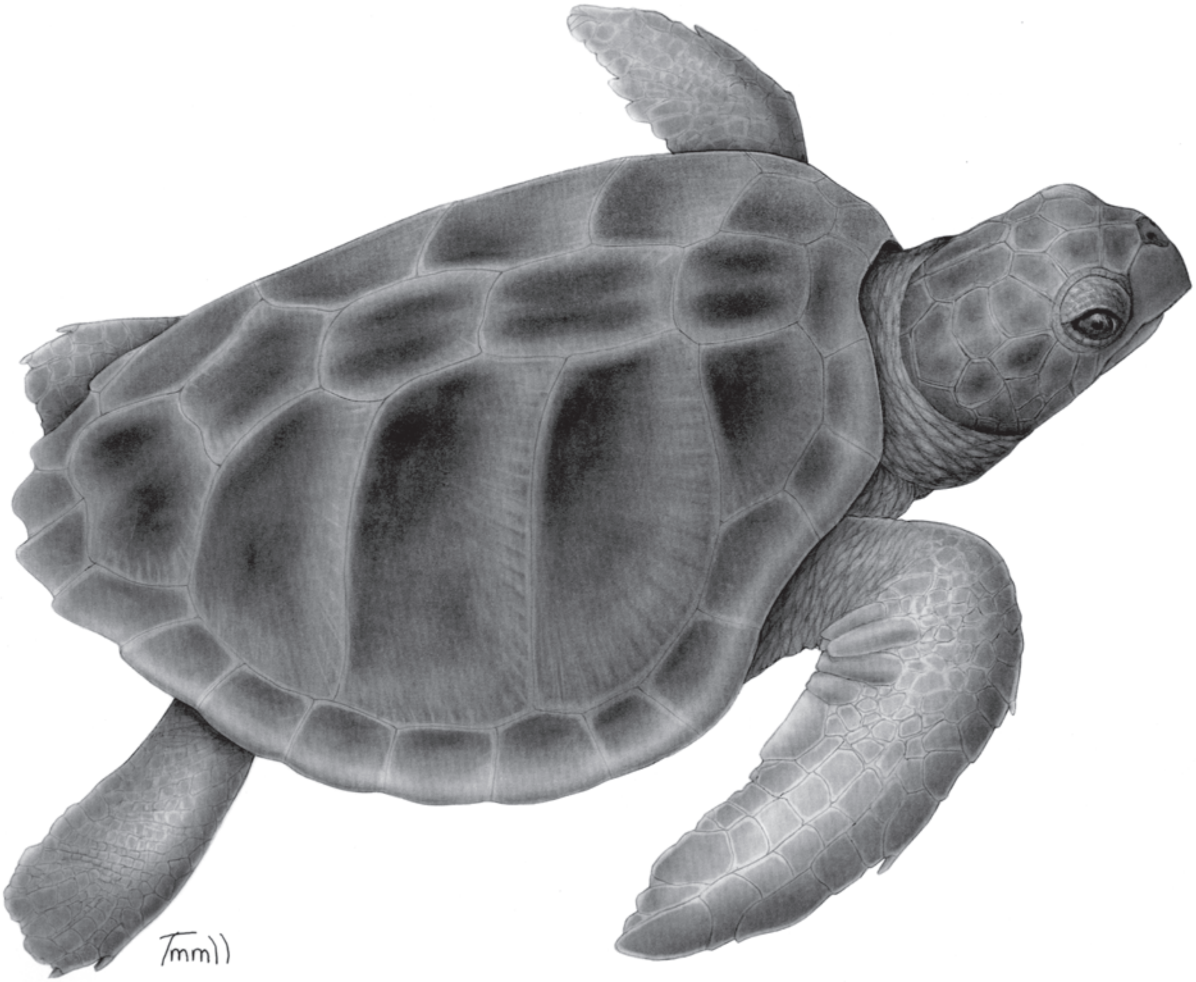
Trauth, S., Wilhide, I., and Holt, A. 1998. Population structure and movement patterns of alligator snapping turtles (*Macroclemys temminckii*) in northeastern Arkansas. Chelonian Conservation and Biology 3:64-70.

Wagner, B.K., Urbston, D., and Leek, D. 1996. Status and distribution of the alligator snapping turtle in Arkansas. Proceedings, Annual Conference, Southeastern Association, Fish and Wildlife Agencies 50:264-270.

Walker, D., and Avise, J.C. 1998. Principles of phylogeography as illustrated by freshwater and terrestrial turtles in the southeastern United States. Annual Review of Ecology and Systematics 29:23-58.

Webb, R. G. 1995. The date of publication of Gray's *Catalogue of Shield Reptiles*. Chelonian Conservation and Biology 1:322-323.

Whetstone, K. N. 1978. Additional record of the fossil snapping turtle *Macroclemys schmidti* from the Marsland Formation (Miocene) of Nebraska with notes on interspecific skull variation within the genus *Macroclemys*. Copeia 1978:159-163.



Loggerhead Sea Turtle, *Caretta caretta* (Cheloniidae).
Drawing by Susan Trammell.

Biology and Conservation of Florida Turtles – Peter A. Meylan, Ed.
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Introduction to the Sea Turtles: Family Cheloniidae

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Living sea turtles include members of two families, the Cheloniidae, all of which have hard shells, and the Dermochelyidae, containing only one living species that has a leathery shell. Florida provides critical habitat for both families; this includes important nesting beaches and/or feeding grounds for four hard-shelled species. A fifth hard-shelled species is known in Florida only as a waif. Recently collected data also indicate that critical habitat is present for pelagic, post-hatchlings of several species that use Florida waters during the earliest stages of their developmental migrations. In order of abundance the cheloniids that occur in Florida waters include the loggerhead (*Caretta caretta*), green turtle (*Chelonia mydas*), Kemp's ridley (*Lepidochelys kempii*), and hawksbill (*Eretmochelys imbricata)*. The olive ridley (*L. olivacea*) has recently been reported from Florida as a waif (Foley et al., 2003).

Content. — Living sea turtles of the family Cheloniidae include five genera and most authors recognize six species. Four of the five genera of hard-shelled (cheloniid) sea turtles are found in Florida. The only genus that is not present is the flatback, *Natator,* whose single species, *N. depressa*, is limited to the waters off the north coast of Australia and adjacent New Guinea (Iverson, 1992).

Relationships. — The closest living relative of the hard-shelled sea turtles is the leatherback. The families to which they belong, Cheloniidae and Dermochelyidae, are usually treated together as a Superfamily, Chelonioidea (Gaffney and Meylan, 1988; Hirayama, 1995; Shaffer et al., 1997). However, the fossil record suggests that the leatherback and cheloniid lineages separated long before the end of the age of dinosaurs, at least 110 million years ago in the early Cretaceous. This date is based on a very well preserved fossil protostegid sea turtle from the Santana Formation of Brazil, *Santanachelys gaffneyi* (Hirayama, 1998). The extinct sea turtle family Protostegidae includes the giant "eagle-beaked" sea turtles like *Archelon*. Protostegids appear to be more closely related to the leatherback than to hard-shelled (cheloniid) sea turtles.

Geological Distribution. — The oldest hard-shelled sea turtles are Cretaceous forms such as *Toxochelys*. Hard-shelled sea turtles are common throughout the Cretaceous and Tertiary (Hirayama, 1997). The earliest records of modern genera are difficult to identify since their names have been applied liberally to fossils without careful consideration of relationships. However, all living genera except *Natator,* are known by the early Pliocene (Dodd and Morgan, 1992).

Geographic Distribution. — The family occurs world-wide with the exception of Arctic and Antarctic waters, but nests mainly on tropical and sub-tropical beaches.

Status. — All of the hard-shelled sea turtle species in Florida waters are considered to be endangered or threatened (Moler, 1992). Two, the hawksbill and Kemp's ridley are considered to be critically endangered. There are many threats to sea turtle survival. They vary from renewed effort to generate international trade in sea turtle products, to incidental capture in marine fisheries, to loss of nesting beaches through armoring and development. All sea turtles are conservation dependent species and careful management of these species in Florida and throughout their ranges will be necessary for their long-term survival. Because these species make extensive developmental and reproductive migrations, international cooperation is a prerequisite to successful conservation efforts.

LITERATURE CITED

Dodd, C.K., Jr. and Morgan, G.S. 1992. Fossil sea turtles from the early Pliocene Bone Valley Formation, central Florida. Journal of Herpetology 26:1-8.

Foley, A.M., Dutton, P.H., Singel, K.E., Redlow, A.E., and Teas, W.G. 2003. The first records of olive ridleys in Florida, USA. Marine Turtle Newsletter 101: 23-25.

Gaffney, E.S. and Meylan, P.A. 1988. A phylogeny of turtles. In: Benton, M.J. (Ed.). The Phylogeny and Classification of Tetrapods. Clarendon Press, Oxford, England, pp. 157-219.

Hirayama, R. 1995. Phylogenetic systematics of chelonioid sea turtles. Island Arc 3:270-284.

Hirayama, R. 1997. Distribution and diversity of Cretaceous chelonioids. In: Callaway, J.M. and Nicholls, E.L. (Eds.). Ancient Marine Reptiles. Academic Press, pp. 225-241.

Hirayama, R. 1998. Oldest known sea turtle. Nature 392:705-708.

Iverson, J.B. 1992. A revised checklist with distribution maps of the turtles of the world. Privately published. Richmond IN, 363 pp.

Moler, P.E. 1992. Rare and Endangered Biota of Florida, Vol. III. Amphibians and Reptiles. University of Florida Presses, 272 pp.

Shaffer, H.B., Meylan, P.A., and McKnight, M. 1997. Tests of turtle phylogeny: molecular, morphological and combined approaches. Systematic Biology 46:235-268.

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Caretta caretta – Loggerhead Sea Turtle

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Summary. – The loggerhead, *Caretta caretta,* is the most common sea turtle nesting on Florida beaches and is found throughout Florida's coastal waters. This species reaches an average straight carapace length (SCL) of 92 cm and is recognized by its brown shell and broad, yellow-orange head. Mitochondrial DNA has provided information showing similarities among the loggerheads that share regional nesting beaches, including Florida. In the western North Atlantic, five genetically distinct nesting assemblages occur: the Yucatan peninsula, the Dry Tortugas, the remaining southern Florida peninsula, the Florida panhandle, and northern Florida through North Carolina. Hatchlings emerging from nests on Florida beaches enter the surf, swim seaward, and grow to 45–80 cm SCL in the open ocean before settling into shallow-water coastal habitats where they feed mostly on large, hard-shelled invertebrates. Loggerheads may pass through multiple developmental habitats in coastal waters during their maturation. Age at adulthood is 15–30 yrs. Adults undergo breeding migrations of several hundred kilometers between foraging areas and nesting beaches. Only two loggerhead nesting assemblages worldwide have more than 10,000 females nesting per year: southern Florida and Masirah (Oman). Loggerheads are Threatened, and their nesting numbers in Florida have recently declined. Major threats include nesting habitat loss from coastal armoring and artificial lighting, as well as incidental mortality from boat strikes, entanglement, debris ingestion, and fisheries, especially long-lines and trawling.

Conservation Status. – FNAI Global - G3 (Rare, Local, or Vulnerable), State - S3 (Rare, Local, or Vulnerable); ESA Federal - LT (Threatened); State - T (Threatened); CITES - Appendix I; IUCN Red List - EN (Endangered).

Species Recognition. — Loggerhead sea turtles are named for their conspicuously large heads. The species is known most commonly throughout English-speaking countries as the loggerhead, loggerhead turtle, or loggerhead sea turtle. Although the latter term best separates it from the loggerhead musk turtle (*Sternotherus minor*), clear differences in size and habitats make for little confusion between the two species. Spanish-speaking people know *Caretta caretta* as *caguama* or *cabezon*.

The loggerhead reaches an adult size slightly larger than that of the hawksbill *(Eretmochelys imbricata*) but smaller than the green turtle (*Chelonia mydas*). Adult female loggerheads measured at the nesting beach just north of Cape Canaveral ranged in size between 74.0 and 107.5 cm straight carapace length (SCL, *n* = 1222) and from 70.2 to 186.8 kg (*n* = 803) in weight (Ehrhart, 1980). Loggerheads (Figs. 3-1, 3-2) are distinguished from other sea turtle species by having two pairs of prefrontal scales between the eyes (these scales commonly have an additional intervening scale or two), nonoverlapping carapace scutes, and five pairs of costal scutes, with the first costal touching the nuchal scale (cervical scale of some authors) (Dodd, 1988).

On emergence from the nest, hatchling loggerheads (Fig. 3-3) are approximately one six-thousandth the weight of an adult. Ehrhart (1980) measured 20 hatchlings from each of 46 nests at an east-central Florida beach and reported weights ranging from 14.5 to 26.6 g and sizes ranging from 3.6 to 5.0 cm SCL. Coloration of hatchlings varies between and within clutches. When wet, the dorsal surface varies from light brown or pale gray to dark brown, charcoal, or black. The trailing margins of the carapace and dorsal surface of the flippers are often lighter than the overall dorsal coloration. The ventral surface is commonly lighter than the dorsal surface and is seldom uniformly pigmented. The lateral head scutes are often darker in light hatchlings, or there may be darker centers to the scutes, giving a freckled-cheek appearance. The carapace and plastron of hatchlings are lumpy, with raised scutes that later become the thickened keels and "spines" of juveniles.

As loggerheads grow from hatchlings into juveniles, the carapace and dorsal scales take on an orange-brown or red-brown color, with faint patterns of radiating streaks within each scute. The presence of dark red, yellow, brown, orange, and black in the pattern is variable, but the color blend normally appears orange-brown from a distance. Ventral surfaces of juveniles become amber yellow. In young juveniles (8–40 cm SCL), those generally distributed in oceanic waters, the rear of each costal

Figure 3-1. A subadult loggerhead sea turtle, *Caretta caretta*, 60 cm SCL, from the Atlantic Ocean off the Florida Keys (Monroe County). Photo by Blair Witherington.

and vertebral scute is thickened so that three carapace keels are apparent. The central carapace keel comprises the three middle vertebrals, which form pronounced backward projections. These spines accompany serrate marginal scutes and thickly keeled inframarginal and plastral scutes to provide what may be protective armor against some oceanic predators.

Larger juveniles (> 45 cm SCL) that have begun to feed in shallow coastal waters have lost their thickened shell scutes, and their carapace coloration is often masked by fouling organisms such as algae, hydroids, and barnacles (Fig. 3-1). The carapace in larger juveniles and adults most often has variably peeling layers of scute material with numerous *Chelonibia testudinaria* barnacles covering and imbedded into the scutes. An astounding variety of plants and animals grow within the crevices of a loggerhead's back (reviewed by Dodd, 1988). The carapace of adults is more elongate than that of juveniles and lacks marginal serrations. All size classes have a pronounced suprapygal hump at the posterior carapace. A casual observer seeing a loggerhead breathe at the surface will recognize the turtle by its large golden and orange-brown head.

Taxonomic History. — Linnaeus first described the loggerhead turtle as *Testudo caretta* in 1758, and Rafinesque assigned it to the genus *Caretta* in 1814. Stejneger (1904) presented the species as *Caretta caretta*. Detailed synonymies for *Caretta caretta* can be found in Dodd (1988).

Perceived differences between Indian–Pacific loggerheads and Atlantic loggerheads led Deraniyagala (1933) to treat the two forms as distinct species, then later (1939) as subspecies. An Indian-Pacific form (*C. caretta gigas*) was described as having an average of 13 marginal scutes and 7–12 neural bones, whereas an Atlantic form (*C. caretta caretta*) averaged 12 marginal scutes and 7–8 neural bones (Deraniyagala, 1939). Brongersma (1961) examined numerous specimens of *Caretta* from a wide range of localities and found that all sites had turtles with counts of marginal scutes between 12 and 13. With this evidence, more recent species accounts for *Caretta* have not recognized subspecies (Pritchard, 1979; Pritchard and Trebbau, 1984; Dodd, 1988; Kamezaki and Matsui, 1997). Analyses of genetic material from globally distributed sites have provided no support for dividing *C. caretta* into subspecies (Bowen et al., 1994; Bowen, 2003).

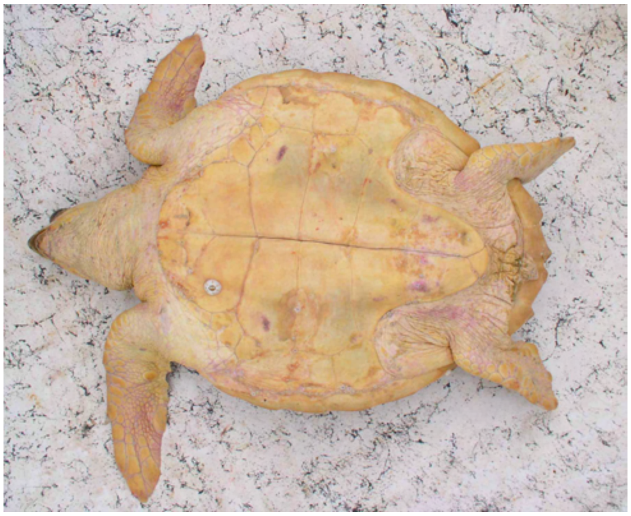

Figure 3-2. A subadult loggerhead sea turtle, *Caretta caretta*, 74 cm SCL, from the Atlantic Ocean off St. Lucie County, Florida. Photo by Blair Witherington.

Figure 3-3. A hatchling loggerhead, *Caretta caretta,* 4.5 cm SCL, from a nest on Melbourne Beach, Brevard County, Florida. Photo by Blair Witherington.

Relationships Among Populations. — As is the case for other sea turtle species, the genetic identities of loggerhead populations are best known where they nest, and natal-beach homing of females influences relatedness among these nesting assemblages. The idea that loggerheads return to nest on the same stretch of beach they left as hatchlings has been supported by evidence of spatial population structure in Atlantic and Mediterranean loggerheads (Bowen et al., 1993; Encalada et al., 1998; Laurent et al., 1998). Differences in maternally inherited mitochondrial DNA have shown that most nesting assemblages throughout the Atlantic and Mediterranean share only a few females per generation (Bowen, 2003).

The geographic distances between nesting assemblages necessary to produce genetic differences between populations of nesting females has been studied. Pearce (2001) surveyed mitochondrial DNA diversity at 12 nesting locations in Florida. Many adjacent nesting groups were not significantly different, but there were genetic differences between regional clusters of beaches that were separated by more than 100 km of sparsely nested coastline.

Worldwide, the greatest genetic differences occur between Indian–Pacific loggerheads and Atlantic–Mediterranean loggerheads (Bowen et al., 1994; Bowen, 2003). In the western North Atlantic, mitochondrial DNA has shown genetically distinct nesting assemblages from the Yucatan peninsula, southern Florida peninsula, Florida panhandle, and north Florida through North Carolina (Encalada et al., 1998). Additional genetic differences may exist between these nesting groups and loggerheads nesting in the Dry Tortugas, Florida (Pearce, 2001).

The four hypothesized subpopulations of loggerheads nesting in Florida—southern Florida peninsula, Florida panhandle, northeastern Florida northward, and Dry Tortugas (Encalada et al., 1998; Pearce, 2001)—have nearly complete nest-census data in recent years (FWC-FWRI Statewide Nesting Beach database). The largest subpopulation is the southern Florida group (peninsular Florida) with a mean of approximately 75,000 nests per year (approximately 18,000 females nesting per year) between 1998 and 2002. The second largest subpopulation is the northern group, which extends north from Amelia Island, Florida, through North Carolina. The northern subpopulation averaged approximately 5000 nests annually between 1989 and 1998 (adapted from TEWG, 2000) but the contribution of Florida nests to this subpopulation averaged only 75 nests per year during this same period (approximately 18 female loggerheads per year from Florida). The third largest Florida subpopulation nests in the panhandle, where there were an average of approximately 1000 nests per year (250 females nesting per year) between 1998 and 2002. The smallest of the Florida loggerhead subpopulations nests in the Dry Tortugas. Nesting there averaged approximately 200 nests per year (50 females nesting per year) between 1997 and 2001.

Male loggerheads often breed away from their natal beach and this tendency provides for some genetic exchange between nesting assemblages. In studies of biparentally inherited nuclear DNA, genetic differences were observed only in populations separated by hundreds to thousands of kilometers (FitzSimmons et al., 1996; Schroth et al., 1996). In Florida, Pearce (2001) found no differences in nuclear DNA to match the differences observed in maternally inherited mitochondrial DNA. As in other sea turtles, the relatedness of loggerhead nesting assemblages follows lines of geographical separation and is due to natal-site fidelity of nesting females. One consequence of genetic differences that occur only in females is that several generations or more (representing hundreds of years) would be necessary to replenish an extirpated nesting group.

Loggerheads foraging in Florida waters come from multiple nesting assemblages. In a sample of immature loggerheads drawn from Atlantic coastal waters near St. Lucie County, Witzell et al. (2002) found that at least three subpopulations were represented: southern Florida (69%), Mexico (20%), and northeastern Florida through North Carolina (10%).

DISTRIBUTION

Geographic Distribution. — The total range of the loggerhead turtle includes foraging areas, migration corridors, and nesting beaches distributed throughout the subtropical and temperate oceans of the world (Dodd, 1988). Unlike most other sea turtles, the loggerhead is more thinly distributed in the tropics than it is in temperate waters. Most loggerhead nesting beaches are also outside of the tropics. Nearly all nesting occurs between 19 and 36 degrees latitude in each hemisphere.

Beaches with the greatest loggerhead nesting are distributed around the western rims of the Atlantic and Indian oceans. Only two loggerhead nesting assemblages have more than 10,000 females nesting per year: southern Florida and Masirah (Oman) (reviews by Ehrhart et al., 2003, and Baldwin et al., 2003). Beaches with 1000

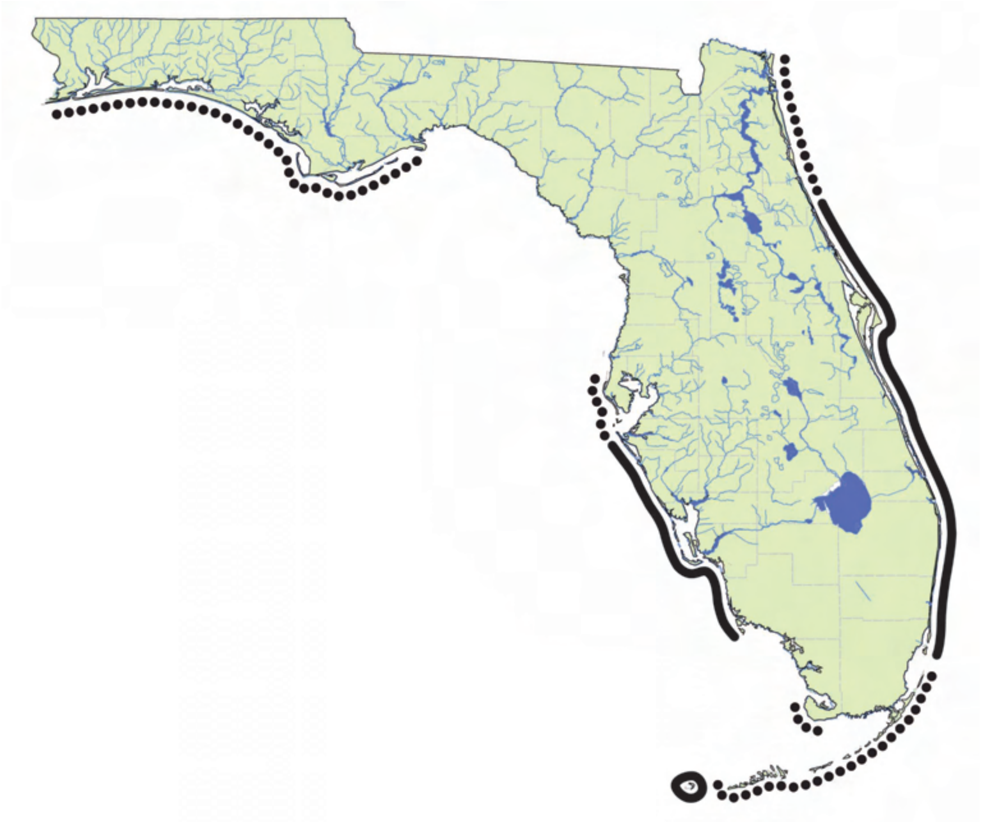

Figure 3-4. The distribution of loggerhead sea turtle (*Caretta caretta*) nesting on Florida beaches. Solid lines indicate nesting > 10 nests/km/season during the period 2001–2005, and dotted lines < 10 nests/km/season during the same period (FWC-FWRI Statewide Nesting Beach Survey database.

to 10,000 females nesting each year are in northeastern Florida through North Carolina, Cape Verde Islands (Spain, eastern Atlantic off Africa), and Western Australia (Australia) (reviews by Ehrhart et al., 2003, and Baldwin et al., 2003). Smaller nesting aggregations with fewer than 1000 nesting females annually occur in northwestern Florida, Cay Sal Bank (Bahamas), Quintana Roo and Yucatán (Mexico), Sergipe and northern Bahia (Brazil), southern Bahia to Rio de Janerio (Brazil), Tongaland (South Africa), Mozambique, Oman's Arabian Sea coast, Halaniyat Islands (Oman), Cyprus, Peloponnesus (Greece), Zakynthos (Greece), Turkey, Queensland (Australia), and the Ryukyu Islands (Japan) (Ehrhart et al., 2003; Baldwin et al., 2003; Margaritoulis, 2003; Limpus and Limpus, 2003a; Kamezaki et al., 2003).

The majority of US nesting occurs in peninsular Florida, although at least some loggerhead nesting has been recorded on beaches from Texas to Virginia (rarely as far north as New Jersey). Approximately 80% of the annual 53,000-92,000 nests in the U.S. (1989–98, TEWG, 2000) occur in six Florida counties (Brevard, Indian River, St. Lucie, Martin, Palm Beach, and Broward) (Ehrhart et al., 2003, Florida Fish and Wildlife Research Institute [FWC-FWRI] Statewide Nesting Beach Survey database).

Florida is the center of loggerhead abundance in the western hemisphere and may have more nesting loggerheads than any other population. There has been loggerhead nesting recorded for every coastal Florida county except for those bordering the Big Bend between Wakulla and Pasco counties (FWC-FWRI, Statewide Nesting Beach Survey database) (Fig. 3-4). Prominent peaks in nesting distribution occur on the Atlantic coast in southern Brevard County, St. Lucie and Martin counties, and northern Palm Beach County, and on the gulf coast in Sarasota County. The peaks lie between 28.5 and 26.5 degrees north latitude where coastal development is sparse and on beaches that are the greatest distance from ocean inlets and passes (Witherington et al., 2004). Nesting in the panhandle is highest in Bay, Gulf, and Franklin counties. Nesting in the keys is sparse except on Boca Grande, the Marquesas keys, and Dry Tortugas keys.

Loggerheads are present throughout Florida's coastal waters, bays, and lagoons. Locations where loggerheads are commonly observed throughout the year include Port Canaveral and other ship channels; areas of hard bottom in the Gulf of Mexico and in the Atlantic west of the Gulf Stream; Mosquito and Indian River lagoons; and reefs, hardbottom areas, channels, and seagrass pastures of Florida Bay, the Florida Keys, the Marquesas, and the Dry Tortugas (Ehrhart, 1983; Schroeder et al., 1998; Hopkins-Murphy et al., 2003; Bresette and Herren, 2003). Records of stranded turtles indicate that loggerheads are most abundant between southwestern Florida and the northeastern corner of the state (FWC-FWRI Sea Turtle Stranding and Salvage Network database).

Ecological Distribution. — Loggerheads nest nocturnally on the sandy beaches of mainland shores and barrier islands. Hatchlings that leave these nests enter the sea and disperse into the open ocean or the Gulf of Mexico. Posthatchlings and early juveniles forage at or near the ocean surface and are dispersed by currents throughout ocean basins (Witherington, 2002; Bolten, 2003).

The oceanic juvenile life-stage is better understood in loggerheads than in other sea turtles. Posthatchling loggerheads begin foraging before they disperse out of neritic (< 200 m depth) waters. These neonate loggerheads feed on organisms associated with convergence zones at the ocean surface, such as wind-dispersed pleuston and members of the *Sargassum* community (Witherington, 2002). Young loggerheads in the Atlantic disperse into oceanic (> 200 m depth) waters and are known from the Grand Banks off Newfoundland, Canada, and from the Azores Current frontal eddy off the Azores and Madeira (Bolten, 2003). Loggerheads remain in this oceanic juvenile stage for approximately 6.5 to 11.5 years (Bjorndal et al., 2000) and their sizes (from observations off the Azores) range widely from 8 to 80 cm curved carapace length (Bjorndal et al., 2000). The Azores Current frontal eddy occurs in a region where seamounts and other subsurface features of the Mid-Atlantic Ridge create a complex swirl of convergence zones. These convergence zones create concentrations of buoyant organisms upon an otherwise barren sea surface.

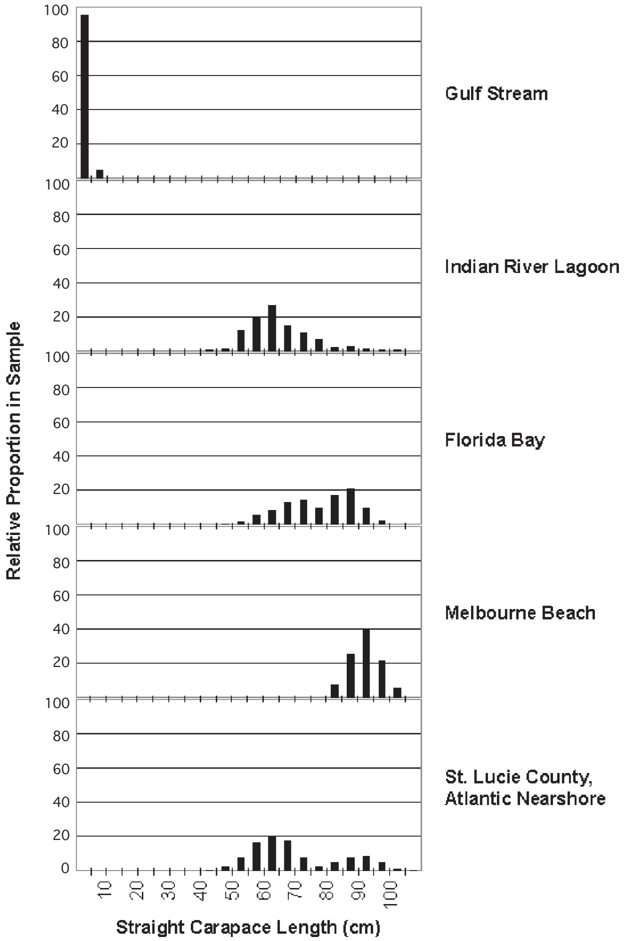

Figure 3-5. Sizes of loggerhead sea turtles (*Caretta caretta*) from Florida locations, expressed as Relative Proportion in Sample (0 to 100% for each location). Data are from the Gulf Stream off central Florida (*n* = 712, Witherington, 2002, and BW, unpubl. data), Indian River Lagoon near Sebastian Inlet (*n* = 452, Ehrhart et al., 1996), Florida Bay (*n* = 484, B. Schroeder, A. Foley, and B. Witherington, unpubl. data), Melbourne Beach (nesting females, *n* = 122, Witherington, 1986), and Atlantic nearshore hardbottom off St. Lucie County (St. Lucie Power Plant intake canal captures, *n* = 3760, MB, unpubl. data).

Immature loggerheads are not commonly seen in shallow coastal waters until they are larger than 40 cm SCL (Carr, 1987; Musick and Limpus, 1996; Hopkins-Murphy et al., 2003). The transition between epipelagic foraging in oceanic habitats and benthic foraging in neritic habitats occurs within a range of sizes (and, perhaps, ages). Immature loggerheads known from temperate coastal waters in the western North Atlantic are typically between 45 and 80 cm SCL. Although immature loggerheads are generally uncommon in the tropics, one significant assemblage has been observed in the southwestern Caribbean in a Panama lagoon (Engstrom et al., 2002).

Large immature (75–90 cm SCL) and adult loggerheads (> 90 cm SCL) that are not breeding or migrating to breed are known from the same temperate coastal waters as smaller immature turtles, but most of these large loggerheads are distributed in more subtropical waters. Habitats where benthic-foraging immature and adult loggerheads are found include coral reef and hardbottom between 0.5 and 200 m deep, seagrass pastures between 0.5 and 10 m deep, and shallow estuarine lagoons, sounds, and bays (Hopkins-Murphy et al., 2003; Limpus and Limpus, 2003b; FWC-FWRI Sea Turtle Stranding and Salvage Network database).

Migration corridors between foraging habitats and nesting beaches are commonly along continental shelf areas (Schroeder et al., 2003) but may also parallel major currents like the Florida Current (Dodd and Byles, 2003). Both males and females migrate seasonally along corridors where courtship and breeding occur.

Loggerhead populations in and outside Florida have similar ecological distributions. Much of the ecological information on loggerhead distribution in general comes from western Atlantic loggerheads, including those from Florida. Although most life stages occur in Florida waters (Fig. 3-5), it is clear that few if any Florida loggerheads complete their life cycle without traveling thousands of kilometers away from the state.

Within Florida, loggerheads are found on sandy beaches both as hatchlings and as nesting females. Posthatchlings are known from weed lines and other downwelling areas between the Gulf Stream (Florida Current) and the Florida peninsula. Large benthic-foraging neritic juveniles and adults are distributed throughout the marine and estuarine waters of the state.

HABITAT RELATIONS

Seasonality and Movements. — Loggerhead turtles can be found in Florida's coastal waters throughout the year, although seasonal abundance varies among size classes and geographic regions. In most Atlantic coastal waters, adult loggerheads are predominately observed throughout the spring and summer months during the mating and nesting season. More than 90% of all adult loggerheads captured from south-central Atlantic waters at the St. Lucie Power Plant were captured between April and August (Quantum Resources, 2002).

Juvenile loggerheads in Florida have similar winter and summer ranges (FWC-FWRI Sea Turtle Stranding and Salvage Network database), but it is clear that some seasonal movements occur throughout the species' western Atlantic range. Hopkins-Murphy et al. (2003) reviewed data for loggerheads in this region and generalized that spring movements of loggerheads were offshore to inshore and south to north, and that fall movements were the opposite of spring movements. Tag-return data from juvenile loggerheads captured at the St. Lucie Power Plant (St. Lucie Co.) support this seasonal pattern. Immature loggerheads originally tagged at the power plant have been found in the coastal waters of Virginia, North Carolina, South Carolina, and Georgia exclusively during the summer months (MB, unpubl. data). In one case, a loggerhead captured at the power plant in March 1995 was later captured five times during July and August of that year in the pound-net fisheries in Pamlico Sound, North Carolina. Morreale and Standora (2005) reported that many loggerheads forage in the coastal waters of New York during the summer and overwinter west of the Gulf Stream off North Carolina or near Cape Canaveral, Florida.

Although many juvenile loggerheads make extensive seasonal migrations, others are resident in Florida waters throughout the year. One resident loggerhead has been captured at the power plant site 36 times between 1989 and 2005. This turtle was captured during every season throughout the 17 years it resided in the nearshore Atlantic waters near the power plant (Herren et al., 2005).

Occasionally in winter, water temperatures in coastal lagoon habitats are low enough to cause hypothermic torpor in loggerheads (Witherington and Ehrhart, 1989). These cold-stunning events have occurred several times in Mosquito Lagoon, a coastal embayment with no southern exit. At least one Florida site, the Canaveral Ship Channel on the Atlantic coast, has been identified as a location where loggerheads assemble and bury in soft sediment to overwinter (Carr et al., 1980).

As described above, many loggerheads undergo seasonal movements, but within the seasons, loggerheads can be faithful to particular plots of foraging habitat. B. Schroeder, A. Foley, and B. Witherington (unpubl. data) have extensive recapture records for loggerheads in Florida Bay, where turtles are distributed among discrete basins. Many recaptures span five years or more between captures and nearly all turtles are recaptured within the same corner of the particular basin (within a few hundred meters) where they were originally captured.

Long-distance movements of juvenile loggerheads occur during seasonal migrations and during major shifts between developmental habitats (each described above). As with other sea turtles, pelagic juveniles may circle entire oceans, perhaps more than once. In the Pacific, genetic links between oceanic loggerheads and nesting populations have uncovered transoceanic movements of tens of thousands of kilometers (Bowen, 2003).

Loggerheads make successive developmental migrations between foraging habitats throughout their lives. In a review of loggerhead sizes at known foraging locations in the eastern US, Hopkins-Murphy et al. (2003) concluded that there is a gradual ontogenetic shift south along the Atlantic coast and into the southeastern Gulf of Mexico.

The largest regular movements that loggerheads make are between foraging and breeding areas. Female loggerheads that have nested on the beaches of Florida's central Atlantic coast are known to migrate to foraging areas in the Bahamas, Cuba, Mexico, the Florida Keys, and the eastern Gulf of Mexico (Meylan et al., 1983; Schroeder et al., 2003; Dodd and Byles, 2003). The periodicity of these movements is covered in the section on reproductive biology.

Return migrations between foraging areas and nesting beaches show remarkable precision. With migration distances that range from hundreds to thousands of kilometers, interseasonal distances between nest sites are only a few kilometers. In data reported by Ehrhart (1980), about two thirds of 39 loggerheads recorded in multiple seasons nested within 5 km of their nest site of a previous nesting season. Within a season, distances between nest sites are commonly between 0 and 17 km (Hughes, 1974; Bell and Richardson, 1978; Limpus, 1985).

Home Range. — Limited information on loggerhead home ranges describes these turtles as faithful to core areas but with occasional wide movements. Data from Florida Bay loggerheads (B. Schroeder, A. Foley, and B. Witherington, unpubl. data) show that some foraging loggerheads spend a high proportion of their time within plots of foraging habitat little more than a few hectares in area. Renaud and Carpenter (1994) tracked loggerheads with satellite telemetry and found broader home ranges for turtles near oil production platforms in the Gulf of Mexico. Four turtles tracked for 5–10.5 months showed a wide range in the extent of their movements, from 90 to 4297 km^2 for core areas and from 954 to 28,833 km^2 total home range.

Loggerheads that assemble within shallow coastal waters to forage in benthic habitats have an opportunity to interact with conspecifics. These interactions, either agonistic behavior or scramble competition, are not commonly reported. However, with the opportunity to ob-

Table 3-1. Loggerhead (*Caretta caretta*) growth rates from four mark-recapture studies in western Atlantic neritic habitats. GR = mean growth rate in cm/yr ± one standard deviation. Studies are of loggerheads from [a] Hutchinson Island, Florida (Herren et al., 2001); [b] Mosquito Lagoon, Florida (Mendonca, 1981); [c] Great Inagua, Bahamas (Bjorndal and Bolten, 1988); and [d] Chesapeake Bay, Virginia (Klinger and Musick, 1995).

SCL (cm)	[a] Hutchinson Island		[b] Mosquito Lagoon		[c] Great Inagua		[d] Chesapeake Bay	
	n	GR	*n*	GR	*n*	GR	*n*	GR
40-50	-	-	-	-	3	15.7+1.3	-	-
50-60	15	1.9+2.2	2	7.4+1.4	-	-	2	3.0+0.1
60-70	49	0.8+1.1	7	6.0+2.3	-	-	9	1.5+1.2
70-80	8	0.2+0.5	4	5.0+3.5	2	5.2+0.8	-	-
80-90	3	0.3+0.1	-	-	-	-	6	1.2+0.9
>90	3	0.2+0.3	-	-	-	-	-	-

serve loggerhead interactions in clear water, Limpus and Limpus (2003b) described occasional gaping displays directed at conspecifics and reported that some turtles bore bite marks from more violent interactions.

GROWTH AND REPRODUCTION

Growth. — Early estimates from young captive loggerheads placed the age of sexual maturity at 6 to 7 yrs (Uchida, 1967), but these estimates are now believed to be misleading (Bjorndal and Zug, 1995). More applicable growth rates from wild loggerheads spanning many sizes have provided estimates of age at maturity that range from 15 yrs to over 30 yrs, with the most complete data supporting the high end of this range (Parham and Zug, 1997; Bjorndal et al., 2000).

In general, growth is faster in small (young) loggerheads, gradually slows in larger juveniles, and becomes negligible at the size of a sexually mature adult (Mendonca, 1981; Frazer and Ehrhart, 1985; Bjorndal and Bolten, 1988; Parham and Zug, 1997). Oceanic loggerheads in the North Atlantic (20–50 cm SCL) grew approximately 9–21% in carapace length annually, Florida neritic loggerheads (50–80 cm SCL) grew 2–5%, and adult females on Florida beaches (80–110 cm SCL) grew 0.5–0.8% (from a review of growth rates by Bjorndal, 2003).

Loggerhead growth rates vary between populations and individuals and within the same individual (Chaloupka, 1998). For example, Florida loggerheads from Atlantic coastal waters grow slower than loggerheads from shallow lagoons (Table 3-1). It is likely that growth rates vary with differing diets, water temperatures, seasonal effects, genetics, and energy expenditures (Witham and Futch, 1977; Bjorndal and Bolten, 1988; Klinger and Musick, 1995).

Dimorphism. — In external appearance, immature males and females are essentially identical. Adults are sexually dimorphic. Adult males have a thick prehensile tail that extends far beyond the posterior margin of the carapace and a strongly recurved claw at the leading edge of each front flipper (the claws are straighter and shorter in females) (Fig. 3-6). On average, adult males are believed to be slightly larger (by a few centimeters SCL) and have broader heads than adult females (Pritchard and Trebbau, 1984).

Figure 3-6. An adult male loggerhead, *Caretta caretta*, 89 cm SCL, from Florida Bay, Monroe County. Photo by Blair Witherington.

Courtship and Mating. — Courtship and mating between loggerheads takes place mostly along migration routes and only rarely near nesting beaches (Limpus and Limpus, 2003b). The most detailed account of courtship and mating behavior is given by Miller et al. (2003), who described nuzzling and biting consistent with signals showing receptivity and fitness. Mating behavior, courtship, competitive interactions between males, and multiple paternity in clutches collectively suggest promiscuous mating with some level of female choice (Harry and Briscoe, 1988; Miller et al., 2003).

Mating takes place weeks or months before the first nesting of the summer season. Evidence in support of this includes healed mating scars (from the foreclaws of

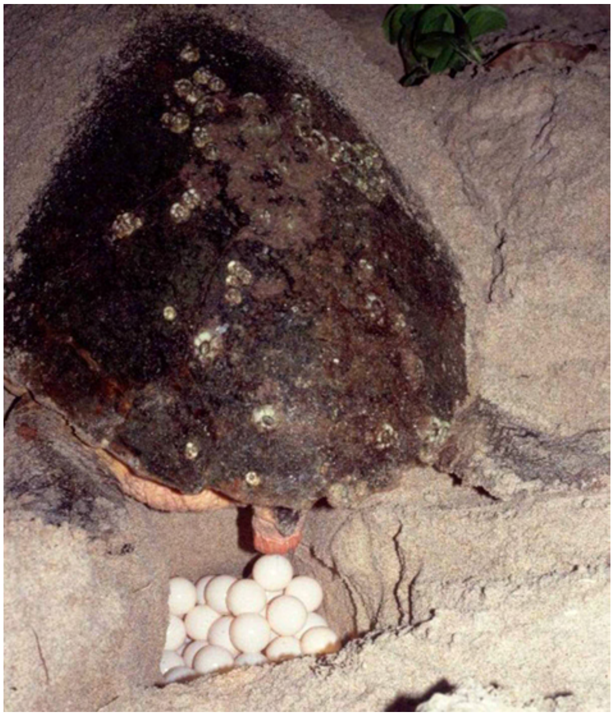

Figure 3-7. Nesting female loggerhead, *Caretta caretta*, from Palm Beach Co., Florida, in the process of laying eggs. Photo by George Heinrich.

Figure 3-8. Nesting female loggerhead, *Caretta caretta*, from Brevard County, Florida, in the process of returning from nesting. Photo by Blair Witherington.

males) on nesting females (Miller et al., 2003), early spring captures of migratory male loggerheads near Atlantic nesting beaches (Henwood, 1987), and direct observations of midspring mating in the Florida Straits (Meylan et al., 1983; BW, *pers. obs*.).

Nest Site Selection and Seasonality. — Nesting in the Northern Hemisphere begins in late April and ends in early September, whereas nesting in the Southern Hemisphere is typically between October and March (Dodd, 1988; Meylan et al., 1995). Hatchlings may emerge from Florida nests as early as late June and as late as November.

Loggerhead nests are made on open ocean beaches, typically between the high tide line and the dune front (Witherington, 1986; Hailman and Elowson, 1992). Loggerheads prefer nesting on relatively narrow, steeply sloped, coarse-grained beaches (Provancha and Ehrhart, 1987; Wood and Bjorndal, 2000).

Nesting Behavior. — Female loggerheads on nesting beaches (Figs. 3-7, 3-8) crawl with alternating limb movements. This characteristic gait, the size of the turtle, and the shortness of its flippers and tail result in a unique track that can be distinguished from the tracks of other turtles nesting on Florida beaches. Loggerhead tracks on soft-sand beaches average approximately 95 cm in width, have alternating flipper marks, and bear no mark from a tail drag down the center.

The appearance of a loggerhead nest site reflects the turtle’s stereotypical behavior and the nature of the sand substrate into which she has dug. Away from obstacles that could impede digging, a loggerhead nest appears as a 10–20 cm deep pit, approximately 1.7 m in diameter, at the base of a circular flat mound slightly larger than the diameter of the pit.

Differences in male and female philopatry are discussed in the section on population genetics. Other differences between the sexes may include breeding frequencies. Although loggerhead females remigrate to breed only every 1–9 years, with most showing a 2- to 4-yr cycle (Limpus, 1985; Dodd, 1988), males may breed each season (Wibbels et al., 1990).

During the nesting season, female loggerheads emerge onto beaches at night to nest. Undisturbed turtles complete approximately half of their nesting attempts (FWC-FWRI Index Nesting Beach database). The nesting process has been described by Bustard et al. (1975) and by Hailman and Elowson (1992). In 15 loggerhead females timed at Melbourne Beach, Florida, mean total nesting time was one hour and 35 minutes; turtles spent approximately 36% of this time preparing the nest site, 24% of the time laying eggs, and 40% of the time covering and camouflaging the site (BW, unpubl. data).

Estimates of mean remigration interval and clutch frequency are critical to estimating adult female population size from nest counts (the most readily available index of sea turtle abundance). Some cautions in using these estimates are given in the account for the green turtle in this volume. A widely accepted average remigration interval for Florida loggerheads is 2.7 years between successive reproductive migrations, and an accepted average clutch frequency for Florida loggerheads is 4.1 nests per female per reproductive migration (Dodd, 1988; Schroeder et al., 2003). Within a season, successive clutches are separated by a period of approximately two weeks (Dodd, 1988).

Clutch Size and Incubation. — The average number of eggs per clutch within a population is remarkably constant among years, although this parameter can vary considerably between populations. In Florida, loggerhead clutches at Melbourne Beach averaged 116 eggs (70–165 eggs, *n* = 100; Witherington, 1986).

Incubation period varies between locations and within the nesting season, largely due to effects from incubation temperature. The average time between oviposition and emergence of hatchlings from nests sampled throughout the season at Melbourne Beach was 53 days (49–58 days, *n* = 67, Witherington, 1986). The social facilitation behavior that facilitates nest escape by hatchlings is covered in the account for the green turtle.

POPULATION BIOLOGY

Population Structure. — As with other sea turtle species, the sex of loggerhead hatchlings is determined by incubation temperature. Nest temperatures higher than the pivotal temperature (at which a 1:1 sex ratio occurs) produce mostly females, and lower temperatures produce mostly males. The pivotal temperature for loggerhead turtles ranges from approximately 28.0 to 30.0ºC (Wibbels, 2003). Estimating hatchling sex ratios is complex because of variations in geography, nest placement, time of season, and weather. In Florida, the loggerhead hatchling sex ratio appears to be strongly female-biased at 9:1 (Mrosovsky and Provancha, 1989; Hanson et al., 1998). Despite seemingly skewed sex ratios in individual populations, there is little reason to believe that the primary sex ratio (the ratio at fertilization) measured over a sufficiently long period would not conform to the

1:1 ratio predicted by theory (Fisher, 1930). Even so, sex ratio studies of immature loggerheads in Florida have shown a female bias: Hutchinson Island 2:1 (Wibbels et al., 1991), Indian River Lagoon 1.6:1 (Ehrhart et al., 1999), and Cape Canaveral 1.5:1 (Wibbels et al., 1987). Because of the difficulty of capturing turtles at sea and of sampling bias from sex-specific migration patterns, adult sex ratios are more difficult to determine. Henwood (1987) reported an approximate 1:1 sex ratio of adults near Cape Canaveral, Florida, yet Quantum Resources (2003) reported a female-biased adult sex ratio of 9.5:1 for Atlantic waters near the St. Lucie Power Plant, Hutchinson Island, a site adjacent to an important nesting beach that would be expected to show a female bias.

Other than hatchlings and posthatchlings, loggerheads in Florida waters generally range from 40 to 110 cm SCL (Fig. 3-5). The size-class distribution for loggerheads captured at the St. Lucie Power Plant is very similar to that found in other studies conducted along Florida's east coast in that close to 80% of the sample contains juveniles (Henwood, 1987; Schmid, 1995; Ehrhart et al., 1996). Within most Florida foraging assemblages, there are relatively few of the largest immature loggerheads (75 to 85 cm SCL). It is likely that many loggerheads nearing maturity move to adult foraging grounds in south Florida, the Bahamas, and the northern Caribbean. Support for this comes from the predominately large loggerheads found in Florida Bay and in the lower Florida Keys (Schroeder et al., 1998; Bresette and Herren, 2003) (Fig. 3-5).

Survivorship. — Survivorship from egg to hatchling is highly variable both within and among Florida nesting beaches. The rate is affected predominantly by predation, especially from raccoons, and by acute beach erosion such as that caused by heavy surf from tropical weather systems. Average survival from egg to hatchling on beaches of southern Brevard County—beaches on which approximately 40% of Florida's loggerhead nesting takes place—has ranged between 55 and 62% (Witherington, 1986; Owen et al., 1994; FWC-FWRI hatchling production database). In 2001, egg-to-hatchling survivorship was 55%, as revealed by a weighted mean of 2347 nests on representative beaches throughout Florida. In a subsample of 2068 nests not affected by erosion from a late-season tropical storm, survival was 59% (FWC-FWRI hatchling production database).

Figure 3-9. Raccoons, *Procyon lotor*, destroy more sea turtle eggs in Florida than any other predator. Photo by Steve Johnson.

Hatchling mortality on the beach is minimal except where artificial lighting or other impediments to seaward orientation are present. Witherington (1997) estimated that mortality from misdirection by artificial lighting in Florida takes hundreds of thousands of loggerhead hatchlings each year. The proportion of all emerging hatchlings that die as a result of beach lighting may be as high as 5–10% (Witherington et al., 1996).

Hatchling survivorship at sea is known only from observations spanning the first several minutes, hours, or days of the hatchling swim frenzy. Fish predation accounts for all quantified mortality observed in swimming loggerhead hatchlings from Florida. Stewart and Wyneken (2004) observed 5% mortality from fish predation in the initial 15 min of swimming (*n* = 217 hatchlings at Boca Raton), Witherington and Salmon (1992) recorded 6.8% mortality in the initial 50–120 min of swimming (*n* = 74 hatchlings from Ft. Pierce, Wabasso, and Cape Canaveral), and Witherington (1995) observed 7% mortality in hatchlings tracked for 5–81 hrs (*n* = 15 hatchlings from Wabasso Beach).

Loggerhead survivorship probably increases with body size, but there are no detailed, empirical measurements of this effect. Based on catch-curve analyses and occasional long-term mark-recapture studies, Chaloupka (2003) and Heppell et al. (2003) modeled age-dependent survivorship and presented reviews and assessments of model parameters and results. In models for western Atlantic loggerheads, Heppell et al. (2003) used stage-based (small, medium, and large juveniles and breeding and nonbreeding adults) annual survivorship estimates that ranged from 0.68 to 0.85 in turtles between hatchling size and adulthood. An important conclusion from these modeling efforts was that changes in survival rates of oceanic and neritic juveniles have a large effect on population growth rates.

Reproductive value of a life stage is calculated as a function of both survival beyond that stage and the potential for ensuing reproduction; it is related to the number of offspring an animal is likely to produce. A stage-based model for the loggerhead that revealed reproductive value was first proposed by Crouse et al. (1987). In their seven-stage model, reproductive value increases by a factor of 20 as small benthic immatures (58.1–80.0 cm SCL, termed "large juveniles") survive to become large benthic immatures (80.1–87.0 cm, termed "subadults"), and all stages of adults have reproductive values that are four to five times higher than those for the largest immatures. From a conservation perspective, the oldest members of a population (breeding adults) are its most valuable members, and those just about to mature are not far behind.

INTERSPECIFIC INTERACTIONS

Diet and Feeding. — Posthatchlings feed in pelagic surface waters on a wide variety of plant and animal material. Common items flushed from the esophagus of posthatchling loggerheads off Florida included animals of the *Sargassum* community such as hydroids, copepods, polychaetes, and bryozoans; other pelagic animals such as medusae, wind-dispersed snails and siphonophores; carrion such as insects; plants such as *Sargassum* and seagrasses; and debris, including plastics and tar (Witherington, 2002). Juveniles in the open ocean feed on a variety of coelenterates, salps, pelagic snails, barnacles, and pelagic crabs (Bjorndal, 1997).

Hopkins-Murphy et al. (2003) reviewed information on the diet of neritic, benthic-feeding loggerheads in the western Atlantic. They generalized that these medium-sized to large (> 40 cm SCL) turtles feed principally on slow-moving or sessile macroinvertebrates and occasionally on fisheries bycatch carrion. In most studies of loggerhead diet, the most common items are large crustaceans and hard-shelled mollusks (Lutcavage and Musick, 1985; Ruckdeschel and Shoop, 1988; Burke and Standora, 1993; Plotkin et al., 1993; Youngkin, 2001). One observed feeding behavior in loggerheads involves scraping away at the bottom sediment and biting at the exposed substrate containing buried invertebrates (Preen, 1996).

Predation. — As in other turtles, most predation on loggerheads occurs during the egg and hatchling stages. In 2001, 635 of 3110 sample nests on Florida beaches were invaded by identifiable predators (FWC-FWRI hatchling production database). Identified predators listed in decreasing order of number of eggs destroyed are raccoons (*Procyon lotor*, Fig. 3-9), ghost crabs (*Ocypode quadrata*), nine-banded armadillos (*Dasypus novemcinctus*), foxes (*Vulpes* or *Urocyon*), domestic dogs (*Canis domesticus*), feral pigs (*Sus scrofa*), spotted skunks (*Spilogale putorius*), and unidentified larval insect species. In addition to the egg predators above, predators on hatchlings in the nest included fish crows (*Corvus ossifragus*), red imported fire ants (*Solenopsis invicta*), and bobcats (*Lynx rufus*). Predation on properly oriented hatchlings on Florida beaches is probably low and is principally from ghost crabs (Witherington, 1986).

Predation on hatchlings in the water is principally by fishes. Stewart (2001) recorded observations of fish predation on hatchlings dispersing from Palm Beach County beaches and found tarpon (*Megalops atlanticus*) to be the most common predator, followed by small sharks (Carcharhinidae). In Florida, loggerhead hatchlings have been recovered from the stomachs of other fishes and marine predators: hardhead catfish (*Arius felis*), blue runner (*Caranx crysos*), great barracuda (*Sphyraena barracuda*), mangrove snapper (*Lutjanus griseus*), red grouper (*Epinephelus morio*), dolphinfish (*Coryphaena hippurus*), and reef squid (*Sepiateuthis sepiodea*) (Witham, 1974; Wyneken et al., 2000; Stewart, 2001; Vose and Shank, 2003).

Other than humans, sharks are likely to be the principal predators of loggerheads larger than dinner plates. Many stranded loggerheads in Florida have shark-bite injuries (FWC-FWRI Sea Turtle Stranding and Salvage database), but it is unclear in most cases whether the sharks were preying or scavenging (i.e., whether bites occurred before or after death). One shark species that dominates the records of predation on large loggerheads is the tiger shark (*Galeocerdo cuvier*), a species that may specialize in loggerheads and other large sea turtles (Gudger, 1949; Witzell, 1987; Heithaus et al., 2002).

THREATS

Florida's sea turtle species are threatened by factors affecting sea turtles worldwide. Thorough descriptions of the threats to loggerheads and other sea turtles can be found in Parsons (1962), NRC (1990), NMFS and USFWS (1991), Lutcavage et al. (1997), Thorbjarnarson et al. (2000), and Witherington (2003). Many of the threats faced by loggerheads are incidental to human activities and occur because of overlap between areas of human activity and loggerhead distributions (Witherington, 2003).

A common threat on Florida beaches comes from efforts to protect coastal development from beach erosion. One of these protective efforts is coastal armoring, which includes seawalls, rocks, fences, and other structures designed to retain sand or lessen dune erosion from waves. Armoring that is exposed on the beach prevents turtles from accessing suitable (dry) nesting habitat (Mosier, 1998). Although coastal armoring can protect dune property from erosion, these structures commonly affect the beach itself by increasing erosion caused by wave scour and by interrupting beach-dune sand dynamics (Pilkey and Wright, 1988).

Another common measure to protect developed coastal property is to construct artificial beaches, a process that is termed beach nourishment. In this process, dredged sand is pumped as slurry onto the beach or is trucked onto the beach and spread with earth-moving equipment. In Florida, these activities are often permitted to occur during the nesting season, but permits generally require nest-monitoring, and as many nests as possible are translocated. Between 1995 and 2002, 139 km of loggerhead nesting beaches in Florida were nourished with sand (Greene, 2002).

From the perspective of sea turtle conservation, it seems clear that protecting dune property by sand-nourishing beaches is preferable to coastal armoring, but beach nourishment is not without its own negative effects. Some of these effects come from the covering of undiscovered nests with sand (presumably destroying all nests covered). Where beach nourishment takes place during the nesting season, approximately 7% of nests are

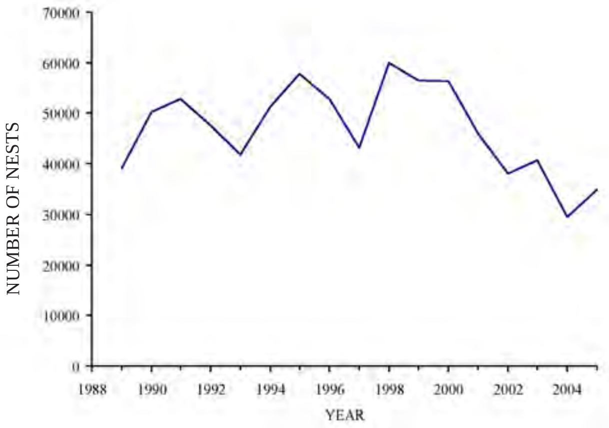

Figure 3-10. Annual loggerhead sea turtle (*Caretta caretta*) nesting at core index beaches in Florida for the period 1989–2005. Nesting survey effort did not vary between years. Loggerhead nests at core index beaches make up approximately 65% of total loggerhead nesting in the state. Data are from Florida Fish and Wildlife Research Institute (FWC-FWRI) Statewide and Index Nesting Beach Survey databases; information found at http://research.myfwc.com/features/category_sub.asp?id=3618.

likely to be missed by even the most highly trained monitors (FWC-FWRI index nesting beach database on nest identification accuracy). Other effects come from an inability on the part of engineers and contractors to make a beach that is similar to the one that has eroded away. Compared to natural beaches, artificial beaches tend to be wider, flatter, and have more compact sands. Other differences are in sand-grain size and sorting, sand color, compaction, general beach profile, and increased formation of escarpments (Crain et al., 1995). Loggerheads will nest on artificial beaches, and increases in nesting have been observed where sand is added to coastline with little or no dry beach, but in comparison to beaches with natural profiles, artificial beaches generally have increased rates of nest-site abandonment (Steinitz et al., 1998; Herren and Ehrhart, 2000). Despite design specifications for sands used in nourishment projects to mimic the native material on the beach, nourished beaches are often composed of poorer quality material. In terms of sea turtle hatchling success, poor-quality material can mean difficult digging in compact sands, reduced gas exchange for eggs, poorly drained sediments, and reduced hatching and emerging success rates (Crain et al., 1995).

Another serious threat to loggerhead populations is incidental catch in marine fisheries that target other species. Trawling for shrimp and other marine species has had a profound adverse effect on loggerheads. In recent years, the use of TEDs (turtle excluder devices) has shown the potential to reduced the impact from trawlers. However, the use of TEDs is not universal, and their continued use must be monitored and enforced. The importance of TEDs to marine turtle conservation is discussed below and in the Kemp's Ridley account in this volume.

Another fishery found to cause high loggerhead mortality is the longline catch of tunas and swordfish (Lewison et al, 2004). This fishery hooks, entangles, and drowns oceanic juvenile loggerheads in numbers sufficient to prevent recovery of populations. U.S. longline fleets, which are a small part of the global fishing effort, are currently experimenting with changes in fishing methods and gear that have been proposed to reduce loggerhead mortality.

STATUS

The loggerhead sea turtle is listed as Threatened, using criteria of both FCREPA (Dodd, 1992) and the U.S. Endangered Species Act (NMFS and USFWS, 1991). The loggerhead sea turtle is considered by IUCN to be Endangered, and is listed by CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora) as an Appendix I species. TEWG (2000) and Ehrhart et al. (2003) gave a complete review of abundance and distribution of Atlantic loggerheads, and an extensive USFWS/NMFS Atlantic loggerhead recovery team document is currently being prepared that will outline demography, quantify threats, and revise recovery goals.

Although historical abundance of loggerheads in Florida is uncertain, published accounts from the European colonization of the Caribbean clearly refer to tremendous numbers of sea turtles not seen today (Meylan et al., 1995). Take of loggerheads and their eggs from Florida beaches and turtle mortality caused by fisheries are likely to have depleted Florida loggerheads long before they could be effectively counted. In the 1970s and 1980s, when nesting surveys on Florida beaches were just getting underway, loggerheads foraging in the southeastern US and Gulf of Mexico had already been exposed to several decades of bottom-trawling. These fisheries killed the most reproductively valuable members of the population at an annual rate estimated to range higher than the total annual number of nesting females in the population (NRC, 1990).

The best assessment of loggerhead abundance in Florida comes from nest counts on beaches. Between 1989 and 2005, total nest counts and trends at index beach sites suggest that loggerheads are not recovering (Fig. 3-10). An approximate census with variable monitoring revealed that the mean number of loggerhead nests in Florida between 2001 and 2005 was approximately 59,000 nests/yr, which corresponds to approximately 15,000 females nesting per year (FWC-FWRI Statewide Nesting Beach database, http://research.myfwc.com/features/category_sub.asp?id=3618).

Temporal trends for loggerheads foraging in Florida waters are less clear because of the inherent difficulty in having standardized in-water monitoring. Perhaps the most reliable sampling of foraging loggerheads comes from the St. Lucie power plant. The power plant's intake canal has drawn water and turtles from the nearshore Atlantic since 1977. Between 1987 and 2005, 3449 loggerheads have been captured. The annual rate of capture of immature loggerheads (SCL < 85 cm) has increased significantly during the 19-year period ($r^2 = 0.55$, $p < 0.0007$). It is unclear how well this single site represents all immature loggerheads in Florida waters.

An overall assessment of population trends in Florida loggerheads is that there has not been significant recovery over the past 17 years. Although increases have been observed in immature loggerheads captured at a single location on the Atlantic coast, we hesitate to apply this trend in assessing immature loggerheads statewide. Nesting on beaches, our best index of adult abundance, shows no indication of a recovery substantial enough to change the status of Florida loggerheads from that of Threatened, and data from recent years indicate that a decline in nesting is occurring (Fig. 3-10). In our opinion, loggerheads in Florida remain depleted and have yet to overcome important threats to their survival, many of which occur outside Florida. Monitoring into the next decade, which would complete a generation-length of time since a consistent effort to count loggerheads began, is necessary to detect any subtle recovery or decline that may now be developing.

CONSERVATION OPTIONS AND SOLUTIONS

The principal milestone in loggerhead conservation was the protection afforded in 1978 with the listing of loggerhead populations under the U.S. Endangered Species Act. In the past 25 years, directed take has been nearly eliminated, and concerted efforts have been made by regulatory agencies to manage indirect take (Witherington and Frazer, 2003; Witherington, 2003).

Loggerhead conservation achievements in Florida include the development of local ordinances banning lighting of nesting beaches, a statewide prohibition of entangling nets in Florida waters, and acquisition and protection of beachfront properties within refuges, such as the Archie Carr National Wildlife Refuge in Brevard and Indian River counties. However, the greatest loggerhead conservation achievement in the past two decades has probably been the implementation of turtle excluder device (TED) regulations for shrimp trawlers (a staggered implementation that began in 1989). Because drowning mortality in trawl nets affected large numbers of the most reproductively valuable segment of the loggerhead population, TED regulations, even with only partial effectiveness, are thought to have greatly promoted recovery (Witherington, 2003). But confirming recovery will require patience. If demographic projections by Crowder et al. (1994) are correct, reduced juvenile mortality due to TED implementation would be expected to produce positive changes in counts on nesting beaches by approximately 2060.

Understanding loggerhead life history has revealed that conservation actions restricted to Florida are unlikely to complete the recovery of loggerheads swimming in the state's waters. Many threats occur outside Florida waters, and some critical threats, chiefly mortality from longline fishing, occur in international waters (Bolten, 2003; Lewison et al., 2004). As is true for other sea turtle species, a key to conserving loggerheads lies in the development of international agreements to manage fishing effort and other human activities at sea.

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LITERATURE CITED

BALDWIN, R., G. R. HUGHES, AND R. I. T. PRINCE. 2003. Loggerhead turtles in the Indian Ocean. In: A. B. Bolten and B. E. Witherington (Ed.). Loggerhead Sea Turtles. Smithsonian Institution Press, Washington DC, pp. 218-232.

BELL, R., AND J. I. RICHARDSON. 1978. Analysis of tag recoveries from loggerhead sea turtles (*Caretta caretta*) nesting on Little Cumberland Island, Georgia. Florida Marine Research Bulletin 33:20-24.

BJORNDAL, K.A. 1997. Foraging ecology and nutrition of sea turtles. In: Lutz, P.L. and J. A. Musick (Eds.). The biology of sea turtles. CRC Press, Boca Raton, pp. 199-231.

BJORNDAL, K.A. 2003. Roles of loggerhead sea turtles in marine ecosystems. In: Bolten, A.B. and B.E. Witherington (Eds.). Loggerhead Sea Turtles. Smithsonian Institution Press, Washington DC, pp. 233-254.

BJORNDAL, K.A., AND A.B. BOLTEN. 1988. Growth rates of juvenile loggerheads, *Caretta caretta*, in the southern Bahamas. Journal of Herpetology 22:480.

BJORNDAL, K.A., AND G.A. ZUG. 1995. Growth and age of sea turtles. In: Bjorndal, K.A. (Ed.). Biology and Conservation of Sea Turtles (Revised Edition). Smithsonian Institution Press, Washington DC, pp. 599-600.

BJORNDAL, K.A., A.B. BOLTEN, AND H.R. MARTINS. 2000. Somatic growth model of juvenile loggerhead sea turtles *Caretta caretta*:

duration of pelagic stage. Marine Ecology Progress Series 202:265-272.

Bolten, A.B. 2003. Active swimmers-passive drifters: the oceanic juvenile stage of loggerheads in the Atlantic system. In: A. B. Bolten and B. E. Witherington (Eds.). Loggerhead Sea Turtles. Smithsonian Institution Press, Washington DC, pp. 63-78.

Bowen, B.W. 2003. What is a loggerhead turtle? The genetic perspective. In: A. B. Bolten and B. E. Witherington (Eds.). Loggerhead Sea Turtles. Smithsonian Institution Press, Washington DC, pp. 7-27.

Bowen, B.W., J. C. Avise, J. I. Richardson, A. B. Meylan, D. Margaritoulis, and S. R. Hopkins-Murphy. 1993. Population structure of loggerhead turtles (*Caretta caretta*) in the northwestern Atlantic Ocean and Mediterranean Sea. Conservation Biology 7:834-844.

Bowen, B.W., N. Kamezaki, C. J. Limpus, G. H. Hughes, A. B. Meylan, and J. C. Avise. 1994. Global phylogeography of the loggerhead turtle (*Caretta caretta*) as indicated by mitochondrial DNA haplotypes. Evolution 48:1820-1828.

Bresette, M. J. and R. M. Herren. 2003. Demographic composition of marine turtles in the Key West National Wildlife Refuge, 2002. Technical report to U.S. Fish and Wildlife Service.

Brongersma, L. D. 1961. Notes upon some sea turtles. Zoologische Verhandelingen, Leiden, 51: 1-46.

Burke, V. J., and E. A. Standora. 1993. Diet of juvenile Kemp's ridley and loggerhead sea turtles from Long Island, New York. Copeia 1993:1176-1180.

Bustard, H. R., P. Greenham, and C. J. Limpus. 1975. Nesting behaviour of loggerhead and flatback turtles in Queensland, Australia. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen Series C Biological and Medical Sciences 78:111-122.

Carr, A. 1987. New perspectives on the pelagic stage of sea turtle development. Conservation Biology 1: 103-121.

Carr, A., L. Ogren, and C. McVea. 1980. Apparent hibernation by the Atlantic loggerheadturtle, *Caretta caretta*, off Cape Canaveral. Biological Conservation 19:7-14.

Chaloupka, M. 1998. Polyphasic growth in pelagic loggerhead sea turtles. Copeia 1998:516-518.

Chaloupka, M. 2003. Simulation modeling of population viability for loggerhead sea turtles exposed to competing mortality risks in the western South Pacific region. In: A. B. Bolten and B. E. Witherington (Eds.). Loggerhead Sea Turtles. Smithsonian Institution Press, Washington DC, pp. 274-294.

Crain, D.A., A.B. Bolten, and K.A. Bjorndal. 1995. Effects of beach renourishment on sea turtles: review and research initiatives. Restoration Ecology 3:95-104.

Crouse, D.T., L.B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412-1423.

Crowder, L.B., D.T. Crouse, S.S. Heppell, and T.H. Martin. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. Ecological Applications 4:437-445.

Deraniyagala, P.E.P. 1933. The loggerhead turtles (*Carettidae*) of Ceylon. Ceylon Journal of Science B. Zoology and Geology (Spolia Zeylanica) 18: 61-73.

Deraniyagala, P.E.P. 1939. Order Testudinata. The Tetrapod Reptiles of Ceylon. Vol. 1. Testudinates and Crocodilians. Colombo Museum, Colombo, Sri Lanka, and Dulau and Co., Ltd., pp. 24-242.

Dodd, C.K., Jr. 1988. Synopsis of the biological data on the loggerhead sea turtle *Caretta caretta* (Linnaeus 1758). U.S. Fish and Wildlife Service Biological Report 88(14).

Dodd, C.K., Jr. 1992. Loggerhead sea turtle, *Caretta caretta* (Linnaeus). In: Moler, P. E. (Ed.). Rare and Endangered Biota of Florida. Vol. III. Amphibians and Reptiles. University Press of Florida, Gainesville, pp. 128-134.

Dodd, C.K., Jr., and R. Byles. 2003. Post-nesting movements and behavior of loggerhead sea turtles (Caretta caretta) departing from east-central Florida nesting beaches. Chelonian Conservation and Biology 4:530-536.

Ehrhart, L.M. 1980. A survey of marine turtles nesting at the Kennedy Space Center Cape Canaveral Air Force Station, North Brevard County, Florida. Report to Division of Marine Resources, Florida. 216 pp.

Ehrhart, L.M. 1983. Marine turtles of the Indian River Lagoon System. Florida Scientist 46:337-346.

Ehrhart, L.M., W.E. Redfoot, and D.A. Bagley. 1996. A study of the population ecology of in-water marine turtle populations on the east-central Florida coast from 1982-96. Comprehensive Final Report, NOAA, National Marine Fisheries Service, Miami, Florida, 164 pp.

Ehrhart, L.M., W.E. Redfoot and D.A. Bagley. 1999. A study of the population ecology of in-water marine turtle populations on the east-central Florida coast in 1997-98. Final report to NOAA & National Marine Fisheries Service, 56 pp.

Ehrhart, L. M., D. A. Bagley, and W. E. Redfoot. 2003. Loggerheads in the Atlantic Ocean: geographic distribution, abundance, and population status. In: A. B. Bolten and B. E. Witherington (Eds.). Loggerhead Sea Turtles. Smithsonian Institution Press, Washington DC, pp. 157-174.

Encalada, S.E., K.A. Bjorndal, A.B. Bolten, J.C. Zurita, B. Schroeder, E. Possardt, C.J. Sears, and B.W. Bowen. 1998. Population structure of loggerhead turtle (*Caretta caretta*) nesting colonies in the Atlantic and Mediterranean regions as inferred from mtDNA control region sequences. Marine Biology 130:567-575.

Engstrom, T. N., P. A. Meylan, and A. B. Meylan. 2002. Origin of juvenile loggerhead turtles (*Caretta caretta*) in a tropical developmental habitat in Caribbean Panama. Animal Conservation 5: 125-133.

Fisher, R. A. 1930. The Genetical Theory of Natural Selection. Oxford University Press.

FitzSimmons, N. N., C. Moritz, C. J. Limpus, J. D. Miller, C. J. Parmenter, and R. Prince. 1996. Comparative genetic structure of green, loggerhead, and flatback populations in Australia based on variable mtDNA and nDNA regions. In: B. W. Bowen and W. N. Witzell, (Eds.). Proceedings of the International Symposium on Sea Turtle Conservation Genetics. NOAA Technical Memorandum NMFS-SEFSC-396, pp. 25-32.

Frazer, N.B. and L.M. Ehrhart. 1985. Preliminary growth models for green, *Chelonia mydas*, and loggerhead, *Caretta caretta*, turtles in the wild. Copeia 1985:73-79.

Greene, K. 2002. Beach nourishment: a review of the biological and physical impacts. ASMFC Habitat Management Series #7. Atlantic States Marine Fisheries Commission, Washington DC, 174 pp.

Gudger, E.W. 1949. Natural history notes on tiger sharks, *Galeocerdo tigrinus*, caught at Key West, Florida, with emphasis on food and feeding habits. Copeia 1949: 39-47.

Hailman, J. P., and A. M. Elowson. 1992. Ethogram of the nesting female loggerhead (*Caretta caretta*). Herpetologica 48:1-30.

Hanson, J., T. Wibbels and R. E. Martin. 1998. Predicted female bias in sex ratios of hatchling loggerhead sea turtles from a Florida nesting beach. Canadian Journal of Zoology 76:1850-1861.

Harry, J. L., and D. A. Briscoe. 1988. Multiple paternity in the loggerhead turtle (*Caretta caretta*). Journal of Heredity 79:96-99.

Heithaus, M. R. A. Frid, and L. M. Dill. 2002. Shark-inflicted injury frequencies, escapeability, and habitat use of green and loggerhead turtles. Marine Biology 140: 229-236.

Henwood, T. A. 1987. Movements and seasonal changes in loggerhead turtle *Caretta caretta* aggregations in the vicinity of Cape Canaveral, Florida (1978-84). Biological Conservation 40:191-202.

Heppell, S. S., L. B. Crowder, D. T. Crouse, S. P. Epperly, and N. B. Frazer. 2003. Population models for Atlantic loggerheads: past, present, and future. In: A. B. Bolten and B. E. Witherington (Eds.). Loggerhead Sea Turtles. Smithsonian Institution Press, Washington DC, pp. 255-272.

Herren, R.M., and L.M. Ehrhart. 2000. The effect of beach nourishment on loggerhead nesting and reproductive success at Sebastian Inlet, Florida. In: H. J. Kalb and T. Wibbels, compilers. Proceedings of the Nineteenth Annual Symposium on Sea Turtle Biology and Conservation, 2-6 March 1999. NOAA Technical Memorandum. NMFS-SEFSC-443. pp. 221-224.

Herren, R.M., M.J. Bresette, and D.A. Singewald. 2005. Loggerhead (*Caretta caretta*) growth rates from nearshore Atlantic waters. Proceedings of the Twenty-First Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-528. pp. 186-187.

Hopkins-Murphy, S., D. W. Owens, and T. M. Murphy. 2003. Ecology of loggerheads on foraging grounds and in internesting habitat in the eastern United States. In: A. B. Bolten and B. E. Witherington (Eds.). Loggerhead Sea Turtles. Smithsonian Institution Press, Washington DC, pp. 79-92.

Hughes, G. R. 1974. The sea turtles of South-east Africa, II. Investigational Report no. 36 of the Oceanographic Research Institute, Durban, South Africa.

Kamezaki, N., and M. Matsui. 1997. Allometry in the loggerhead turtle, *Caretta caretta*. Chelonian Conservation and Biology 2:421-425.

Kamezaki, N., Y. Matsuzawa, O. Abe, H. Asakawa, T. Fujii, K. Goto, S. Hagino, M.Hayami, M. Ishii, T. Iwamoto, T. Kamata, H. Kato, J. Kodama, Y. Kondo, I. Miyawaki, K. Mizobuchi, Y. Nakamura, Y. Nakashima, H. Naruse, K. Omuta, M. Samejima, H. Suganuma, H. Takeshita, T. Tanaka, T. Toji, M. Uematsu, A. Yamamoto, T. Yamato, and I. Wakabayashi. 2003. Loggerhead turtles nesting in Japan. In: A. B. Bolten and B. E. Witherington (Eds.). Loggerhead Sea Turtles. Smithsonian Institution Press, Washington DC, pp. 210-217.

Klinger, R. C. and J. A. Musick. 1995. Age and growth of loggerhead turtles (*Caretta caretta*) from Chesapeake Bay. Copeia 1995:204-209

Laurent, L., P. Casale, M. N. Bradai, B. J. Godley, G. Gerosa, A. C. Broderick, W. Schroth, B. Schierwater, A. M. Levy, D. Freggi, E. M. Abd El-Mawla, D. A. Hadoud, H. E. Gomati, M. Domingo, M. Hadjichristophorou, L. Kornaraky, F. Demirayak, and C. Gautier. 1998. Molecular resolution of the marine turtle stock composition in fishery bycatch: a case study in the Mediterranean. Molecular Ecology 7:1529-1542.

Lewison, R.L., Freeman, S.A., and Crowder, L. 2004. Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. Ecology Letters 7:221-231.

Limpus, C. J. 1985. A study of the loggerhead sea turtle, *Caretta caretta*, in eastern Australia. Ph. D. Dissertation, University of Queensland, St Lucia, Australia.

Limpus, C. J., and D. J. Limpus. 2003a. The loggerhead turtle in the equatorial and southern Pacific Ocean: a species in decline. In: A. B. Bolten and B. E. Witherington (Eds.). Loggerhead Sea Turtles. Smithsonian Institution Press, Washington DC, pp. 199-209.

Limpus, C. J., and D. J. Limpus. 2003b. The biology of the loggerhead turtle in western South Pacific Ocean foraging areas. In: A. B. Bolten and B. E. Witherington (Eds.). Loggerhead Sea Turtles. Smithsonian Institution Press, Washington DC, pp. 93-113.

Lutcavage, M., and J. A. Musick. 1985. Aspects of the biology of sea turtles in Virginia. Copeia 1985:449-456.

Lutcavage, M. E., P. Plotkin, B. E. Witherington, and P. L. Lutz. 1997. Human impacts on sea turtle survival. In: Lutz, P. L., and Musick, J. A. (Eds.). The Biology of Sea Turtles. CRC Marine Science Series, CRC Press, Boca Raton. pp 387-409

Margaritoulis, D., R. Argano, I. Baran, F. Bentivegna, M. N. Bradai, J. Antonio Camiñas, P. Casale, G. De Metrio, A. Demetropoulos, G. Gerosa, B. J. Godley, D. A. Haddoud, J. Houghton, L. Laurent, and B. Lazar. 2003. Loggerhead turtles in the Mediterranean: present knowledge and conservation perspectives. In: A. B. Bolten and B. E. Witherington (Eds.). Loggerhead Sea Turtles. Smithsonian Institution Press, Washington DC, pp. 175-198.

Mendonca, M. T. 1981. Comparative growth rates of wild immature *Chelonia mydas* and *Caretta caretta* in Florida. Journal of Herpetology 15:447-451.

Meylan, A. B., K. A. Bjorndal, and B. J. Turner. 1983. Sea turtles nesting at Melbourne Beach, Florida, II. Post-nesting movements of *Caretta caretta*. Biological Conservation 26:79-80.

Meylan, A., B. Schroeder, and A. Mosier. 1995. Sea turtle nesting activity in the State of Florida 1979-1992. Florida Marine Research Publications 52: 1-51.

Miller, J. D., C. J. Limpus, and M. H. Godfrey. 2003. Nest site selection, oviposition, eggs, development, hatching, and emergence of loggerhead turtles. In: A. B. Bolten and B. E. Witherington (Eds.). Loggerhead Sea Turtles. Smithsonian Institution Press, Washington DC, pp. 125-143.

Morreale, S. J., and E. A. Standora. 2005. Western North Atlantic waters: crucial developmental habitat for Kemp's ridley and loggerhead sea turtles. Chelonian Conservation and Biology 4:872-882.

Mosier, A. E. 1998. The impact of coastal armoring structures on sea turtle nesting behavior at three beaches on the east coast of Florida. Unpublished Master's Thesis. University of South Florida, Tampa, Florida, USA.

Mrosovsky, N. and J. Provancha. 1989. Sex ratios of loggerhead sea turtles hatching on a Florida beach. Canadian Journal of Zoology 67:2533-2539.

Musick, J.A., and C.J. Limpus. 1997. Habitat utilization and migration in juvenile sea turtles. In: P.L. Lutz, and J. A. Musick (Eds.). The biology of sea turtles. CRC Marine Science Series, CRC Press, Boca Raton, pp. 137-163.

National Research Council (USA), Committee on Sea Turtle Conservation. 1990. Decline of the Sea Turtles: Causes and Prevention. National Academy Press, Washington DC.

NMFS and USFWS (National Marine Fisheries Service and US Fish and Wildlife Service). 1991. Recovery plan for U.S. population of loggerhead turtle (*Caretta caretta*). National Marine Fisheries Service, Washington DC.

Owen, R.D., S.A. Johnson, W.E. Redfoot, and L.M. Ehrhart. 1994. Marine turtle nest production and reproductive success at Archie Carr NWR: 1982-1993. In Bjorndal, K.A., A.B. Bolten, D.A. Johnson, and P.J. Eliazar (compilers). Proceedings of the Fourteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-351, pp. 109-111.

Parham, J.F. and G.R. Zug. 1997. Age and growth of loggerhead sea turtles (*Caretta caretta*) of coastal Georgia: An assessment of skeletochronological age-estimates. Bulletin of Marine Science, 61:287-304.

Parsons, J.J. 1962. The Green Turtle and Man. University of Florida Press, Gainesville, Florida.

Pearce, A. F. 2001. Contrasting population structure of the loggerhead turtle (*Caretta caretta*) using mitochondrial and nuclear DNA markers. Master's Thesis, University of Florida, Gainesville, Florida, USA.

Pilkey, O. H., and H. L. Wright III. 1988. Seawalls versus beaches. In: N. C. Kraus and O. H. Pilkey, (Eds.). Journal of Coastal Research, Special Issue No. 4. pp. 41-66.

Plotkin, P. T., M. K. Wicksten, and A. F. Amos. 1993. Feeding ecology of the loggerhead sea turtle *Caretta caretta* in the Northwestern Gulf of Mexico. Marine Biology 115:1-15.

Preen, A.R. 1996. Infaunal mining: a novel foraging method of loggerhead turtles. Journal of Herpetology 30: 94-96.

Pritchard, P.C.H. 1979. Encyclopedia of Turtles. T.F.H Publications, Inc. Ltd, Neptune NJ.

Pritchard, P.C.H. and P. Trebbau. 1984. The Turtles of Venezuela. Contributions to Herpetology, 2. Society for the study of Amphibians and Reptiles.

Provancha, J.A. and Ehrhart, L.M. 1987. Sea turtle nesting trends at Kennedy Space Center and Cape Canaveral Air Force Station, Florida, and relationships with factors influencing nest site selection. In: W. N. Witzell (Ed.). Ecology of East Florida Sea Turtles, Proceedings of the Cape Canaveral, Florida, Sea Turtle Workshop, Miami, Florida, USA, February 26-27, 1985. NOAA Technical Report NMFS No. 53. pp. 33-44.

Quantum Resources. 2002. Florida Power and Light Company St. Lucie Unit 2 Annual Environmental Operating Report 2001. Prepared by Quantum Resources Inc. for Florida Power and Light Company, Juno Beach, Florida.

Quantum Resources. 2003. Florida Power and Light Company St. Lucie Unit 2 Annual Environmental Operating Report 2002. Prepared by Quantum Resources Inc. for Florida Power and Light Company, Juno Beach, Florida.

Renaud, M.L., and J.A. Carpenter. 1994. Movements and submergence patterns of the loggerhead turtles (*Caretta caretta*) in the Gulf of Mexico determined through satellite telemetry. Bulletin of Marine Science 55:1-15.

Ruckdeschel, C.A., and C.R. Shoop. 1988. Gut contents of loggerheads: Findings, problems, and new questions. In: B. A. Schroeder, compiler. Proceedings of the Eighth Annual Workshop on Sea Turtle Biology and Conservation. National Oceanic and Atmospheric Administration Technical Memorandum, NMFS-SEFC-214: 97-98.

Schmid, J.R. 1995. Marine turtle populations on the east-central coast of Florida: results of tagging studies at Cape Canaveral, Florida 1986-1991. Fishery Bulletin 93:139-151

Schroeder, B.A., A.M. Foley, B.E. Witherington, and A.E. Mosier. 1998. Ecology of marine turtles in Florida Bay: population structure, distribution, and occurrence of fibropapilloma. In: S. P. Epperly, and J. Braun (compilers). Proceedings of the Seventeenth Annual Sea Turtle Symposium. NOAA Technical Memorandum NMFS-SEFSC-415: 265-267.

Schroeder, B.A., A.M. Foley, and D.A. Bagley. 2003. Nesting patterns, reproductive migrations, and adult residence habitat of loggerhead turtles. In: A. B. Bolten and B. E. Witherington (Eds.). Loggerhead Sea Turtles. Smithsonian Institution Press, Washington DC, pp. 114-124.

Schroth, W., B. Streit, and B. Schierwater. 1996. Evolutionary handicap for turtles. Nature 384:521-522.

Steinitz, M.J., M. Salmon, and J. Wyneken. 1998. Beach renourishment and loggerhead turtle reproduction: A seven year study at Jupiter Island, Florida. Journal of Coastal Research 14:1000-1013.

Stejneger, L. 1904. The herpetology of Porto Rico. Annual Report to the U.S. National Museum, No. 129. pp. 549-724.

Stewart, K.R. 2001. The risk of hatchling loss to nearshore predators at a high-density loggerhead nesting beach in southeast Florida (*Caretta caretta*). Master's Thesis. Florida Atlantic University, Boca Raton.

Stewart, K.R., and J. Wyneken. 2004. Predation risk to loggerhead hatchlings at a high-density nesting beach in Southeast Florida. Bulletin of Marine Science 74:325-335.

Thorbjarnarson, J. B., C. J. Lagueux, D. Bolze, M. W. Klemens, and A. B. Meylan. 2000. Human use of turtles: a worldwide perspective. In: Klemens, M. W. (Ed.). Turtle Conservation. Smithsonian Institution Press, Washington DC, pp. 33-84.

Turtle Expert Working Group. 2000. Assessment update for the Kemp's ridley and loggerhead sea turtle populations in the western North Atlantic. US Department of Commerce, National Oceanic and Atmospheric Administration Technical Memorandum, NMFS-SEFSC-444.

Uchida, I. 1967. On the growth of the loggerhead turtle *Caretta caretta*, under rearing conditions. Bulletin of Japanese Society of Fisheries 33:497-507.

Vose, F. E., and B. V. Shank. 2003. Predation on Loggerhead and Leatherback Post-Hatchlings by Gray Snapper. Marine Turtle Newsletter 99:11-13.

Wibbels, T. 2003. Critical approaches to sex determination in sea turtles. In: P. L. Lutz, J.A. Musick and J. Wyneken (Eds.). The Biology of Sea Turtles Volume II, CRC Press, Boca Raton, pp. 103-134.

Wibbels, T., D.W. Owens, and M.S. Amoss. 1987. Seasonal changes in the serum testosterone titers of loggerhead sea turtles captured along the Atlantic coast of the United States. In: W. N. Witzell (ed.). Ecology of east Florida sea turtles. NOAA technical Report. NMFS No. 53:59-64.

Wibbels, T., D.W. Owens, C.J. Limpus, P.C. Reed, and M.S. Amoss, Jr. 1990. Seasonal changes in serum gonadal steroids associated with migration, mating and nesting in the loggerhead sea turtle (*Caretta caretta*). General and Comparative Endocrinology 79:154-164.

Wibbels, T., R.E. Martin, D.W. Owens, and M.S. Amoss, Jr. 1991. Female-biased sex ratio of immature loggerhead sea turtles inhabiting the Atlantic coastal waters of Florida. Canadian Journal of Zoology 69: 2973-2977.

Witham, R. 1974. Neonate sea turtles from the stomach of a pelagic fish. Copeia 1974:548.

Witham, R. 1980. The 'lost year' question in young sea turtles. American Zoologist 20:525-530.

Witherington, B.E. 1986. Human and Natural Causes of Marine Turtle Clutch and Hatchling Mortality and Their Relationship to Hatchling Production on an Important Florida Nesting Beach. M.S. Thesis. University of Central Florida, Orlando.

Witherington, B. E. 1995. Observations of hatchling loggerheads during the first few days of the lost year(s). In: Richardson J.I. and T. H. Richardson (compilers) Proceedings of the Twelfth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-361:154-157.

Witherington, B. E. 1997. The problem of photopollution for sea turtles and other nocturnal animals. In: J. R. Clemmons and R. Buchholz (Eds.). Behavioral Approaches to Conservation in the Wild. Cambridge University Press, Cambridge UK, pp. 303-328.

Witherington, B.E. 2002. Ecology of neonate loggerhead turtles inhabiting lines of downwelling near a Gulf Stream front. Marine Biology (Berlin) 140:843-853.

Witherington, B.E. 2003. The biological conservation of loggerheads: challenges and opportunities. In: A. B. Bolten and B. E. Witherington (Eds.). Loggerhead Sea Turtles. Smithsonian Institution Press, Washington DC, pp. 295-311.

Witherington, B.E., and L.M. Ehrhart. 1989. Hypothermic stunning and mortality of marine turtles in the Indian River Lagoon System, Florida. Copeia 1989: 696-703.

Witherington, B.E., and N.B. Frazer. 2003. Social and economic aspects of sea turtle conservation. In P. L. Lutz, J. Musick, and J. Wyneken (Eds.). Biology of sea turtles, volume II. CRC Press, Boca Raton, pp. 355-384.

Witherington, B.E., and M. Salmon. 1992. Predation on loggerhead turtle hatchlings after entering the sea. Journal of Herpetology 26:226-228.

Witherington, B.E., C. Crady, and L. Bolen. 1996. A ‘Hatchling Orientation Index’ for assessing orientation disruption from artificial lighting. In: J. A. Keinath, D. E. Barnard, J. A. Musick, and B. A. Bell (compilers). Proceedings of the Fifteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-387: 344-347.

Witherington, B.E., L. Lucas, and C. Koeppel. 2004. Nesting sea turtles respond to the effects of ocean inlets. In: M. S. Coyne, and R. D. Clark (compilers). Proceedings of the Twenty-First Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-528:355-356.

Witzell, W.N. 1987. Selective predation on large cheloniid sea turtles by tiger sharks (*Galeocerdo cuvier*). Japanese Journal of Herpetology 12: 22-29.

Witzell, W.N., A.L. Bass, M.J. Bresette, D.A. Singewald, and J.C. Gorham. 2002. Origin of immature loggerhead sea turtles (*Caretta caretta*) at Hutchinson Island, Florida: evidence from mtDNA markers. Fishery Bulletin 100:624-631.

Wood, D.W., and K.A. Bjorndal. 2000. Relation of temperature, moisture, salinity, and slope to nest site selection in loggerhead sea turtles. Copeia 2000:119-128.

Wyneken, J., L. Fisher, M. Salmon, and S. Weege. 2000. Managing relocated sea turtle nests in open-beach hatcheries. Lessons in hatchery design and implementation in Hillsboro Beach, Broward County, Florida. In: H. J. Kalb, and T. Wibbels (Compilers) Proceedings of the Nineteenth Annual Symposium on Sea Turtle Biology and Conservation. U.S. Dept. Commerce. NOAA Tech. Memo. NMFS-SEFSC-443:193-194.

Youngkin, D. 2001. A long-term dietary analysis of loggerhead sea turtles (*Caretta caretta*) based on strandings from Cumberland Island, Georgia. M.S. Thesis. Florida Atlantic University, Boca Raton, Florida.

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Chelonia mydas – Green Turtle

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Summary. – The green turtle, *Chelonia mydas*, is second to the loggerhead as the most common sea turtle on Florida nesting beaches and is found throughout Florida's coastal waters. This species reaches an average straight carapace length (SCL) of 98 cm and is recognized by its broad oval shell and two prefrontal scales between the eyes. Mitochondrial DNA has provided information showing similarities among the green turtles that share regional nesting beaches, including Florida. Next to Costa Rica, Florida is likely second or third in green turtle nesting among the geopolitical units rimming the western Atlantic. Approximately 99% of the green turtle nesting in Florida occurs on the Atlantic coast. Hatchlings emerging from nests on Florida beaches enter the surf, swim seaward, and grow to 20–30 cm SCL in the open ocean before settling into shallow water coastal habitats where they feed on seagrasses and macroalgae. Green turtles may pass through multiple developmental habitats in coastal waters during their maturation. Age at adulthood is 20–40 yrs. Adults undergo breeding migrations of several hundred kilometers between foraging areas and nesting beaches. Florida green turtles are Endangered, but there are indications that the Florida population is recovering. Threats in Florida include nesting habitat loss from coastal armoring and artificial lighting; incidental mortality from boat strikes, entanglement, debris ingestion, and fisheries; fibropapilloma disease; and directed take principally outside US waters.

Conservation Status. – FNAI Global - G3 (Rare, Local, or Vulnerable), State - S2 (Imperiled); ESA Federal - LT (Threatened); State - E (Endangered); CITES - Appendix I; IUCN Red List - EN (Endangered).

Species Recognition. — Green turtles are named for the color of their green fat, not for their outer appearance. Their name reveals the circumstances under which green turtles first came to be known, that is, by being eaten. Other English names given the green turtle include green sea turtle, green-back turtle, and the culinary descriptors, soup turtle and edible turtle (Pritchard and Trebbau, 1984; Hirth, 1997).

The green turtle reaches the largest size of any hard-shelled turtle alive today. Among living turtles, only the leatherback is larger (the largest specimens of giant soft-shell turtles from Asia approach green turtle size). Of 20 adult female green turtles measured on the nesting beach just north of Cape Canaveral, sizes ranged from 88 cm straight carapace length (SCL) and 104 kg to 109 cm SCL and 177 kg (Ehrhart, 1980). Of 27 adult female green turtles measured on Melbourne Beach, sizes ranged from 83 cm to 114 cm SCL (Witherington, 1986). Green turtles are distinguished from other sea turtle species by the presence of a single pair of large prefrontal scales between the eyes, a strongly serrated lower jaw, non-overlapping carapace scutes, and four pairs of costal scutes (Pritchard and Trebbau, 1984) (Figs. 4-1, 4-2, 4-3).

The contrasting coloration of hatchlings is striking. Hatchlings are countershaded: the ventral surface is typically cream white except for dark pigmentation centered at the distal half of each flipper, and the dorsal surface is typically blue-black except for light margins at the trailing edge of the carapace and flippers (Fig. 4-4).

As green turtles grow from hatchlings into juveniles, the carapace and other dorsal scutes take on patterns of radiating streaks. The presence of yellows, browns, greens, and black in the pattern is variable among and within populations. Plastron coloration is an immaculate white in the smallest juveniles, a size class found in the open ocean or recently recruited into coastal waters. The ventral surfaces become light yellow in coastal juveniles, and darker yellow in turtles approaching adulthood. Carapace coloration in adult green turtles from Florida is usually faded from the radiating streaks in the juvenile pattern. Most adults have a carapace with an olive tone spattered by light and dark spots radiating within each scute.

Taxonomic History. — Linnaeus first described the green turtle as *Testudo mydas* in 1758 from a specimen taken at Ascension Island, and Brongniart first assigned the green turtle to the genus *Chelonia* in 1800. A detailed synonymy for the green turtle can be found in Hirth (1997).

As the worldwide distribution of the green turtle (*Chelonia mydas*) was discovered, the species came to be known as one having a number of morphologically distinct forms. Currently, there is uncertainty concerning the taxonomy of these forms. Recent attention has focused on the recognition of two possible subspecies: the green turtle, *Chelonia mydas mydas*, and the black turtle, *Chelonia mydas agassizii* (Bocourt, 1868) (reviews are given by Pritchard and Trebbau, 1984; Groombridge and Luxmoore, 1989; Hirth, 1997).

Figure 4-1. A subadult green turtle, *Chelonia mydas*, 54 cm SCL, from the Atlantic Ocean off Monroe County, Florida Keys. Photo by Blair Witherington.

Black turtles are found almost exclusively in the eastern Pacific near the Galapagos Islands and off the western coast of the Americas. They are generally recognized as being the most different of the various forms. However, studies of nuclear and mitochondrial DNA haplotypes suggest that black turtles are only one of several genetically distinct and geographically separated assemblages of *Chelonia* (Bowen et al., 1992; Karl et al., 1992; Bowen and Karl, 2000).

Relatedness Among Populations. — The global genetics of green turtle populations has been well studied where they nest, and the relatedness among these nesting assemblages is strongly influenced by the natal beach homing of females. The idea that green turtles return to nest on the same stretch of beach they left as hatchlings has been supported by comparisons of maternally inherited mitochondrial DNA (Meylan et al., 1990). Mitochondrial DNA also has provided information showing genetic similarities among green turtles that share regional nesting beaches (Bowen et al., 1992; Allard et al., 1994). Male green turtles are less faithful to specific nesting beaches (Karl et al., 1992); comparisons of nuclear DNA (genetic material passed on by both males and females) show that male-mediated gene flow between nesting assemblages regularly occurs but is limited by distances between breeding sites. Thus, the overall relatedness of green turtle nesting assemblages worldwide appears to follow lines of geographical separation.

The greatest genetic differences among the world's green turtles occur between stocks from two ocean regions, the Atlantic-Mediterranean and the Indian-Pacific (Bowen et al., 1992). However, there are many genetically distinct

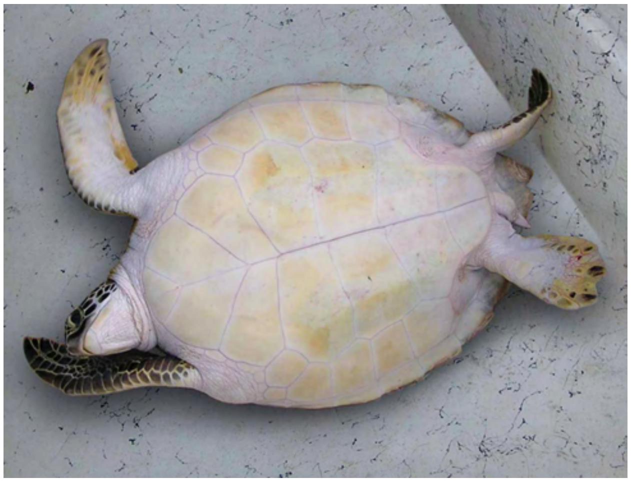

Figure 4-2. A subadult green turtle, *Chelonia mydas*, 54 cm SCL, from the Atlantic Ocean off Monroe County, Florida Keys. Photo by Blair Witherington.

Figure 4-3. An adult female green turtle, *Chelonia mydas*, camouflaging a nest site on Melbourne Beach, Brevard County, Florida. Photo by L. M. Ehrhart.

Figure 4-4. A hatchling green turtle, *Chelonia mydas*, 5.2 cm SCL, from a nest on Melbourne Beach, Brevard County, Florida. Photo by Blair Witherington.

nesting stocks within each of these ocean regions. In the western Atlantic, most green turtle nesting occurs in the wider Caribbean Sea. There, the most distinctive genetic split is between two stocks in the northwestern region (Florida/Mexico and Costa Rica) and two in the southeastern region (Isla Aves and Surinam). Each of the four nesting stocks is genetically distinct (Lahanas et al., 1994).

Green turtles found in Florida waters come from nesting beaches widely scattered throughout the Atlantic. Juvenile green turtles from Atlantic coast sites (Port Canaveral, Indian River Lagoon, and southeastern Florida nearshore reefs) were found to have come predominantly from the Florida/Quintana Roo stock (42–94%) and from the Costa Rica stock (3–54%), although stocks from Aves Island or Surinam (1–4%), Ascension Island or Guinea Bissau (0–3%), and Cyprus (0–2%) were also represented (Bass and Witzell, 2000; D. Bagley, unpubl. data).

DISTRIBUTION

Geographic Distribution. — Although most green turtle populations are greatly depleted, the species retains much of its historical distribution. The total range of the green turtle includes foraging areas, migration corridors, and nesting beaches that are interspersed throughout the tropical and subtropical oceans of the world (Hirth, 1997). Within this range, green turtles are least common in the east-central Pacific and in the northeast Atlantic. At least six green turtle rookeries have been extirpated, and of these, two were located in the western Atlantic (Bermuda and Grand Cayman; Groombridge and Luxmoore, 1989).

Green turtles nest on both island and continental beaches between 30ºN and 30ºS latitudes. The largest Atlantic nesting rookery is in Tortuguero, Costa Rica; the largest Indian Ocean rookeries are in Oman, at each of a number of islands surrounding Madagascar (Europa, Tromelin, and the Comores), and among the Indonesian islands (with severely declining populations that may no longer rival the others mentioned here); and the largest Pacific rookery is at Raine Island, Queensland, Australia (Hirth, 1997; Seminoff, 2002).

Although Florida is near the northern extent of the green turtle's Atlantic nesting range, the peninsula's beaches host a significant proportion of the region's green turtle nesting. Other than Costa Rica, Florida is likely second or third in the annual number of nests made on beaches rimming the western Atlantic. Green turtle nesting in Florida has only recently surpassed nesting numbers for Aves Island (Venezuela), and perhaps Surinam (Solé and Medina, 1989; Weijerman et al., 1998; Florida Fish and Wildlife Conservation Commission's Marine Research Institute [FWC-FWRI] Statewide Nesting Beach Survey database).

Green turtle nesting in Florida has occurred in every coastal county except those bordering the Big Bend area: Wakulla through Pasco counties (FWC-FWRI, Statewide Nesting Beach Survey database) (Fig. 4-5). Although nesting on Florida's Gulf coast was unrecorded before 1987, nesting in the panhandle now occurs on a regular basis. In the panhandle region, Okaloosa County receives the most nesting. Southwestern Florida remains sparsely nested, although Sarasota, Charlotte, Lee, and Collier counties have each had several nests during some recent seasons.

Approximately 99% of the green turtle nesting in Florida occurs on the Atlantic coast of the peninsula, with Brevard through Broward counties hosting the greatest nesting activity. There are peaks in green turtle nesting in southern Brevard, St. Lucie, Martin, and Palm Beach counties where coastal development is sparse and on beaches that are farthest from ocean inlets. Although little nesting occurs in the Florida Keys, the Dry Tortugas has received dozens of nests each season in recent years.

Green turtles are known from much of Florida's coastal waters where there is sufficient seagrass or algae to support their foraging. Green turtles forage through the winter in Mosquito Lagoon and the Indian River Lagoon (Ehrhart, 1983; Bresette et. al., 2002); within Port Canaveral (Redfoot and Ehrhart, 2000); on nearshore Atlantic reefs from Brevard to Broward counties (Guseman and Ehrhart, 1990; Wershoven and Wershoven, 1992; Bresette et al., 1998); on seagrass pastures of Florida Bay, the Florida Keys, and the Marquesas (Schroeder et al., 1998; MB, unpubl. data); and near the Ten Thousand Islands, western Everglades (Witzell and Schmid, 2002) . In summer, the center of green turtle abundance remains within their winter range, although green turtles are known from waters as far north as Massachusetts. In Florida, summer foraging extends north in the Gulf of Mexico from Tarpon Springs to Yankeetown (Caldwell and Carr, 1957; Carr, 1967; Schmid, 1998) and within St. Joseph Bay (E. McMichael, *pers. comm.*).

Ecological Distribution. — Green turtles nest predominantly at night on the sandy oceanic beaches of mainland shores, barrier islands, volcanic islands, and atolls. Hatchlings that leave these nests enter the sea and disperse away from land into the open ocean. It is likely that post-hatchlings and early juveniles forage at or near the ocean surface and are dispersed throughout ocean basins by currents (Caldwell, 1969; Carr and Meylan, 1980; Witham, 1980). Although little is known about green turtle ecology during this oceanic stage, there is some evidence that young green turtles feed on organisms associated with convergence zones at the ocean surface, such as wind-dispersed pleuston and members of

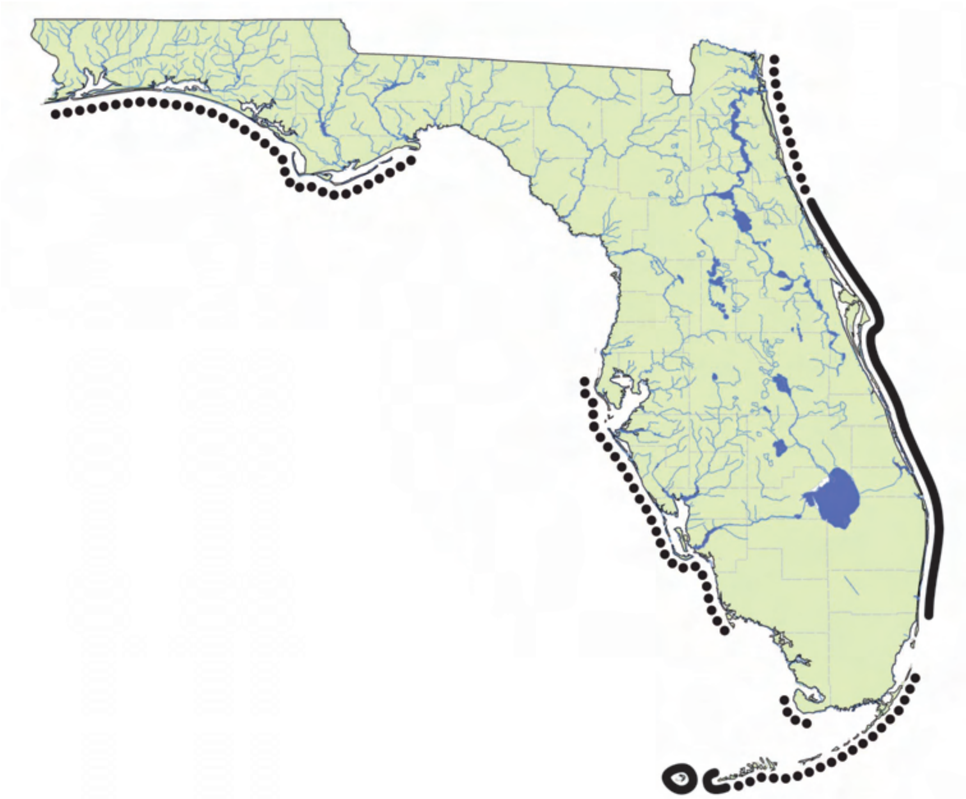

Figure 4-5. The distribution of green turtle, *Chelonia mydas*, nesting on Florida beaches. Solid lines indicate nesting greater than one nest/km/season during the period 2001–2005, and dotted lines indicate less than one nest/km/season during the same period (FWC-FWRI Statewide Nesting Beach Survey database.

the *Sargassum* community (Carr, 1987; BW, unpubl. data). Juvenile green turtles are not commonly seen in shallow coastal waters until they are approximately 20–30 cm in carapace length (Musick and Limpus, 1997). Growth rates during the previous oceanic stage are speculative, but it is likely that a 30-cm green turtle, newly recruited to coastal (neritic) waters, has spent approximately 3–5 yrs in the oceanic environment (Zug and Glor, 1998).

Green turtles that range in size from 30-cm juveniles to adults (90–120 cm SCL) forage in coastal waters near mainland shores, islands, reefs, and shelves. These turtles feed on benthic macroalgae and seagrasses that grow in waters mostly shallower than 10 m. Green turtles lodge themselves into corals, sponges, rocky ledges, and soft mud in order to rest without drifting, and habitats with these features that are adjacent to foraging areas may be important to green turtles.

Migration corridors between foraging habitats and nesting beaches are also important for green turtles. These corridors lie along coastlines and reefs and may span the open water between landmasses. Both males and females migrate seasonally to nesting beaches along corridors where courtship and breeding may also occur.

Juveniles and adults may have different habitat requirements and are rarely observed in Florida waters within the same foraging areas. For example, only one of 1062 green turtles netted by Ehrhart et al. (1996) in the Indian River Lagoon between 1982 and 1996 was determined to be an adult.

Green turtles nesting in Florida seem to prefer barrier-island beaches that receive high wave energy and that have coarse sands, steep slopes, and prominent foredunes. The greatest nesting is on sparsely developed beaches that have minimal levels of artificial lighting. Green turtles typically deposit their eggs near the base of the primary dune.

The hatchlings that emerge from green turtle nests on Florida's Atlantic beaches swim away from land and toward the Gulf Stream. We hypothesize that driftlines at convergence fronts (downwellings) near the western edge of the Gulf Stream provide accumulations of floating material where young green turtles begin their first feeding. Post-hatchlings that have stranded dead following storms contained ingested material including *Sargassum* and animals from the *Sargassum* community known from Gulf Stream driftlines (BW, unpubl. data). However, after extensive efforts to observe green turtles in this habitat off Florida (Witherington, 2002), and with approximately 1300 observations of loggerhead post-hatchlings in western Gulf Stream driftlines, only 17 green turtles have been observed (BW, unpubl. data). The active swimming pattern seen in these turtles suggested that young green turtles are able to disperse beyond the surface advection and downwelling at driftlines, and actively evade both potential predators and human observers. A post-hatchling's countershaded coloration suggests this sort of free-swimming epi-pelagic lifestyle, although limited capture records show a strong association with *Sargassum* and other drift material.

After years of feeding in the open ocean, green turtles that have come from Florida nests move into coastal waters. Although many of these turtles may settle within Florida waters, others begin benthic foraging as far east as Bermuda (A. Meylan, *pers. comm.*) and as far south as Nicaragua (Bass et al., 1998). On these widespread foraging grounds and among Florida sites, each assemblage of juveniles seems to be a mix of turtles from various western Atlantic rookeries. Although varied, the mix appears to be nonrandom. For instance, juveniles found in Florida waters were equally likely to have come from Florida beaches as from Costa Rica (Bass and Witzel, 2000; D. Bagley, unpubl. data) even though the hatchlings produced by Costa Rica outnumber Florida hatchling production by nearly ten to one.

Juvenile green turtles from Florida that are smaller than approximately 60 cm SCL are most common from shallow, restricted waters such as enclosed embayments and turbulent surf-zone reefs (Ehrhart, 1983; Guseman and Ehrhart, 1990; Wershoven and Wershoven, 1992; Bresette et al., 1998; Schroeder et al., 1998; Redfoot and Ehrhart, 2000; Bresette et al., 2002; E. McMichael, *pers. comm.*). At approximately 60–70 cm SCL (ca. 50 kg) and a decade or more away from maturity, most green turtles leave Florida's coastal waters and migrate south. Although it is uncertain how widely these turtles might travel, a number of Florida-tagged turtles have been recaptured in Caribbean waters. Sixteen green turtles that were tagged by L. Ehrhart (*pers. comm.*) and his students working in lagoon and nearshore waters of east-central Florida have been recovered from Nicaragua (n = 7), Cuba (n = 7), Belize (n = 1), and the Dominican Republic (n = 1).

It is uncertain why a size milestone in immature turtles would prompt such a shift in developmental habitats. Recently, the Inwater Research Group (*pers. comm.*) has discovered large (69–109 cm SCL, n = 24) subadult green turtles in waters west of the Marquesas, south of the Florida peninsula. These turtles were found in open (unenclosed) waters slightly deeper (4–6 m) than most Florida embayments where smaller juveniles are observed. This suggests that in addition to their movements to more tropical waters, larger immature green turtles moving south also may be seeking deeper, more open grazing habitats.

Except for the waters off nesting beaches during late spring and summer, adult green turtles of either sex in Florida waters are restricted to the southernmost reach of the peninsula. Female green turtles tagged with satellite transmitters on Florida east-coast beaches (n = 18) were tracked southward down the coast to waters near the northeastern Florida Keys, the Dry Tortugas, and along the extreme southwestern coast of Florida (B. Schroeder, *pers. comm.*). One of the 18 females took up long-term residence in Bahamian waters. Continued contact with five of the tracked turtles revealed that they returned to the same foraging areas after subsequent nesting migrations. Three adult males captured and transmittered off east-coast beaches were found to occupy the same region of south Florida as the tracked females (B. Schroeder, *pers. comm.*).

HABITAT RELATIONS

Ecological Role. — At levels of historical green turtle abundance, there probably was localized but considerable grazing competition among green turtles for seagrasses and algae (Jackson, 1997; Jackson et al., 2001). Today, although seagrasses are depleted, it is probable that green turtles are even more depleted than seagrasses, and it is unlikely that green turtles in Florida waters are near the carrying capacity of regional habitats. However, within local patches of habitat in the Bahamas, Bjorndal et al. (2000) have shown that green turtle growth rates are negatively correlated with abundance. This suggests that green turtles do compete for food resources. If these density-dependent limitations occur as Florida green turtle populations recover, the evidence for it will probably first be seen at the densely foraged Atlantic nearshore reefs such as those off Indian River County. There, green turtles forage at densities an order of magnitude greater than at other known Florida sites (Ehrhart et al., 1996).

Other interactions between green turtles may include the mutualistic, selfish herding that many animals show. Ogden et al. (1983) reported that green turtles in the waters of the U.S. Virgin Islands were seen most often foraging alone but were occasionally observed in groups of two or three. Mellgren and Mann (2000) hypothesized that groups of green turtles may facilitate foraging behavior through a process called local enhancement. Their results in the laboratory supported the hypothesis but were based on post-hatchlings fed a fish diet. Preliminary evidence from a long term study of turtles off Hutchinson Island, Florida, suggests that small cohesive groups of juvenile green turtles occur in the wild and may have members that stay together for several years (MB, unpubl. data).

Seasonality. — Green turtles are most seasonal in their nesting. Within the tropics, nesting may span all seasons of the year, but there is often a peak during the rainy season. Outside the tropics the nesting peak is in the summer months. In Florida, green turtles begin nesting in significant numbers by late May, plateau in nesting frequency during July, and taper off in nesting August through September. Hatchlings may emerge from Florida nests as early as late July and as late as December.

Adult green turtles are seldom observed in Florida waters outside the nesting season. Of 51 adult green turtles captured in the Atlantic near the St. Lucie power plant between 1976 and 2002, 49 were captured during the months of May through September (MB, unpubl. data).

Some information on the seasonality of juvenile green turtles in Florida is discussed in the section on geographic distribution. The seasonal abundance of foraging turtles seems to track water temperature. Green turtles in the Gulf of Mexico from Cedar Key northward and in Atlantic coastal lagoons from Mosquito Lagoon northward appear to move

Table 4-1. A summary of green turtle, *Chelonia mydas*, growth rates (cm/yr) by size class from the Western Atlantic. Growth rate (GR) is reported as mean ± one standard deviation.

	Florida						West Indies					
Size Class (cm SCL)	Hutchinson Island [a]		Mosquito Lagoon [b]		Broward County [c]		Great Inagua [d]		Puerto Rico [e]		U.S. Virgin Islands [f]	
	n	GR	*n*	GR	*n*	GR	*n*	GR	*n*	GR	*n*	GR
20-30	11	0.9 ± 0.9	–	–	–	–	–	–	4	3.6 ± 0.8	4	6.9 ± 2.9
30-40	105	2.2 ± 1.1	4	5.3 ± 2.8	13	3.5 ± 1.6	10	8.8 ± 1.0	6	5.1 ± 3.2	26	5.0 ± 1.7
40-50	76	2.5 ± 1.1	–	–	11	3.6 ± 2.9	40	4.9 ± 2.0	9	6.0 ± 1.8	12	4.7 ± 3.0
50-60	22	2.6 ± 0.8	2	3.1 ± 1.8	11	1.9 ± 1.9	67	3.1 ± 1.6	4	3.8 ± 1.0	5	3.5 ± 1.8
60-70	–	–	3	2.8 ± 1.2	–	–	22	1.8 ± 1.4	3	3.9 ± 3.5	2	1.9 ± ----
70-80	–	–	3	2.2 ± 1.1	–	–	9	1.2 ± 0.9	–	–	–	–

[a] updated from Bresette and Gorham (2001); [b] from Mendonca (1981); [c] calculated from Wershoven and Wershoven (1992); [d] from Bjorndal and Bolten (1988); [e] adapted from Collazo et al. (1992); [f] from Boulon and Frazer (1990).

south ahead of winter (FWC-FWRI Sea Turtle Stranding and Salvage database). These turtles are occasionally trapped by embayments with no southern exit and succumb to hypothermia when temperatures drop rapidly (Witherington and Ehrhart, 1989a). This type of entrapment resulted in an extensive early-winter cold stunning of green turtles in St. Josephs Bay, Gulf County, where the hook of St. Josephs Peninsula may either trap resident turtles or catch turtles attempting to move southward along the coast out of cooling panhandle waters (Summers et al., 2004).

Green turtles inhabiting bays and lagoons are uncommon in the northern regions of Florida during the late fall and winter months (J. Provancha, *pers. comm*.; E. McMichael, *pers. comm.*) and are most common in some southern regions during the winter and spring months (Ehrhart et al., 1996; Bresette et al., 2002), but these seasonal trends are not as pronounced in some nearshore Atlantic waters. Of more than 3900 juvenile green turtles captured from the Atlantic at the St. Lucie power plant between 1976 and 2004, 26% were captured during the fall, 29% during winter, 27% during spring, and 18% during the summer months (MB, unpubl. data). In comparison to green turtles inhabiting bays and lagoons, turtles in nearshore Atlantic waters are likely to experience more stable water temperatures, which may reduce the temperature-driven movements of juveniles.

Movements. — Although green turtles migrate extensively, they do not migrate continually. Green turtles go through extensive periods of residency and often have a tight fidelity to specific features in their environment. Tracking experiments in Mosquito Lagoon, Florida, and elsewhere have shown that juveniles make scheduled movements between specific diurnal foraging areas and nocturnal resting areas (Mendonca, 1983; Ogden et al., 1983). In Hawaii, Balazs (1982) has found that nearly all recaptures of green turtles tagged in foraging areas occur in the same resident neighborhood where they were originally captured.

Long-distance movements of juvenile green turtles may occur during seasonal migrations and during major shifts between developmental habitats (each described above). After juveniles settle into coastal foraging areas, their next large-scale movements may not take place until they near adulthood. Juveniles that have foraged in Florida waters are known to travel to subsequent developmental habitats throughout the Caribbean as far south as Nicaragua and as far east as the Dominican Republic (L. Ehrhart, unpubl. data).

Migrations of breeding adults between foraging areas and nesting beaches are the most frequent long-distance movements made by green turtles. Green turtles from other populations are known to travel hundreds or thousands of kilometers to nest. If, as suggested by satellite tracking results, the waters at the southern tip of the peninsula prove to be the principal foraging area for Florida's nesting green turtles, their breeding migrations to the major nesting beaches would range from less than 100 km to approximately 700 km.

One aspect of green turtle movement occurs within the nest. The socially facilitated thrashing of hatchlings in the nest results in their vertical movement 40–70 cm from clutch center to the surface. Low sand-surface temperature, predominantly at night, prompts the group of hatchlings to emerge *en masse* (Mrosovsky, 1968). Movement from nest to sea is guided by light cues. To hatchlings, the ocean is identified by a broad and comparatively bright horizon (Witherington and Martin, 2000). The time that a properly oriented group of hatchlings spends crawling from nest to sea is approximately 5–10 minutes.

Home Range. — Mendonca (1983) found that juvenile green turtles in Mosquito Lagoon moved within a range of approximately 3 km during warm-water periods and within a range of 5–10 km during cooler weather. Telemetry of adult green turtles in Florida suggests that their home ranges on foraging grounds are similarly small (B. Schroeder, *pers. comm.*).

GROWTH AND REPRODUCTION

Growth. — Estimates of age at sexual maturity based on wild growth rates indicate that green turtles take 20–40 yrs to reach adult size (Limpus and Walter, 1980; Frazer and Ehrhart, 1985; Frazer and Ladner, 1986; Bjorndal and Zug, 1995; Limpus and Chaloupka, 1997). Growth rates from green turtles in the western Atlantic are available from populations in Florida, the Bahamas, Puerto Rico, and the

U.S. Virgin Islands (Table 4-1). It is likely that the rates vary with differing diets, water temperatures, seasonal effects, and the age and health of turtles (Witham and Futch, 1977; Bjorndal and Bolten, 1988; Boulon and Frazer, 1990). Growth rates in Florida are known for turtles in both estuarine and nearshore waters (Table 4-1). Higher growth rates in estuarine waters may be related to availability of food (see below).

Some generalities about green turtle growth and maturation are that they grow more slowly as they age, and virtually cease to grow as adults. Green turtles require decades to reach maturity in the wild, have growth rates that vary with geography, and are very difficult if not impossible to accurately age as adults (Bjorndal and Zug, 1995).

Sexual Dimorphism. — In external appearance, immature males and females are essentially identical. Adults are sexually dimorphic. An adult male differs from an adult female by having a thick prehensile tail that extends far beyond the posterior margin of its carapace and by having a strongly recurved claw at the leading edge of each front flipper (the claws are straighter and shorter in females). On average, adult males are smaller than adult females by a few centimeters in carapace length (Limpus, 1993; Godley et al., 2002).

Courtship and Mating. — Courtship and mating in green turtles has been studied from both behavioral (Booth and Peters, 1972; Green, 2000) and genetic perspectives (Karl et al., 1992; Peare et al., 1994). Courtship and competitive interactions between green turtles suggest promiscuous mating with some level of female choice and occasionally high male-male competition.

Although male green turtles are known to mount any object with an approximate sea turtle size and shape (Ehrhart, 1982), encounters with actual females show extensive communication of receptivity or refusal. Males often approach females cautiously and nip at the female's neck and flippers before maneuvering to mount. Females will turn to face approaching males and may perform a number of behaviors to indicate receptivity or refusal. Booth and Peters (1972) concluded that females turning to a vertical body pitch with their plastron toward an approaching male are able to deny copulation to some males. Males that are successful in mounting typically approach females rapidly from behind, commonly at the surface, and hold their relatively soft, flexible plastron to the female's carapace. The male holds this position by hooking the recurved pollex claws of his foreflippers to the leading edge of the female's carapace, by grasping the rear margin of the carapace with the hallux claws of the hind flippers, and by curling his strong prehensile tail beneath the female where cloacae come into contact and intromission occurs. The bifurcated sperm duct of the male's penis allows semen to enter each of the female's oviducts (Miller, 1997).

Males may remain mounted for several hours. Where there is high competition between males, rival males may deliver severe biting injuries to the flippers, tail, and head of both mounted males and females that refuse copulation (Limpus, 1993). Copulation is often conspicuous in green turtles because of their tendency to mate just off nesting beaches and to float at the surface for long periods.

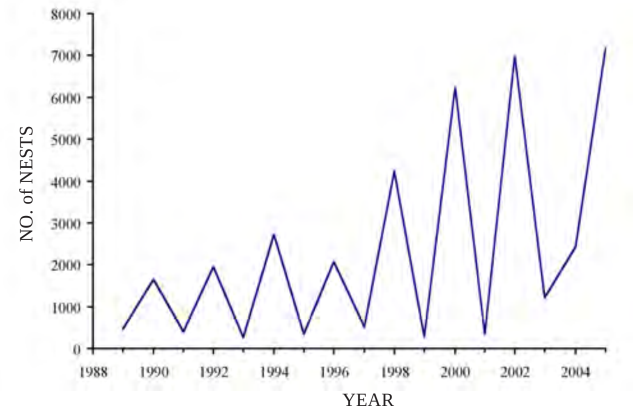

Figure 4-6. Annual green turtle, *Chelonia mydas*, nesting at core index beaches in Florida for the period 1989–2005. Nesting survey effort did not vary between years. Green turtle nests at core index beaches make up approximately 70% of total green turtle nesting in the state. Data are from Florida Fish and Wildlife Research Institute (FWC-FWRI) Statewide and Index Nesting Beach Survey databases; information found at http://research.myfwc.com/features/category_sub.asp?id=3618.

Green turtles are promiscuous breeders and multiple paternity is common (Peare et al., 1994). Males are not as philopatric (faithful to their natal beach) as are females, which leads to some male-mediated gene flow between nesting beaches (Karl et al., 1992). However, males in some populations are believed to be remarkably faithful to specific breeding sites (Limpus, 1993). Males breed with females both directly off nesting beaches and at courtship areas widely separated from nesting beaches. Because males make annual migrations to breeding sites more frequently than females (Balazs, 1980; Limpus, 1993), there is a potential for operational sex ratios to be biased toward males.

Nesting. — Female green turtles on nesting beaches crawl by moving their limbs simultaneously. This gait, the size of the turtle, and the length of its flippers and tail result in a unique track that can be distinguished from the tracks of other nesting turtles. Green turtle tracks average approximately 120 cm in width; have parallel flipper marks, including slashes from the front flippers at the margins of the track; and have a straight, thin, tail-drag mark down the center that is often punctuated by backward points between each limb stroke.

The appearance of a green turtle's nest site is dictated by her stereotypical behavior and by the nature of the sand substrate into which she has dug. Away from obstacles that could impede digging, a green turtle nest appears as a pit, approximately 2 m in diameter, at the base of an oval mound that is approximately 2 m by 3–5 m.

Remigration interval is the number of years between successive migrations to the nesting beach by reproductive females. Because the interval is measured by reobserving previously tagged turtles at the nesting beach, its measurement is subject to error from tag loss and incomplete beach coverage. Some error may also occur as observed remigration intervals are translated into reproductive cycles, because females with longer remigration intervals are more likely to die before they can be observed again on the beach (Frazer, 1989). The estimated remigration interval is predominately two years in Florida (Witherington and Ehrhart, 1989b; Johnson and Ehrhart, 1994). Among the world's green turtle populations, modal remigration intervals range from 2 to 5 years (Hirth, 1997). The two-year interval for Florida green turtles matches a clear biennial pattern of high and low nesting years (Fig. 4-6).

Nesting females emerge onto beaches at night and are susceptible to being turned away by a human approach. Although undisturbed green turtles will complete approximately half of their nesting attempts, females in the site-preparation stage of their nesting behavior, prior to egg-laying, seldom continue their attempt if they detect a moving person (BW, *pers. obs*.). A description of the two-hour nesting process can be found in Hirth and Samson (1987). Green turtles spend approximately 40% of this time preparing the nest site, 13% of the time laying eggs, and 47% of the time covering and camouflaging the site.

Clutch frequency is the number of nests deposited by a female in a single season. As with estimation of remigration intervals, error in estimating clutch frequency can result from tag loss and incomplete beach coverage. Fortunately, the interval between nestings is relatively constant at 9–15 days (Hirth, 1997), which allows an identification of some missed nests, except for the first and last nests of the season. Because beach monitors are likely to miss some nests, clutch frequencies are generally underestimated. Johnson and Ehrhart (1994) reported clutch frequency in Florida green turtles to be an average of 3.6 nests per season. Average clutch frequency among green turtle populations worldwide ranges from 2.0 to 5.5 nests per season (Hirth, 1997).

Clutch Size. — Although the average number of eggs per clutch within a population is remarkably constant between years (Bjorndal and Carr, 1989), average clutch size can vary considerably between populations. At 13 widely separated beaches examined by Hirth (1980), average clutch size ranged from 104 to 147 eggs. In Florida, green turtle clutches average 136 eggs (90–199 eggs, *n* = 130; Witherington and Ehrhart, 1989b).

Judging by successive observations of green turtles on nesting beaches, there is a slight but significant increase in clutch size with age (Bjorndal and Carr ,1989) and a moderate increase in clutch frequency with age (Bjorndal 1980). However, it is unclear how fecundity may vary throughout the reproductive lifespan of a green turtle and whether they may ever reach reproductive senility. Among the longest spans that green turtles have been repeatedly observed nesting are 20 years (Tortuguero; Carr et al., 1978) and 22 years (Heron Island, Great Barrier Reef; FitzSimmons et al., 1995). These observations are a function of the persistence of tags as well as turtles and likely underestimate possible reproductive longevity. There is also the possibility that these long-term observations are of outliers that would provide an overestimate of actual reproductive longevity.

Incubation and Hatching. — Length of incubation period is inversely correlated with nest temperature. On a relatively sunny but temperate beach in Florida, most nests were found to incubate 52–56 days before producing hatchlings (Witherington, 1986), and at a rainy, tropical beach in Costa Rica, this period was commonly 60–65 days (Horikoshi, 1992). Some Florida clutches deposited in September and incubated through rainy and cool periods may take nearly four months to produce hatchlings. Hatchling green turtles are approximately one six-thousandth the weight of an adult. Ehrhart (1980) measured 560 green turtle hatchlings from 28 nests at an east-central Florida beach and reported sizes ranging from 21 to 37 g and from 4.4 to 5.8 cm SCL.

Hatchling Behavior. — Green turtles take part in important intraspecific interactions immediately after escaping their eggshells. In the nest, hatchlings thrash in coordinated periodic bouts that cause sand above the turtles to fall beneath them. This activity results in group-movement toward the surface and eventual escape from the nest (Carr

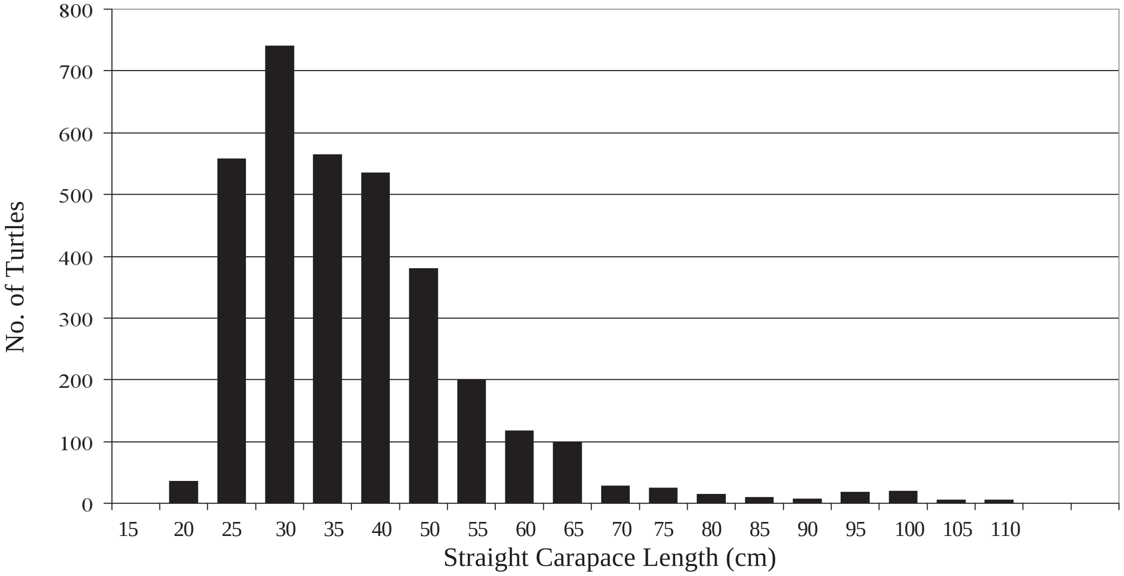

Figure 4-7. Size frequencies (in 5-cm SCL ranges [15–19, 20–24, etc.]) of green turtles, *Chelonia mydas*, captured at the St. Lucie power plant at Hutchinson Island, Florida, 1976–2002 (*n* = 3354) (MB, unpubl. data).

and Hirth, 1961). This brief collaboration, what Carr (1967) described as “mindless teamwork,” ends when hatchlings scramble out of the nest and move toward the water. Once in the open ocean, contact between neonate turtles is probably as rare as encounters between any other group of drifting objects. It is not until they recruit to shallow coastal feeding grounds where juveniles concentrate that there are opportunities for interactions with other green turtles.

POPULATION BIOLOGY

Population Structure. — Green turtles in Florida coastal waters range from 25 to 110 cm SCL, with a size distribution that is skewed toward smaller size-classes (Fig. 4-7). This size-class distribution also gives an indication of the variable size at which green turtles arrive in neritic habitats, the variable size at which they leave for other developmental habitats, and the size of adults that have seasonally returned to breed (Fig. 4-7).

The sex ratio of green turtle hatchlings is determined by incubation temperature: higher incubation temperatures produce mostly females, and lower temperatures produce mostly males. The pivotal temperature for green turtles (at which a 1:1 ratio occurs) is approximately 28.5–30.3ºC (Spotila et al., 1987). Despite the potential for skewed sex ratios in individual populations, there is little reason to believe that primary sex ratio (the ratio at fertilization) measured over a sufficiently long period will not conform to the 1:1 ratio predicted by theory (Fisher, 1930). Over the short term, however, sex ratio at hatching is often different from 1:1 and is observed to vary with geography, nest placement, time of the season, and weather. At Tortuguero, Spotila et al. (1987) estimated hatchling sex ratio during a relatively dry year to be 67% female, and Horikoshi (1992) estimated this ratio during a relatively wet year to be only 10% female. At Heron Island, green turtle nests on the warmer, north-facing side of the island produced 63% females, and nests on the cooler, south side of the island produced 30% females (Limpus et al., 1983).

Green turtle sex ratios examined on foraging grounds have been found to be approximately 1:1 at a variety of sites: Bermuda (Meylan et al., 1992), the southern Bahamas (Bolten et al., 1992), Heron Reef (Limpus and Reed, 1985), and Hawaii (Wibbels et al., 1993). However, sex ratios that are considerably female-biased (approximately two-thirds female) are observed at both Indian River Lagoon, Florida (Schroeder and Owens, 1994), and Moreton Banks, southeastern Queensland, Australia (Limpus et al., 1994).

Survivorship. — Survivorship of eggs is highly variable both within and among Florida nesting beaches. The rate is affected predominantly by predation, especially from raccoons, and by acute beach erosion such as that caused by heavy surf from tropical weather systems. Average annual survival from egg to hatchling on beaches of south Brevard County (beaches having approximately 40% of Florida’s nesting) has ranged 26–75% (Witherington, 1986; Redfoot and Ehrhart, 1989; Johnson and Ehrhart, 1994, FWC-FWRI hatchling production database). In 2001, egg-to-hatchling survivorship was 29%, determined from a weighted mean of 227 nests on representative beaches between Brevard and Broward counties. In a subsample of those nests not affected by erosion from a late-season tropical storm, survival from egg to hatchling was 53% (FWC-FWRI hatchling production database).

Hatchling survivorship is poorly known. On naturally lighted beaches, the proportion of eggs that result in hatchlings that enter the sea is often close to the proportion of eggs that hatch in the nest (Witherington, 1986; Horikoshi, 1992). However, artificial lighting, which disrupts hatchlings’ seaward movement and draws them into the dune or other hazards, can cause some nests to have 100% mortality among emerging hatchlings. Predation by fish in the surf and nearshore zones may be extensive. Gyuris (1994) reported that fish-predation mortality of green turtle hatchlings leaving the beach at Australia’s Great Barrier Reef was 31%.

Although it is reasoned that mortality from predation lessens once young green turtles leave the nearshore zone, predation and survival at sea have not been adequately measured. Indications in the FWRI Sea Turtle Stranding and Salvage database are that many human-caused and seemingly size-independent factors (entanglement, boat strikes) result in juvenile green turtle mortality. Tag returns from Florida green turtles taken by directed fisheries in other countries reveal that levels of human predation may be high (L. Ehrhart, unpubl. data).

Bjorndal (1980) reported that approximately 60–90% of all nesters observed at Tortuguero during the period 1969 to 1978 were new recruits. From 14 cohorts of adult females, Bjorndal calculated that instantaneous death rates (d) ranged from 29 to 51%. This low survivorship was thought to be due to extensive exploitation at the Costa Rica nesting beach and on Nicaraguan foraging grounds (approximated at the time to be 25% of all adults harvested annually). Because adult green turtles nesting in Florida are protected from harvest on beaches and throughout most of the areas where they forage, their survival is likely to be higher than that of the Tortuguero population.

Based upon net reproductive rate and adult abundance (from Carr et al., 1978), Bjorndal (1980) calculated that the proportion of Tortuguero green turtle eggs surviving to adulthood that would maintain a stable population was approximately one in 250. This estimate may be high if the Tortuguero population was declining rather than stable during the period that the estimate was made (Frazer ,1986).

INTERSPECIFIC INTERACTIONS

Diet and Feeding. — Post-hatchlings begin feeding in oceanic surface waters on both plant and animal material. In turtles of this size-class that have stranded during storms, ingested material is predominantly *Sargassum* and many of the hydroids, bryozoans, and polychaetes found living attached to this floating brown alga (BW, unpubl. data). Other commonly ingested animals include surface-drifting cnidarians, such as the blue-button (*Porpita*) and by-the-wind sailor (*Velella*). Most stranded post-hatchlings have also consumed significant amounts of plastics or tar (BW, unpubl. data).

When juvenile green turtles enter coastal waters after reaching 20–30 cm SCL they make a dietary shift to herbivory. From this stage through adulthood, green turtles in Florida feed almost exclusively on seagrasses and macroalgae. This diet shift is marked by a lengthening of the large intestine relative to the small intestine by a factor of four (Davenport et al., 1989). The large gut in green turtles accommodates a high-volume cellulose diet; digestion is aided by microbial fermentation (Bjorndal, 1979). Gut microflorae are believed to be specific to either seagrasses or macroalgae; turtles feeding on both are thought to lose digestive efficiency (Bjorndal, 1985).

Holloway-Adkins (2001) compared the diet of juvenile green turtles from five foraging areas on Florida's east coast and found differences in diet based largely on availability. Turtles from Mosquito Lagoon fed predominantly on seagrasses (chiefly manatee grass, *Syringodium filiforme*), turtles from two Indian River Lagoon sites fed on either seagrasses (five species) or macroalgae (chiefly red algae, *Rhodophyta*), and turtles foraging on hard substrates at Port Canaveral and nearshore reefs ate mostly red algae.

Holloway-Adkins found only a small (0–4% by volume) amount of ingested animal material and concluded that this part of the diet was incidental. However, examples of green turtles feeding on fish and squid in captivity and observations of wild green turtles feeding on fish caught in nets and on baited hooks suggest that green turtles opportunistically take animal food (BW, *pers. obs*.).

Predation. — The vast majority of predation on green turtles occurs when they are within eggs and as hatchlings. In 2001, 28 of 229 monitored nests on east Florida beaches were invaded by identifiable predators (FWC-FWRI hatchling production database). Identified predators listed in order of number of eggs destroyed are: raccoons (*Procyon lotor*), ghost crabs (*Ocypode quadrata*), and nine-banded armadillos (*Dasypus novemcinctus*). Predation on properly oriented hatchlings on the beach is probably low.

Predation on small green turtles in the water is thought to be high, but the only well documented predation by fishes in Florida is Witham's (1974) account of predation by dolphinfish (*Coryphaena hippurus*). Fish predation over the relatively featureless bottom near most Florida nesting beaches may not occur to the extent seen off Great Barrier Reef islands (Gyuris, 1994). Most predation on Florida hatchlings may occur in open ocean waters as Witham's report indicates.

There are numerous records of shark-bite injuries to green turtles stranded in Florida (FWC-FWRI Sea Turtle Stranding and Salvage database), but it is unclear in most cases whether the sharks were preying or scavenging (i.e., whether bites occurred before or after death). Two observations of tiger sharks (*Galeocerdo cuvier*) eating green turtles in Florida waters (MB, unpubl. data; L. Ehrhart, unpubl. data) are similarly unclear, although it is reasonable to assume that such a large shark could easily catch and consume a live green turtle.

THREATS

Florida's sea turtle species and sea turtles worldwide share similar threats. Thorough descriptions of the threats to sea turtles can be found in Parsons (1962), NRC (1990), NMFS and USFWS (1991), Lutcavage et al. (1997), and Thorbjarnarson et al. (2000). Two threats particularly acute in Florida are the artificial lighting of nesting beaches and the high frequency of fibropapilloma disease.

Artificial lighting that is visible from the beach discourages females from emerging onto the beach to nest (Witherington, 1992a) and disrupts the orientation of hatchlings in their attempt to find the sea after emerging from their nest (Witherington, 1997). Because light pollution has been shown to change spatial nesting patterns (Salmon et al., 2000) and cause mass mortality in misdirected hatchlings (Witherington, 1997), managing light on sea turtle nesting beaches has become an important conservation goal.

In part, hatchlings reach the sea by orienting toward the brightest horizon (Verheijen and Wildschut, 1973; Mrosovsky and Kingsmill, 1985; Salmon et al., 1992;

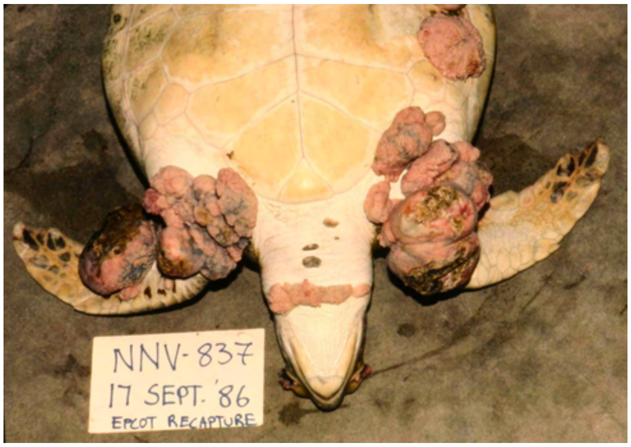

Figure 4-8. A juvenile green turtle, *Chelonia mydas*, with fibropapilloma lesions, from the Indian River Lagoon System, Brevard County, Florida. Photo by Blair Witherington.

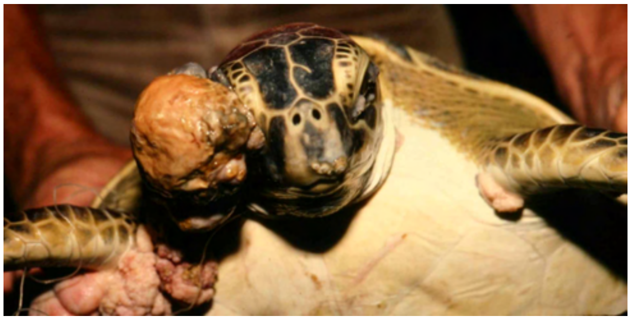

Figure 4-9. A juvenile green turtle, *Chelonia mydas*, with fibropapilloma lesions, from the Indian River Lagoon System, Brevard County, Florida. Photo by Blair Witherington.

Witherington, 1992b; Witherington and Martin, 2000). The brightness of artificial lighting can lead hatchlings away from the sea and leave them vulnerable to dehydration, exhaustion, and predation. The problem is particularly evident on Florida's developed beaches. Statewide, approximately 20% of sea turtle nests show signs that the hatchlings emerging from them were misdirected by lighting (Witherington et al., 1996). Although hatchling mortality from this misdirection is uncertain, this rate may reach 50% of misdirected hatchlings (10% of all hatchlings). Additional debilitating effects may occur in hatchlings that reach the water after prolonged, misdirected crawling on the beach. Witherington (1997) estimated that hundreds of thousands of hatchling sea turtles are killed as a result of artificial lighting in Florida each year.

Sea turtles worldwide are threatened by a tumor disease that produces fibropapilloma growths on the skin and internal organs (Figs. 4-8, 4-9) (for reviews see Jacobson et al., 1991; Herbst, 1994; Herbst and Jacobson, 1995). Although fibropapilloma tumors were first observed in green turtles from the Florida Keys in the 1930s (Smith and Coates, 1938), the disease was subsequently unreported until the 1980s. Fibropapilloma tumors are now common in green turtles and are regularly found in loggerheads; cases of tumors have been reported in both species at several locations around the state (Foley et al., 2005). Two hotspots for the disease are the Indian River Lagoon and Florida Bay, estuarine waters where more than half of all captured green turtles show external fibropapilloma tumors (Ehrhart, 1991; Schroeder et al., 1998). Fibropapillomas growing on the skin and eyes of green turtles can become pendulous and abraded and reach 30 cm in diameter (Herbst, 1994).

Fibropapilloma tumors are clearly linked to debilitation and death of turtles although the rate of survival in afflicted turtles is uncertain. In 4519 green turtles that stranded dead or debilitated between 1980 and 1998, Foley et al. (2005) reported no fibropapilloma tumors in green turtles that stranded north of 29º N (southern Volusia County), but south of 29ºN, 23% of 2990 stranded turtles had tumors. Turtles with fibropapillomas were more likely to be emaciated or tangled in debris such as fishing line. Tumors were rare in the smallest and largest juveniles, which may indicate that juveniles acquire the disease after recruiting to coastal waters and that older juveniles either die or recover from the disease.

STATUS

The Florida population of green turtles is listed as Endangered by criteria of both FCREPA (Ehrhart and Witherington, 1992) and the U.S. Endangered Species Act (NMFS and USFWS, 1991). Both Witherington and Ehrhart (1989b) and Ehrhart and Witherington (1992) presented status reviews for Florida. In a recent global status review, Seminoff (2002) estimated that green turtle populations worldwide have declined 37 to 61% in the last three generations and that according to the 2001 IUCN Red List Criteria, a status of Endangered was justified.

It is unclear how greatly green turtle nesting in Florida has been reduced from historical levels (Dodd, 1981), although one account indicates that nesting in Florida's Dry Tortugas may now be only a small fraction of what it once was (Audubon, 1926). Total nest counts and trends at index beach sites during the past 15 years suggest that Florida green turtles are recovering (Fig. 4-6), but only in the previous decade has nesting reached an average of greater than 1000 nests per year (Meylan et al., 1995; FWC-FWRI Statewide Nesting Beach database, http://research.myfwc.com/features/category_sub.asp?id=3618). Increases in Florida green turtle nesting mirror trends seen at the largest western Atlantic nesting colony, Tortuguero, Costa Rica (Bjorndal et al., 1999).

The two-year remigration interval for Florida green turtles warrants combining biennial nesting cohorts to get total counts. With the additional assumption of four nests per female per year (Johnson and Ehrhart, 1994), we calculate that the number of reproductively active females in Florida ranged from 2200 to 2600 between 1999 and 2002. However, methodological limitations make the clutch frequency number (4 nests/female/year) an underestimate, and the true number of green turtles nesting in Florida may be as low as half of the estimate above.

Counting green turtles foraging in Florida waters is difficult because there are few sites where in-water monitoring protocols are standardized. Perhaps the most reliable sampling of foraging green turtles comes from the St. Lucie power plant. The power plant's intake canal has drawn water and turtles from the nearshore Atlantic since 1977. Between 1977 and 2002, 3557 green turtles have been captured (the vast majority were released without injury). The annual rate of capture of immature green turtles (SCL < 90 cm) has increased significantly during the 26-year period ($r^2 = 0.48$, $p < 0.001$) (MB, unpubl. data).

Despite the recent encouraging trends in the abundance of Florida's green turtles, we are cautious about changes in status designation and in conclusions about how far the population has progressed toward recovery. In our opinion, Florida green turtle populations remain depleted, and additional severe threats to their survival have become apparent. Monitoring throughout the next two or three decades would complete an assessment through an entire generation of green turtles and would reveal whether these additional threats will alter the recovery that seems to be developing.

CONSERVATION OPTIONS AND SOLUTIONS

The most important factor that has moved Florida green turtles toward recovery is probably the protection afforded them in 1978 by the listing of this population under the U.S. Endangered Species Act. Directed take has been prohibited in the U.S. for a period approaching a green-turtle generation, and this has yielded striking results (see the section on status above). But as direct take has diminished, indirect threats have increased, including adverse effects from an ever-broadening array of human activities.

Milestones in addressing indirect threats and incidental deaths of green turtles in Florida include the promulgation of local ordinances banning lighting of nesting beaches. At this writing, approximately 95% of Florida sea turtle nesting takes place on beaches with light-pollution ordinances, although effective enforcement of these laws remains spotty, and some ordinances provide minimal protections. Another important conservation milestone took place in 1995, when entangling nets that were known to drown juvenile green turtles were prohibited in Florida waters. Other conservation efforts are ongoing, such as the acquisition of beachfront properties for protection within refuges such as the Archie Carr National Wildlife Refuge in Brevard and Indian River counties.

Recommended actions for green turtle conservation in Florida include continuing the local efforts described above and expanding international efforts to reduce take. Because green turtles found in Florida waters have spent and will spend significant portions of their lives in other countries and in international waters, conservation efforts outside Florida are as important as conservation efforts within the state. Key to reducing commercial and indirect take outside Florida are international agreements such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, Washington, 1973), the Convention on the Conservation of Migratory Species of Wild Animals (CMS, Bonn, 1979), the Inter-American Convention on the Protection and Conservation of Sea Turtles (IAC, Caracas, 1996), and the Cooperative Agreement for the Conservation of Sea Turtles of the Caribbean Coast of Costa Rica, Nicaragua, and Panama (Tri-Partite Agreement, San José, 1998).

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LITERATURE CITED

Allard, M. W., M. M. Miyamoto, K. A. Bjorndal, A. B. Bolten, and B. W. Bowen. 1994. Support for natal homing in green turtles from mitochondrial DNA sequences. Copeia 1994: 34-41.

Audubon, J. J. 1926. The Turtlers. Pp. 194-202 In: Delineations of American Scenery and Character, G.A. Baker and Co., New York.

Balazs, G. H. 1980. Synopsis of Biological Data on the Green Turtle in the Hawaiian Archipelago. NOAA Technical Memorandum NMFS. NOAA-TM-NMFS-SWFC-7.

Balazs, G. H. 1982. Growth rates of immature green turtles in the Hawaiian Archipelago. In: K. A. Bjorndal (Ed.). Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Washington DC, pp. 117-125.

Bass, A. L., and W. N. Witzell. 2000. Demographic composition of immature green turtles (*Chelonia mydas*) from the east central Florida coast: evidence from mtDNA markers. Herpetologica 56:357-367.

Bass, A. L., C. J. Lagueux, and B. W. Bowen. 1998. Origin of green turtles, *Chelonia mydas*, at 'Sleeping Rocks' off the northeast coast of Nicaragua. Copeia 1998:1064-1069.

Bjorndal, K.A. 1979. Cellulose digestion and volatile fatty-acid production in the green turtle *Chelonia mydas*. Comparative Biochemistry and Physiology A 63:127-134.

Bjorndal, K.A. 1980. Demography of the breeding population of the green turtle, *Chelonia mydas*, at Tortuguero, Costa Rica. Copeia 1980:525-530.

Bjorndal, K.A. 1985. Nutritional ecology of sea turtles. Copeia 1985:736-751.

Bjorndal, K. A., and A. B. Bolten. 1988. Growth rates of immature green turtles *Cheloniamydas* on feeding grounds in the southern Bahamas. Copeia 1988:555-564.

Bjorndal, K. A., and A. Carr. 1989. Variation in clutch size and egg size in the green turtle nesting population at Tortuguero, Costa Rica. Herpetologica 45:181-189.

Bjorndal, K. A., and G. A. Zug. 1995. Growth and age of sea turtles. In: K. A. Bjorndal (Ed.). Biology and Conservation of Sea Turtles (Revised Edition). Smithsonian Institution Press, Washington DC, pp. 599-600.

Bjorndal, K. A., J. A. Wetherall, A. B. Bolten, and J. A. Mortimer. 1999. Twenty-six years of green turtle nesting at Torutguero, Costa Rica: an encouraging trend. Conservation Biology 13:126-134.

Bjorndal, K. A., A. Bolten and M. Y. Chaloupka. 2000. Green turtle somatic growth model: evidence for density dependence. Ecological Applications. 10(1), Pp. 269-282.

Bocourt, M. 1868. Description de quelques cheloniens nouveaux appartenant a la faune Mexicaine. Annales des Sciences Naturelles Zoologie et Biologie Animale 10:121-122.

Bolten, A. B., K. A. Bjorndal, S. Grumbles, and D. W. Owens. 1992. Sex ratio and sex-specific growth rates of immature green turtles, *Chelonia mydas*, in the southern Bahamas. Copeia 1992: 1098-1103.

Booth, J., and J. A. Peters. 1972. Behavioral studies on the green turtle (*Chelonia mydas*) in the sea. Animal Behaviour 20:808-812.

Boulon, R.H., Jr., and N. B. Frazer. 1990. Growth of wild juvenile Caribbean green turtles, *Chelonia mydas*. Journal of Herpetology 24: 441-445.

Bowen, B.W., and S. A. Karl. 2000. Meeting report: Taxonomic status of the East Pacific green turtle (*Chelonia agassizii*). Marine Turtle Newsletter No. 89: 20-22.

Bowen, B.W., A. B. Meylan, J. P. Ross, C. J. Limpus, G. H. Balazs, and J. C. Avise. 1992. Global population structure and natural history of the green turtle (*Chelonia mydas*) in terms of matriarchal phylogeny. Evolution 46: 865-881.

Bresette, M.J. and J.C. Gorham. 2001. Growth rates of juvenile green turtles (*Chelonia mydas*) from Atlantic coastal waters of St. Lucie County, Florida, USA. Marine Turtle Newsletter No. 91:5-6

Bresette, M. J., J.C. Gorham, and B.D. Peery. 1998. Site fidelity and size frequencies of juvenile green turtles (*Chelonia mydas*) utilizing nearshore reefs in St. Lucie County, Florida. Marine Turtle Newsletter. No.82:5-7

Bresette, M.J., J.C. Gorham, and B.D. Peery. 2002. Initial assessment of sea turtles in the southern Indian River Lagoon System, Ft. Pierce Florida. In: Mosier, A., A. Foley and B. Brost, (compilers). Proceedings of the Twentieth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-477:271-273.

Caldwell, D. K. 1969. Hatchling green sea turtles *Chelonia mydas* at sea in the northeastern Pacific Ocean. Bulletin of the Southern California Academy of Sciences 68: 113-114.

Caldwell, D. K., and A. Carr. 1957. Status of the sea turtle fishery in Florida. Transactions of the 22nd North American Wildlife Conference, 457-463.

Carr, A. 1967. So Excellent a Fishe. Charles Scribner's Sons, New York.

Carr, A. 1987. New perspectives on the pelagic stage of sea turtle development. Conservation Biology 1: 103-121.

Carr, A. F., M. H. Carr, and A. B. Meylan. 1978. The ecology and migrations of sea turtles, the west Caribbean green turtle colony. Bulletin of the American Museum of Natural History 162: 1-46.

Carr, A., and H. Hirth. 1961. Social facilitation in green turtle siblings. Animal Behaviour 9:68-70.

Carr, A. and A. B. Meylan. 1980. Evidence of passive migration of green turtle hatchlings in *Sargassum*. Copeia 1980: 366-368.

Collazo, J. A., R. Boulon, Jr., and T. L. Tallevast. 1992. Abundance and growth patterns of *Chelonia mydas* in Culebra, Puerto Rico. J. Herpetol. 26: 293-300.

Davenport, J., S. Antipas, and E. Blake. 1989. Observations of gut function in young green turtles, *Chelonia mydas* L. Herpetological Journal 1: 336-342.

Dodd, C. K. 1981. Nesting of the green turtle, *Chelonia mydas* (L.), in Florida: historic review and present trends. Brimleyana 7: 39-54.

Ehrhart, L. M. 1980. A survey of marine turtles nesting at the Kennedy Space Center Cape Canaveral Air Force Station, North Brevard County, Florida. Report to Division of Marine Resources, Florida. 216 pp.

Ehrhart, L. M. 1982. A review of sea turtle reproduction. In: K. A. Bjorndal (Ed.). Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Washington DC. pp. 29-38.

Ehrhart, L. M. 1983. Marine turtles of the Indian River Lagoon System. Florida Sci. 46: 337-346.

Ehrhart, L. M. 1991. Fibropapillomas in green turtles of the Indian River Lagoon, Florida: Distribution over time and area. In: G. H. Balazs and S. G. Pooley (Eds.), Research plan formarine turtle fibropapilloma, U.S. Department of Commerce, NOAA Technical MemorandumNMFS-SWFSC-156: 59-61.

Ehrhart, L. M., and B. E. Witherington. 1992. Green turtle. In: P. E. Moler (Ed.). Rare and Endangered Biota of Florida, Volume III. Amphibians and Reptiles. University Presses of Florida, Gainesville, pp. 90-94.

Ehrhart, L. M., W. E. Redfoot, and D. A. Bagley. 1996. A study of the population ecology of in-water marine turtle populations on the east-central Florida coast from 1982-96. Comprehensive Final Report To NOAA , National Marine Fisheries Service, Miami, Florida.

Fisher, R. A. 1930. The Genetical Theory of Natural Selection. Oxford University Press.

FitzSimmons, N. N., A. D. Tucker, and C. J. Limpus. 1995. Long-term breeding histories of male green turtles and fidelity to a breeding ground. Marine Turtle Newsletter 68: 2-4.

Foley, A. M., B. A. Schroeder, A. E. Redlow, A. E., K. J. Fick-Child, and W. G. Teas. 2005. Fibropapillomatosis in stranded green turtles (*Chelonia mydas*) from the eastern United States (1980-98): Trends and associations with environmental factors. Journal of Wildlife Diseases 41: 29-41.

Frazer, N. B. 1986. Survival from egg to adulthood in a declining population of loggerhead turtles, *Caretta caretta*. Herpetologica 42: 47-55.

Frazer, N. B. 1989. Nesting cycles in sea turtles: typical, but not cycles. In: S. A. Eckert, K. L. Eckert, and T. H. Richardson (compilers). Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology, NOAA Technical Memorandum NMFS-SEFC-232: 61-64.

Frazer, N. B. and L. M. Ehrhart. 1985. Preliminary growth models for green, *Chelonia mydas*, and loggerhead, *Caretta caretta*, turtles in the wild. Copeia 1985: 73-79.

Frazer, N. B. and R. C. Ladner. 1986. A growth curve for green sea turtles, *Chelonia mydas*, in the U.S. Virgin Islands, 1913-1914. Copeia 1986: 798-802.

Godley, B. J., A. C. Broderick, R. Frauenstein, F. Glen, and G. C. Hays. 2002. Reproductive seasonality and sexual dimorphism in green turtles. Marine Ecology Progress Series 226: 125-133.

Green, D. 2000. Mating behavior in Galapagos green turtles. In: Kalb, H. J., and T. Wibbels (Compilers). Proceedings of the Nineteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-443:3-5.

Groombridge, B., and R. Luxmoore. 1989. The Green Turtle and Hawksbill (Reptilia: Cheloniidae): World Status, Exploitation and Trade. Secretariat of the Convention on International Trade in Endangered Species of Wild Fauna and Flora. Lausanne, Switzerland.

Guseman, J. L., and L. M. Ehrhart. 1990. Green turtles on sabellariid worm reefs: initial results from studies on the Florida Atlantic coast. In: T. H. Richardson, J. I. Richardson, and M. Donnelly (compilers). Proceedings of the Tenth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFC-278: 125-127.

Gyuris, E. 1994. The rate of predation by fishes on hatchlings of the green turtle (*Chelonia mydas*). Coral Reefs 13: 137-144.

Herbst, L. H. 1994. Fibropapillomatosis in marine turtles. Annual Review of Fish Diseases 4:389-425.

Herbst, L. H., and E. R. Jacobson. 1995. Diseases of marine turtles. In: K. A. Bjorndal (Ed.). Biology and Conservation of Sea Turtles (Revised Edition). Smithsonian Institution Press, Washington DC. pp. 593-596.

Hirth, H. F. 1997. Synopsis of the biological data on the green turtle Chelonia mydas (Linnaeus 1758). Biological Report 97(1), Fish and Wildlife Service, U.S. Dept of the Interior. 120 pp.

Hirth, H. F. 1980. Some aspects of the nesting behaviour and reproductive biology of sea turtles. American Zoologist 20: 507-523.

Hirth, H. F., and D. A. Samson. 1987. Nesting behavior of green turtles (*Chelonia mydas*) at Tortuguero, Costa Rica. Caribbean Journal of Science 23: 374-379.

Holloway-Adkins, K. G. 2001. A comparative study of the feeding ecology of *Chelonia mydas* (green turtle) and the incidental ingestion of *Prorocentrum* spp. Unpubl. M.S. thesis, University of Central Florida, Orlando, Florida. 138 pp.

Horikoshi, K. 1992. Egg survivorship and primary sex ratio of green turtles, *Chelonia mydas*, at Tortuguero, Costa Rica. Unpubl. Ph.D.

dissertation, University of Florida, Gainesville, Florida. 157 pp.

Jackson, J.B.C. 1997. Reefs since Columbus. Coral Reefs 16, Supplement S23-S33.

Jackson, J.B.C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293: 629-638.

Jacobson, E. R., S. B. Simpson, Jr., and J. P. Sundberg. 1991. Fibropapillomas in green turtles. In: G. H. Balazs, and S. G. Pooley (Eds.). Research Plan for Marine Turtle Fibropapilloma, NOAA-TM-NMFS-SWFSC-156: 99-100.

Johnson, S. A., and L. M. Ehrhart. 1994. Nest-site fidelity of the Florida green turtle. In: B. A. Schroeder and B. E. Witherington (compilers). Proceedings of the Thirteenth Annual Symposium on Sea Turtle Biology and Conservation, NOAA Technical Memorandum NMFS-SEFSC-341: 83.

Karl, S. A., B. W. Bowen, and J. C. Avise. 1992. Global population genetic structure and male-mediated gene flow in the green turtle (*Chelonia mydas*): RFLP analyses of anonymous nuclear loci. Genetics 131: 163-173.

Lahanas, P. N., M. M. Miyamoto, K. A. Bjorndal, and A. B. Bolten. 1994. Molecular evolution and population genetics of Greater Caribbean green turtles (*Chelonia mydas*) as inferred from mitochondrial DNA control region sequences. Genetica 94:57-67.

Limpus, C. J. 1993. The green turtle, *Chelonia mydas*, in Queensland: breeding males in the Southern Great Barrier Reef. Wildlife Research 20: 513-523.

Limpus, C. J., and M. Chaloupka. 1997. Nonparametric regression modeling of green sea turtle growth rates (southern Great Barrier Reef). Marine Ecology Progress Series. 149: 23-34.

Limpus, C. J., and P. C. Reed. 1985. The green turtle, *Chelonia mydas* in Queensland: a preliminary description of the population structure in a coral reef feeding ground. In: G. Grigg, R. Shine, and H. Ehmann (Eds.). Biology of Australasian Frogs and Reptiles. Surrey Beatty and Sons, and the Royal Zoological Society of New South Wales. pp. 47-52.

Limpus, C. J., and D. G. Walter. 1980. The growth of immature green turtles (*Chelonia mydas*) under natural conditions. Herpetologica 36: 162-165.

Limpus, C. J., P. Reed, and J. D. Miller. 1983. Islands and turtles. The influence of choice of nesting beach on sex ratio. In: J. T. Baker, R. M. Carter, P. W. Sammarco, and K. P. Stark (Eds.). Proceedings of the Inaugural Great Barrier Reef Conference, ISBN 0-86443-128-7. pp. 397-402.

Limpus, C. J., P. J. Couper, and M. A. Read. 1994. The green turtle, *Chelonia mydas*, in Queensland: population structure in a warm temperate feeding area. Memoirs of the Queensland Museum 35: 139-154.

Lutcavage, M. E., P. Plotkin, B. E. Witherington, and P. L. Lutz. 1997. Human impacts on sea turtle survival. In: Lutz, P. L., and Musick, J. A. (Eds.). The Biology of Sea Turtles. CRC Marine Science Series, CRC Press. pp 387-409

Mellgren, R. L., and M. A. Mann. 2000. Do green turtles learn about foraging from conspecifics? In: Proceedings of the Nineteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-443. Pp.6-7.

Mendonca, M. T. 1981. Comparative growth rates of wild immature *Chelonia mydas* and *Caretta caretta* in Florida. Journal of Herpetology 15: 447-451.

Mendonca, M. T. 1983. Movements and feeding ecology of immature green turtles *(Chelonia mydas*) in a Florida lagoon. Copeia 1983: 1013-1023.

Meylan A. B., B. W. Bowen, and J. C. Avise. 1990. A genetic test of the natal homing versus social facilitation models for green turtle migration. Science 248: 724-727.

Meylan, A. B., P. A. Meylan, H. C. Frick, and J. N. Burnett-Herkes. 1992. Population structure of green turtles (*Chelonia mydas*) on foraging grounds in Bermuda. In: M. Salmon and J. Wyneken (compilers). Proceedings of the Eleventh Annual Workshop on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFC-302: 73.

Meylan, A., B. Schroeder, and A. Mosier. 1995. Sea turtle nesting activity in the State of Florida 1979-1992. Florida Marine Research Publications 52: 1-51.

Miller, J. D. 1997. Reproduction in sea turtles. In: P.L. Lutz, and J. A. Musick (Eds.). The biology of sea turtles. CRC Marine Science Series, CRC Press. pp. 51-81

Mrosovsky, N. 1968. Nocturnal emergence of hatchling sea turtles: control by thermal inhibition of activity. Nature 220: 1338-1339.

Mrosovsky, N., and S. F. Kingsmill. 1985. How turtles find the sea. Zeitschrift fur Tierpsychologie 67:237-256.

Musick, J. A., and C. J. Limpus. 1997. Habitat utilization and migration in juvenile sea turtles. in P. L. Lutz, and J. A. Musick (Eds.). The biology of sea turtles. CRC Marine Science Series, CRC Press, Boca Raton, pp. 137-163.

National Research Counsel (USA), Committee on Sea Turtle Conservation. 1990. Decline of the Sea Turtles: Causes and Prevention. National Academy Press, Washington DC.

NMFS and USFWS. 1991. Recovery Plan for U.S. Population of Atlantic Green Turtle. NMFS, Washington DC.

Ogden, J. C., L. Robinson, K. Whitlock, H. Daganhardt and R. Cebula. 1983. Diel foraging patterns in juvenile green turtles (*Chelonia mydas*) in St. Croix United States Virgin Islands. Journal of Experimental Marine Biology and Ecology. 66:199-205.

Parsons, J. J. 1962. The Green Turtle and Man. University of Florida Press, Gainesville, Florida.

Peare, T., P. G. Parker, and T. A. Waite. 1994. Multiple paternity in green turtles (*Chelonia mydas*): conservation implications. In: K. A. Bjorndal, A. B. Bolten, D. A. Johnson, and P. J. Eliazar (compilers). Proceedings of the Fourteenth Annual Symposium on Sea Turtle Biology and Conservation, NOAA Technical Memorandum NMFS-SEFSC-351: 115-118.

Pritchard, P. C. H., and P. Trebbau. 1984. The Turtles of Venezuela. Contributions to Herpetology, 2. Society for the Study of Amphibians and Reptiles, 403 pp.

Redfoot, W. E., and L. M. Ehrhart. 1989. Marine turtle nesting and reproductive success in South Brevard County, Florida 1982-1988. In: S. A. Eckert, K. L. Eckert, and T. H. Richardson (compilers). Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology, NOAA Technical Memorandum NMFS-SEFC-232: 249-251.

Redfoot, W. E., and L. M. Ehrhart. 2000. The feeding ecology of juvenile green turtles utilizing the Trident Basin, Port Canaveral, Florida as developmental habitat. In: F. A. Abreu-Grobois, R. Briseno-Duenas, R. Marquez, and L. Sarti (compilers). Proceedings of the Eighteenth International Sea Turtle Symposium. NOAA Technical Memorandum NMFS-SEFSC-436: 33.

Salmon, M., J. Wyneken, E. Fritz, and M. Lucas. 1992. Seafinding by hatchling sea turtles: role of brightness, silhouette and beach slope as orientation cues. Behaviour 122: 56-77.

Salmon, M., B. E. Witherington, and C. D. Elvidge. 2000. Artificial lighting and the recovery of sea turtles. Pages 25-34 in N. Pilcher, and G. Ismail (editors) Sea turtles of the Indo-Pacific. ASEAN

Academic Press.

Schmid, J. R. 1998. Marine turtle populations on the west central coast of Florida: results of tagging studies at the Cedar Keys, Florida, 1986-1995. Fisheries Bulletin, 96:589-602.

Schroeder, B.A., and D.W. Owens. 1994. Sex ratio of immature green turtles in an east central Florida developmental habitat. In: B. A. Schroeder and B. E. Witherington (compilers). Proceedings of the Thirteenth Annual Symposium on Sea Turtle Biology and Conservation, NOAA Technical Memorandum NMFS-SEFSC-341: 157-161.

Schroeder, B.A., A.M. Foley, B.E. Witherington, and A.E. Mosier. 1998. Ecology ofmarine turtles in Florida Bay: population structure, distribution, and occurrence of fibropapilloma. In: S. P. Epperly, and J. Braun (compilers). Proceedings of the Seventeenth Annual Sea Turtle Symposium. NOAA Technical Memorandum NMFS-SEFSC-415: 265-267.

Seminoff, J. A. 2002. Marine Turtle Specialist Group Review. IUCN Red List Global Status Assessment. Green turtle (*Chelonia mydas*). Marine Turtle Specialist Group, The World Conservation Union (IUCN), Species Survival Commission, Red List Programme. 93 pp.

Smith, G. M., and C. W. Coates. 1938. Fibro-epithelial growths of the skin in large marine turtles, *Chelonia mydas* (Linnaeus). Zoologica 24: 93-98.

Solé, G., and G. Medina. 1989. The green turtles of Aves Island. In: S. A. Eckert, K. L. Eckert, and T. H. Richardson (compilers). Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology. NOAA Technical Memorandum NMFS. NMFS-SEFC-232: 171-173.

Spotila, J. R., E. A. Standora, S. J. Morreale, and G. J. Ruiz. 1987. Temperature dependent sex determination in the green turtle (*Chelonia mydas*): effects on the sex ratio on a natural nesting beach. Herpetologica 43: 74-81.

Summers, T., Redlow, A., Foley, A., Singel, K., and Blackwelder, J. 2004. Mass marine turtle stranding due to cold stress in St. Joseph Bay, Florida. In: Coyne, M.S. and Clark, R.D. (Compilers). Proceedings of the 21st Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-528, pp. 334-335.

Thorbjarnarson, J. B., C. J. Lagueux, D. Bolze, M. W. Klemens, and A. B. Meylan. 2000. Human use of turtles: a worldwide perspective. In: Klemens, M. W. (Ed.). Turtle Conservation. Smithsonian Institution Press, Washington DC. pp. 33-84

Verheijen, F. J., and J. T. Wildschut. 1973. The photic orientation of sea turtles during water finding behaviour. Netherlands Journal of Sea Research 7:53-67.

Weijerman, M., L. H. G. van Tienen, A. D. Schouten, and W. E. J. Hoekert. 1998. Sea turtles of Galibi, Suriname. In: R. Byles and Y. Fernandez (compilers). Proceedings of the Sixteenth Annual Symposium on Sea Turtle Biology and Conservation, NOAA Technical Memorandum NMFS-SEFSC-412: 142-144.

Wershoven, J. L., and R. W. Wershoven. 1992. Juvenile green turtles in their nearshore habitat of Broward County, Florida: a five year review. In: M. Salmon and J. Wyneken (compilers). Proceedings of the Eleventh Annual Workshop on Sea Turtle Biology and Conservation, NOAA Technical Memorandum NMFS. NMFS-SEFC-302: 121-123.

Wibbels, T., G. H. Balazs, D. W. Owens, and M. S. Amoss, Jr. 1993. Sex ratio of immature green turtles inhabiting the Hawaiian Archipelago. Journal of Herpetology 27: 327-329.

Witham, R. 1974. Neonate sea turtles from the stomach of a pelagic fish. Copeia 1974:548.

Witham, R. 1980. The 'lost year' question in young sea turtles. American Zoologist 20: 525-530.

Witham, R., and C.R. Futch. 1977. Early growth and oceanic survival of pen-reared sea turtles. Herpetologica 33:404-409.

Witherington, B. E. 1986. Human and Natural Causes of Marine Turtle Clutch and Hatchling Mortality and Their Relationship to Hatchling Production on an Important Florida Nesting Beach. Unpubl. M. S. Thesis. University of Central Florida, Orlando.

Witherington, B. E. 1992a. Behavioral responses of nesting sea turtles to artificial lighting. Herpetologica 48: 31-39.

Witherington, B. E. 1992b. Sea-finding behavior and the use of photic orientation cues by hatchling sea turtles. Ph.D. dissertation, Univ. of Florida, Gainesville. UMI Dissertation Information Service, Ann Arbor. 241 pp.

Witherington, B. E. 1997. The problem of photopollution for sea turtles and other nocturnal animals. In: J. R. Clemmons and R. Buchholz (Eds.). Behavioral Approaches to Conservation in the Wild. Cambridge University Press. pp. 303-328.

Witherington, B. E. 2002. Ecology of neonate loggerhead turtles inhabiting lines of downwelling near a Gulf Stream front. Marine Biology (Berlin) 140:843-853.

Witherington, B. E., and L. M. Ehrhart. 1989a. Hypothermic stunning and mortality of marine turtles in the Indian River Lagoon System, Florida. Copeia 1989: 696-703.

Witherington, B. E., and L. M. Ehrhart. 1989b. Status and reproductive characteristics of green turtles (*Chelonia mydas*) nesting in Florida. In: L. Ogren, F. Berry, K. Bjorndal, H. Kumpf, R. Mast, G. Medina, H. Reichart, and R. Witham (Eds.). Proceedings of the Second Western Atlantic Turtle Symposium, NOAA Technical Memorandum NMFS-SEFC-226: 351-352.

Witherington, B. E. and R. E. Martin. 2000. Understanding, assessing, and resolving light-pollution problems on sea turtle nesting beaches. 2nd ed. rev. Florida Marine Research Institute Technical Reports TR-2, 73 pp.

Witherington, B. E., C. Crady, and L. Bolen. 1996. A 'Hatchling Orientation Index' for assessing orientation disruption from artificial lighting. In J. A. Keinath, D. E. Barnard, J. A. Musick, and B. A. Bell (compilers). Proceedings of the Fifteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-387: 344-347.

Witzell, W. N., and J. R. Schmid. 2002. Investigation of immature sea turtles in the coastal waters of southwest Florida. In : Proceedings of the Twentieth Annual Symposium on Sea Turtle Biology and Conservation. Mosier, A., A. Foley and B. Brost, (compilers). NOAA Tech. Memo. NMFS-SEFSC-477. Pp.276-277.

Zug, G. R., and R. E. Glor. 1998. Estimates of age and growth in a population of green sea turtles (*Chelonia mydas*) from the Indian River lagoon system, Florida: a skeletochronological analysis. Canadian Journal of Zoology - Revue Canadienne de Zoologie 76: 1497-1506.

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Eretmochelys imbricata – Hawksbill Turtle

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SUMMARY. – Hawksbills, *Eretmochelys imbricata*, are the rarest of the five species of marine turtles that regularly occur in Florida waters. They occur statewide but are most frequently observed along the southeastern coast, in the Florida Keys, and along the central Gulf Coast. All life stages are represented. Thirty-one nests have been documented from 1979–2003, distributed from Volusia to Monroe counties, with a single record on the west coast in Manatee County. Foraging habitats for juvenile and adult hawksbills exist in Florida, including coral reefs and other hardbottom communities that extend along the southeastern coast from Martin to Monroe counties, as well as off the southwest coast. The convergence of currents from a wide area of the Gulf of Mexico and Caribbean Sea into the Florida Current makes waters off the Keys and the east coast of Florida a dispersal corridor for post-hatchling hawksbills from nesting beaches throughout the region. Pelagic-sized hawksbills off Florida inhabit the *Sargassum* community. Gut contents from a small sample include pelagic forms of *Sargassum* algae, goose barnacles, fish eggs, tunicates, plastics, tar, and styrofoam. Compared to other species of marine turtles in Florida, hawksbills are disproportionately affected by oil pollution. Nearly 12% of stranded hawksbills showed evidence of fouling by oil, compared to 1.1% of the strandings of other species; 22.4% of stranded hawksbills smaller than 22 cm SCL had evidence of oil. Other threats include entanglement, various fisheries, power plant entrapment, boat-related injuries, habitat degradation, and hybridization. Fibropapillomatosis is not documented in Florida hawksbills but is known to occur in hawksbill hybrids. From 1980 to 2002, 379 hawksbills were documented by the Florida Sea Turtle Stranding and Salvage Network; 44.9% of these involved live animals, and 48.9% were smaller than 22 cm SCL and presumably from the pelagic habitat.

CONSERVATION STATUS. – FNAI Global - G3 (Rare, Local, or Vulnerable), State - S1 (Critically Imperiled); ESA Federal - LE (Endangered); State - E (Endangered); CITES - Appendix I; IUCN Red List - CR (Critically Endangered).

Species Recognition. — The hawksbill is a medium-sized sea turtle with a sharply pointed, beak-like mouth and posteriorly overlapping scutes on the carapace (except in hatchlings and some adults). Other diagnostic features include two pairs of prefrontal scales, four pairs of costal scutes with the anteriormost pair not touching the nuchal scute, and two claws on each flipper (Fig. 5-1). The carapace is shield-shaped, tapers posteriorly, and usually has a strongly serrated posterior margin. It is typically boldly patterned with radiating streaks or blotches of yellow, brown, and black. The plastron is white to yellow, sometimes with dark blotches of pigment (Fig. 5-2). The carapace is light to dark brown in hatchlings, usually with a dark brown to black plastron (Fig. 5-3). Carapace measurement terminology used in this account follows Bolten (1999): SCL_{min} (straight carapace length notch-to-notch), $SCL_{n\text{-}t}$ (straight carapace length notch-to-tip), SCL_{max} (straight carapace length tip-to-tip), CCL_{min} (curved carapace length notch-to-notch), etc. If details of the measurement were not available, the data are presented simply as SCL or CCL.

Taxonomic History. — Originally described by Linnaeus (1766) as *Testudo imbricata*, the hawksbill was transferred to its own genus, *Eretmochelys*, by Fitzinger (1843). A specimen exists in the Zoology Museum, Uppsala University, Uppsala, Sweden, that is presumed to be the holotype. Although subspecies have been recognized by some authors (Carr, 1952; Smith and Smith, 1979; Pritchard and Trebbau, 1984), subspecific designations are usually not used today.

DISTRIBUTION

Geographic Distribution. — The hawksbill occurs throughout the world's tropical and subtropical oceans, ranging primarily from 30ºN to 30ºS. It has been documented in 82 geopolitical units and may occur in 26 others (Baillie and Groombridge, 1996). However, most populations are small and are declining or depleted; only five regional populations (Mexico, Seychelles, Indonesia, and two in Australia) remain that have more than 1000 females nesting annually (Meylan and Donnelly, 1999). Hawksbills are most common in the western Atlantic Ocean, the Indian Ocean, and western Pacific Ocean. They are relatively rare in the eastern Atlantic Ocean (Brongersma, 1972; Fretey, 1998; Fretey et al., 2000), either rare or highly depleted in the eastern Pacific Ocean (NMFS&USFWS, 1998), and extremely rare or absent in the Mediterranean Sea (Witzell, 1983; Groombridge, 1990).

Figure 5-1. A 40.5 cm SCL$_{n-t}$ hawksbill turtle *(Eretmochelys imbricata*) captured near Barracuda Keys, Key West National Wildlife Refuge (Monroe County), Florida. Photo by Blair Witherington.

In the western Atlantic Ocean, Gulf of Mexico, and Caribbean Sea, hawksbills occur from the southern U.S. southward along the Central American coast to Brazil and throughout the Bahamas and the Greater and Lesser Antilles. The Yucatan Peninsula of Mexico hosts the largest hawksbill nesting aggregation in the hemisphere, with several thousand nests recorded annually in the states of Campeche, Yucatan, and Quintana Roo (Meylan, 1999a). Other significant but much smaller nesting aggregations occur in Puerto Rico (Mona Island), Cuba, Nicaragua, Panama, the U.S. Virgin Islands, Antigua, and Barbados (Meylan, 1999a; Moncada et al., 1999; Lagueux et al., 2003; Ordoñez et al., in press). However, hawksbills nest in small numbers in many other countries in Central America and the Caribbean. Nesting within the U.S. and the U.S. Caribbean occurs in Puerto Rico (including Mona, Culebra, and Vieques islands), the U.S. Virgin Islands (St. Croix, St. Thomas, and St. John), Florida, Texas, and Hawaii. Foraging areas for hawksbills are widely distributed in the western Atlantic and are closely associated with the distribution of coral reefs and other hardbottom habitats.

Within the continental United States, hawksbills are observed with regularity only in Florida and Texas. Those observed in Texas are principally pelagic-sized individuals and small juveniles recovered by the Texas Sea Turtle Stranding and Salvage Network (Amos, 1989; Shaver, 1998).

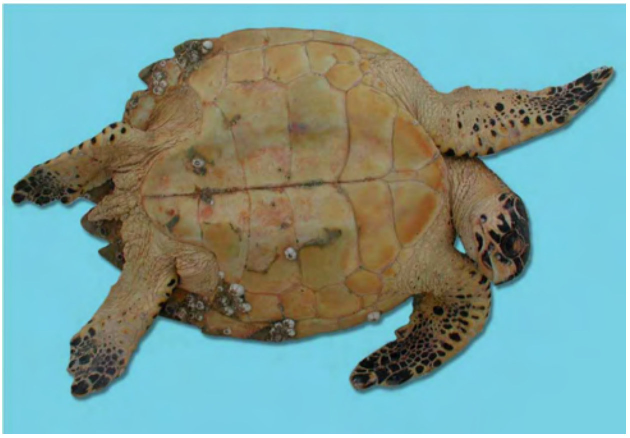

Figure 5-2. Ventral view of a 70.1 cm SCL hawksbill turtle *(Eretmochelys imbricata*) captured in the cooling water intake canal of the St. Lucie Nuclear Plant, Hutchinson Island (St. Lucie County), Florida. Photo by Richard Herren.

Figure 5-3. Hatchling hawksbill turtle (*Eretmochelys imbricata)* from a nest at Bahia Honda State Park, Florida Keys (Monroe County), Florida. Photo by Henry Markey.

Table 5-1. Records of the distribution and relative abundance of hawksbill turtles (*Eretmochelys imbricata* = *E.i.*) in Florida. Records are organized geographically from west to east (see County Map, p. 32). UF = University of Florida Museum of Natural History.

County	Locality	Observation Type	Dates	Turtles Captured		Notes; Source
				Total	*E.i.*	
Gulf	St. Joseph Bay	Strike nets and set nets	Aug 2001-Jan 04	161	0	E. McMichael & R. Carthy, *pers. comm.*
		Cold-stun event	Jan 2001	401	0	Summers et al., 2004
		Cold-stun event	Jan 2003	42	0	E. McMichael & R. Carthy, *pers. comm.*
Levy	Cedar Key	Tangle nets	1986-1995	284	0	Schmid, 1998
	Yankeetown	Museum specimen	Feb 1951		1	45.6 cm SCL$_{\mathrm{min}}$; UF30484
Citrus	Crystal River Nuclear Plant	Entrapment	1998-2003	156	1	21.6 cm SCL$_{\mathrm{n\text{-}t}}$; Nov 2000; D. Bruzek, *pers. comm.*
Pinellas	Tarpon Springs	Museum specimen	1929		1	23.5 cm SCL$_{\mathrm{min}}$; UF5961
	Tampa Bay	Tangle nets, shrimp trawl	1994-1998	2	0	Meylan et al., 2003
		Shrimp trawl	1997-1998	9	0	Nelson, 1999
Collier	Ten Thousand Islands	Strike net	1997-2003	220	0	Witzell and Schmid, 2002, 2003; J. Schmid, *pers. comm.*
Monroe	32 km w of Key West	Sighting			1	Adult; Carr, 1940
	Florida Bay	Nets, rodeo	1990-2003	630	1	38.2 cm SCL$_{\mathrm{n\text{-}t}}$; 3 poss. hybrids; B. Schroeder, *pers. comm.*
	Key West NWR	Nets, rodeo, sightings	2001-2003	68	7	Size range 28.2–50.5 cm SCL$_{\mathrm{n\text{-}t}}$; M. Bresette, *pers. comm.*
Broward	Galt Ocean Mile, Ft. Lauderdale	Scuba	Mar 1986-Nov 89	~81	5	75–150 m offshore; size range 25.7 - 60 cm CCL; Wershoven & Wershoven, 1988; R. Wershoven, *pers. comm.*
Palm Beach	Breakers Reef	Scuba	2003-2004	24	24	L. Wood, pers. comm.
St. Lucie	St. Lucie Nuclear Plant	Entrapment	1976-2003	9542	39	Size range 34.0–83.4 cm SCL$_{\mathrm{min}}$; M. Bresette, *pers. comm.*
	7 km off Hutchinson Is.	Shark gill net	Mar 2001		1	67.5 cm SCL; B. Schroeder, *pers. comm.*
	Jennings Cove, Indian River Lagoon	Set nets	1998-2003	224	0	M. Bresette, *pers. comm.*
Indian River	3 km S of Sebastian Inlet, Indian River Lagoon	Set nets	1982-2003	2442	1	67.6 cm SCL$_{\mathrm{n\text{-}t}}$; L. Ehrhart, *pers. comm.*
	S of Sebastian Inlet,	Set nets	1989-2003	841	1	24.8 cm SCL$_{\mathrm{n\text{-}t}}$; Oct 1989; L. Ehrhart, *pers. comm.*
nearshore						
Brevard	4 km S of Melbourne Beach	Live stranding	Jul 1983		1	19.5 cm SCL; entangled in rope in *Sargassum* wrack; Redfoot et al., 1985
	Indian River Lagoon	Stranding	1974		1	ca. 31 cm SCL; partial carcass; Ehrhart, 1983
		Set nets	1976-1981	100	0	Ehrhart, 1983
		Set nets	1994-2003	149	0	J. Provancha, pers. comm.
		Cold-stunning	1977-78, 1981, 1985-86	467	0	Witherington & Ehrhart, 1989
	46 km ENE Port Canaveral	Dip-net; pers. obs.	Jul-Oct 1997	290	1	26 cm CCL$_{\mathrm{n\text{-}t}}$; captured Aug 2003; B. Witherington, *pers. comm.*
Various NE	Sebastian Inlet to Georgia border	Shrimp trawler	1986-1991	928	0	Concentrated in Cape Canaveral area; Schmid, 1995

A total of 385 hawksbill strandings were recorded in Texas from 1980 to 2002 (D. Shaver, *pers. comm.*). Elsewhere along the northern Gulf of Mexico and the eastern seaboard, observations of hawksbills are rare, with only 17 strandings and incidental captures documented by the National Marine Fisheries Service Sea Turtle Stranding and Salvage Network (STSSN) in states other than Texas and Florida during 1980–2003. A small number of additional observations—most involving immature animals—have been reported in the literature.

To evaluate the distribution and abundance of hawksbills in Florida, we gleaned information from observations of live turtles at sea, in-water capture programs, nesting beach surveys, incidental captures (commercial fisheries, recreational hook-and line captures, and power plant entrapments), cold-stunning events, museum records, and stranding data (Table 5-1; Fig. 5-4). These various data sources document that hawksbills may occur throughout the state but are most frequently observed along the southeastern coast, in the Florida Keys, and off the central Gulf Coast. Hawksbills appear to be rarer than are the other species of marine turtles in Florida. They accounted for only 39 of 6163 turtles captured in inwater projects around the state, 40 of 9648 power plant entrapments, and 0 of 910 cold-stunnings (Table 5-1).

Hawksbills represented less than 2% of statewide strandings from 1980 to 2002. Although stranded animals may be passively transported by currents and may represent a biased sample of the population, stranding distribution patterns can provide useful information, especially when large sample sizes and long time series are available and when potential biases are identified. Compared with strandings of other marine turtle species in the state, an unusually large percentage of hawksbill strandings (44.9% vs. 12.6 % for all other species combined) have involved live animals. Thus, the distribution of stranded hawksbills is likely to be representative of the distribution of healthy animals. From 1980 to 2002, 379 strandings of hawksbills were documented by the Florida Sea Turtle Stranding and Salvage Network (FL STSSN) (Fig. 5-4). During this period hawksbills represented less than 2% of a total of 19,767 sea turtle strandings statewide. This total does not include incidental captures of live, healthy turtles, but it does include captures of injured, sick, or dead turtles. Of all hawksbill strandings in the state from 1980 to 2002, 15.6% took place on the west coast, 23.7% in the Keys, and 60.7% on the east coast (Fig. 5-4).

Hawksbills appear to be very rare in the Florida Panhandle and along the Gulf Coast of the northern Florida peninsula, as evidenced by inwater capture data and cold-stunning events (Table 5-1) and by stranding data (Fig. 5-4). There are only two stranding records of hawksbills for the west coast from the Florida-Alabama border to Hernando County from 1980 to 2002 (FL STSSN).

Hawksbills are more abundant in the Gulf waters off west central Florida than elsewhere along the west coast. Nearly three-quarters (44/59) of all Florida west coast

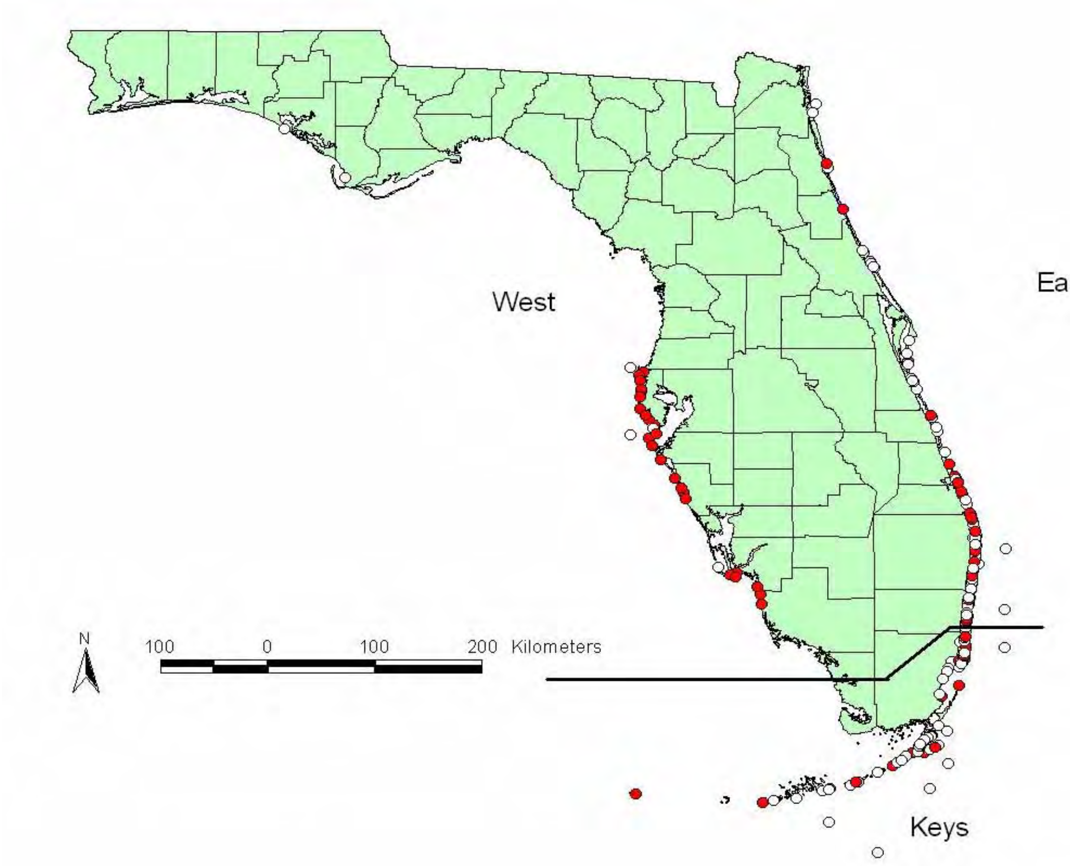

Figure 5-4. Geographic distribution of hawksbill turtles (*Eretmochelys imbricata*) recorded as strandings in Florida, 1980–2002. Open circles denote live strandings (44.9%), filled circles are dead strandings. Source: Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, Sea Turtle Stranding and Salvage Network; *n* = 379. Boundaries of the three regions of the state (West, Keys, and East) referred to in the text are indicated.

hawksbill strandings from 1980 to 2002 occurred in Pinellas, Manatee, and Sarasota counties, with half (28/59) in Pinellas County (FL STSSN) (Figs. 5-4, County Map, p. 32). Twenty-three hawksbills (7 alive) stranded during a four-month period (January through April) in 2001 in Pinellas through Collier counties. The large number of animals, the wide range of sizes affected (25.5–75.0 cm $\text{SCL}_{\text{n-t}}$, mean = 45.1 cm, SD = 11.63), and the coincidence of the event with unusually cold water temperatures in the area suggested to us that these stranded animals had possibly been residing in the area and had succumbed to cold-related stress. No hawksbills were captured or sighted during sampling efforts in Tampa Bay or the Ten Thousand Islands, although one turtle captured at the latter site was a hawksbill/loggerhead hybrid (Table 5-1). The lack of hawksbill stranding records for the Everglades area from southern Collier County to the tip of the peninsula (Fig. 5-4) is likely due to the difficulty observers have gaining access to the coastline and to the type of habitat there (mangrove cays), which makes the discovery of carcasses unlikely. There are relatively few strandings of any marine turtles documented in this area.

The distribution and abundance of hawksbills in the Florida Keys are poorly known. DeSola (1931) described the Florida Keys as the location of the finest fishery of hawksbills in the world, but he provided no other information, and we are unaware of any supporting evidence for this statement. Carr (1940) described hawksbills in Florida as "not common" but singled out the Florida Keys as appropriate habitat. Duellman and Schwartz (1958) noted nine locality records for hawksbills for all of Florida—one in "southern Florida," one at Garden Key (Dry Tortugas, Monroe County), and seven at Key West (Monroe County). No additional data on these specimens were given. The largest reef habitats in Florida exist in Monroe County, where there are an estimated 115,290 ha (W. Jaap, *pers. comm.*) Much of this reef habitat lies within the boundaries of the Florida Keys National Marine Sanctuary and the Dry Tortugas National Park. (Figs. 5-4, County Map, p. 32).

Although hawksbills are regularly sighted in the Florida Keys, there have been only a few studies to document distribution and abundance. Mark-recapture studies suggest that hawksbills are relatively rare in the shallow seagrass and mixed hardbottom habitats of central-western Florida Bay, and more common in the Key West National Wildlife Refuge (Table 5-1). The refuge extends from Key West to just west of the Marquesas Keys. Nearly a quarter (90/379) of all hawksbill strandings in Florida from 1980 to 2002 have occurred in the Florida Keys (FL STSSN).

Hawksbills continue to be not uncommon as live sightings and strandings along the southeastern coast of the peninsula. Carr (1940) listed Dade County (now Miami-Dade County) as a site of occurrence of hawksbills in Florida but did not give specific localities. The county has an estimated 7200 ha of reef habitat (W. Jaap, *pers. comm.*). Nearly 14% (52/379) of statewide hawksbill strandings from 1980 to 2002 occurred in Miami-Dade County, including 16 individuals from Biscayne Bay.

Hawksbills are known to occur on the nearshore reefs off Broward County. A site at Galt Ocean Mile, 7 km north of Port Everglades, appears to serve as a nocturnal resting site (Table 5-1). Hawksbills have also been observed on the hardbottom that lies only 50 m offshore from the coast in the area just north of Hillsboro Beach and on the second and third reef tracts off Broward County (R. Wershoven, *pers. comm.*). An estimated 8300 ha of reef habitat exists in Broward County (W. Jaap, *pers. comm.*). The county accounted for nearly 14% (52/379) of statewide hawksbill strandings from 1980 to 2002.

Hawksbills of various sizes are routinely sighted by scuba divers on the reefs off Palm Beach County (Lund, 1985; N. Rouse, *pers. comm.*; L. Wood, *pers. comm.*). Reef habitat in this county extends over an estimated 12,000 ha (W. Jaap, *pers. comm.*). The county had 66 documented hawksbill strandings from 1980 to 2002, the highest number for any county in the state.

Thirty-nine hawksbills were captured in the intake canal of the St. Lucie Nuclear Plant on Hutchinson Island from 1976 to 2003 (M. Bresette, Quantum Resources, *pers. comm.*). Turtles enter the canal through large-diameter (3.9–4.9 m) pipes that take in cooling water for the plant. The intake structure is located approximately 365 m offshore in the Atlantic Ocean in 7 m of water. The hawksbill captures represented 0.4% of all captures at the plant during this period and did not involve any mortality. Most turtles are not adversely affected by entering the canal (Bresette et al., 1998), and the intake structure is considered to represent a relatively unbiased sampling device for the sea turtles in adjacent inshore waters (Wilcox et al., 1998).

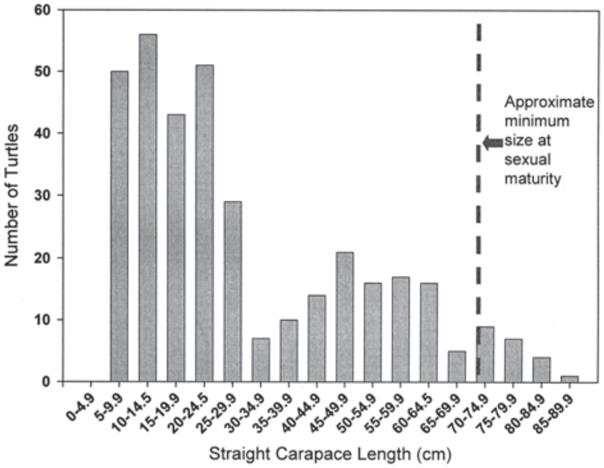

Figure 5-5. Size distribution of hawksbill turtles (*Eretmochelys imbricata*) that were recorded as strandings in Florida, 1980–2002. Size is given as SCL_{n-t}. Source: Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, Sea Turtle Stranding and Salvage Network; *n* = 356.

Hawksbills are poorly represented in inwater studies and cold-stunning events on the central and northeastern coast of Florida despite considerable sampling effort (Table 5-1). Records of hawksbills become increasingly rare as one proceeds northward along the east coast of Florida from Cape Canaveral, although strandings have been documented in every county on the state's east coast (Fig. 5-4).

Ecological Distribution. — Hawksbills pass through several ontogenetic stages during their lifetimes, occupying a sequence of habitats. After entering the sea as hatchlings, an initial pelagic stage occurs that lasts as long as several years, followed by one or more benthic stages that are typically associated with coral reefs and other hard-bottom habitats (Carr et al., 1966, 1982; Meylan, 1984a, b, 1988, 1992; Carr, 1986, 1987a). All life stages of hawksbills appear to be represented in Florida waters. Figure 5-5 shows the size distribution of all hawksbills recovered and measured by the stranding network in Florida over the past 23 years; sizes ranged from 5.5 to 86.5 cm SCL_{n-t} (mean = 30.0 cm, SD = 20.6, *n* = 356). Size data for hawksbills stranded in Florida are presented as straight carapace lengths; when straight-line measurements were not available, they were calculated from curved carapace lengths using the formula $SCL_{n-t} = CCL_{n-t}(0.94158) - 0.187$ ($r^2 = 0.9988$) which was derived from 319 stranded animals for which both carapace measurements were available. Hatchlings are typically about 42 mm when they enter the ocean (Witzell, 1983). As previously noted, nearly half of all hawksbill strandings in Florida involved live animals, making the stranding data more likely to reflect the behavior of wild, healthy hawksbills. Other data on size distribution and ecological distribution include observations of pelagic-sized turtles at sea and of juveniles, subadults, and adults captured by in-water programs, entrapped in power plant structures, or caught on hook-and-line (Table 5-1).

Data on live hawksbills observed in the wild in Florida, although limited, are consistent with observations from other sites in the western Atlantic Ocean that suggest that hawksbills remain in the pelagic environment until they reach approximately 20–26 cm SCL_{min} (Meylan, 1984 a, b, 1988; Boulon, 1994; Mayor et al., 1998; van Dam and Diez, 1998b; Leon and Diez, 1999; Meylan et al., 2003). The smallest hawksbills captured at the St. Lucie Nuclear Plant, the Key West National Wildlife Refuge, and on the reefs off Broward County were 34.0 cm SCL_{min} (*n* = 39; M. Bresette, *pers. comm.*), 28.2 cm SCL_{n-t} (*n* = 7; M. Bresette, *pers. comm.*), and 25.7 cm CCL (*n* = 5; R. Wershoven, *pers. comm.*), respectively.

The size distribution of stranded hawksbills in Florida is bimodal, with the largest number of turtles in the size range 5.0–24.9 cm (Fig. 5-5). The number of strandings drops off in the 25.0–29.9 cm SCL range but peaks again in the 45–64.9 cm range. We believe that the first peak represents hawksbills that were living in the pelagic environment surrounding Florida and that were washed ashore by storms

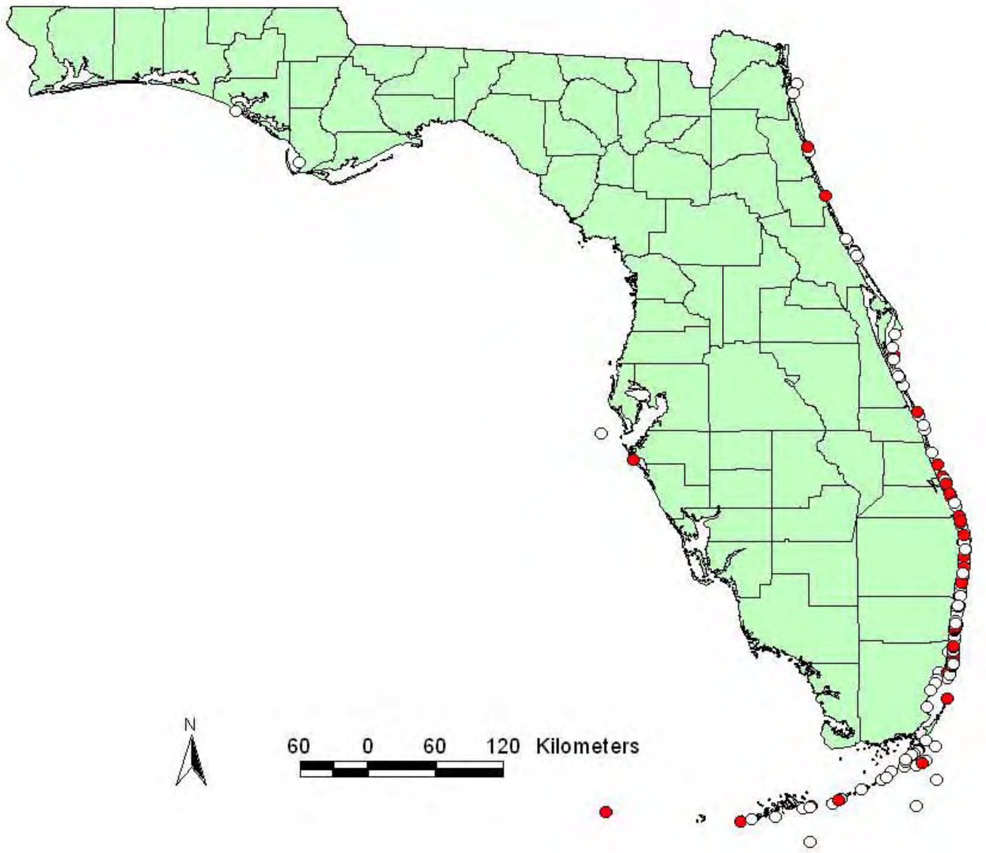

Figure 5-6. Geographic distribution of hawksbill turtles (*Eretmochelys imbricata*) smaller than 22 cm SCL$_{n\text{-}t}$ that were recorded as strandings in Florida, 1980–2002. Open circles denote live strandings (70.7%). Source: Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, Sea Turtle Stranding and Salvage Network; *n* = 174.

or strong winds. Carr (1987a) listed cases of hawksbills less than 25 cm in length stranding after storms or in strong winds in Bermuda, Florida, and Texas and used these to support the hypothesis that hawksbills of this size reside in the pelagic environment in much the same way as do post-hatchling loggerheads and green turtles. Other support for an early pelagic phase is provided by Hornell (1927).

The drop-off in the size distribution of stranded hawksbills in Florida starting at 25 cm (Fig. 5-5) is likely to be correlated with the departure of small hawksbills from the pelagic habitat. Turtles larger than that are typically associated with neritic habitats (< 200 m depth). In Florida, the larger hawksbills that strand tend to be juveniles and subadults, with few adults represented.

Pelagic-sized turtles, defined conservatively herein as those with SCL less than 22 cm SCL$_{n\text{-}t}$ made up 48.9% (174/356 with carapace measurements) of all hawksbill strandings in Florida from 1980 to 2002 (Figs. 5-5, 5-6). Of these, 70.7% were alive when encountered, compared with only 22.5% of hawksbills larger than 22 cm, and 12.6% of all marine turtles of other species.

These smaller sized hawksbills in Florida and elsewhere in the region are frequently found associated with *Sargassum* algae (Gunter, 1981; Carr, 1986, 1987a; Amos, 1989), and it is likely that off Florida's east coast they occupy a "lost year" environment similar to but perhaps not identical to that described by Carr (1986, 1987a) and Witherington (2002) for green turtles and loggerheads. The gut contents of four hawksbills (14.0, 14.0, 20.2, 21.3 cm SCL$_{min}$) that stranded along Florida's southeast coast all included *Sargassum*, and the various food items suggested that they had been surface-feeding (Meylan, 1984a; see Table 5-2 and Feeding). However, Witherington (2002) found no hawksbills when he reported on 293 live post-hatchlings captured or sighted in

Table 5-2. Gut contents of four juvenile hawksbill turtles (*Eretmochelys imbricata*) stranded on Florida's southeast coast (Source: Meylan, 1984a).

Location	SCL (cm)	Gut Contents
Jensen Beach	14.0	*Sargassum fluitans* or *natans* (> 1/2 of volume), unidentified animal matter (w/ nematocysts), plastic (styrofoam, styrofoam precursors), *Syringodium filiforme*, tar droplets, woody plant remains. Animal tarred externally.
Jupiter Island	21.3	Unidentified material, *Sargassum* sp., *Microdictyon* sp. (alga), plastic bead, paper
Ft. Lauderdale	14.0	Unidentified material, *Sargassum* sp. Unidentified alga, tar droplets, plastic particles, shell fragments
Hutchinson Island	20.2	Goose barnacles, fish eggs on *Sargassum*, tunicate, plastic, crab chela, tar droplets, unidentified plant material

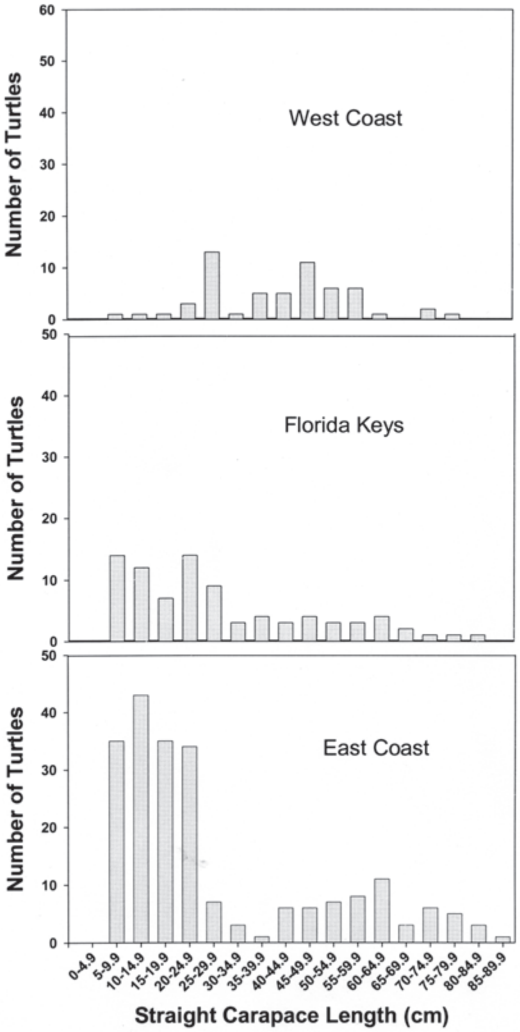

Figure 5-7. Size distribution of hawksbill turtles (*Eretmochelys imbricata*) that were recorded as strandings in three regions of Florida, 1980–2002 (see Fig. 5-4). Mean size on the West coast was 41.0 cm SCL_{n-t} (range 7.0–75, SD = 14.9, *n* = 57); Florida Keys mean = 28.5 cm SCL_{n-t} (range 5.5–81.5, SD = 19.3, *n* = 85); East coast mean = 27.6 cm SCL_{n-t} (range 5.7–86.5, SD = 21.4, *n* = 214). Source: Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, Sea Turtle Stranding and Salvage Network.

drift lines near the Gulf Stream front off east-central Florida. The average size of the turtles he captured, all loggerheads, was only 4.69 cm CL—far smaller than the hawksbills that have been typically found on the east coast and are also presumed occupants of the pelagic environment. One hawksbill (26 cm CCL_{n-t}) has since been captured during the above-mentioned sampling efforts that target pelagic loggerheads off the east-central coast (B. Witherington, *pers. comm.*). Thus, there may be temporal or spatial differences in the use of the pelagic habitats off Florida by hawksbills, there may be behavioral differences that make them more difficult to observe, or they may be as rare as the numbers indicate.

Size-class distributions of stranded hawksbills varied for different regions of the state (Fig. 5-7). The west coast hawksbills had the largest average size, with most animals of juvenile or subadult size, whereas the Keys and east coast had distributions heavily biased towards turtles smaller than 25 cm SCL_{n-t}.

Smaller pelagic-sized hawksbills were rarely reported to strand along the west coast of Florida from 1980 to 2002 (Fig. 5-6), making up only 7% of all west coast hawksbill strandings during this period. Four of the five specimens recorded during this 23-year period were found alive, and several were in good enough condition that they were eventually released after rehabilitation. The hawksbills found in the Panhandle in Bay (14.5 cm SCL_{min}) and Gulf (7.6 cm CCL_{min}) counties stranded two days apart, and we believe it is likely that they were washed ashore by Tropical Storm Allison. The Citrus County hawksbill was entrapped at a power plant (see Florida Distribution); the Hillsborough County specimen (19.4 cm SCL_{n-t}) was found alive, drifting among dead fish 8 km offshore from Egmont Key; and the Manatee County specimen (21.2 cm SCL) was stranded dead on the beach on Longboat Key.

The stranding data suggest that pelagic-sized hawksbills are much more common in the waters of the Florida Keys and along the southeastern Florida coast than along Florida's west coast (Fig. 5-6). They made up 44.7% of all hawksbill strandings (for which carapace measurements were available) within the Florida Keys and 61.7% of those on the east coast. These small hawksbills are presumably derived from nesting beaches in the Gulf of Mexico and Caribbean Sea. There has been only one hawksbill nest recorded on Florida's west coast, and only occasional nesting has been reported in the Florida Keys and on the southeast coast (see Growth and Reproduction). These hawksbills are apparently transported to Florida by the Loop Current, the Caribbean Current, and the Antilles Current (Fig. 5-8) and eventually enter the Florida Current, perhaps joining it at different points and seasons. Hatchlings entrained in the Loop Current could be expected to remain in the Gulf of Mexico for differing amounts of time depending on which branch of the current they enter. The Loop Current occasionally reaches the northern shores of the Gulf of Mexico, which may explain the occasional appearance of pelagic-sized hawksbills in Texas (Amos, 1989), Louisiana, and Mississippi (NMFS Sea Turtle Stranding and Salvage Network database).

The convergence of currents from a wide area of the Gulf of Mexico and Caribbean Sea into the Florida Current may serve to concentrate pelagic hawksbills off the southeastern coast of Florida. It may also explain the abundance of hawksbills along this stretch of coast, where the current is compressed between Florida and the shallow waters of the Bahamas and passes close to shore. Nearly half (170/356) of all strandings of hawksbills of pelagic size in Florida from 1980 to 2002 were found in the three southernmost counties of Florida's east coast: Palm Beach, Broward, and Miami-Dade (Figs. 5-6, County Map, p. 32). Thus, evidence continues to accumulate suggesting that Florida serves as a dispersal corridor for hawksbill post-hatchlings produced on nesting beaches elsewhere in the Gulf and Caribbean region (Meylan, 1992).

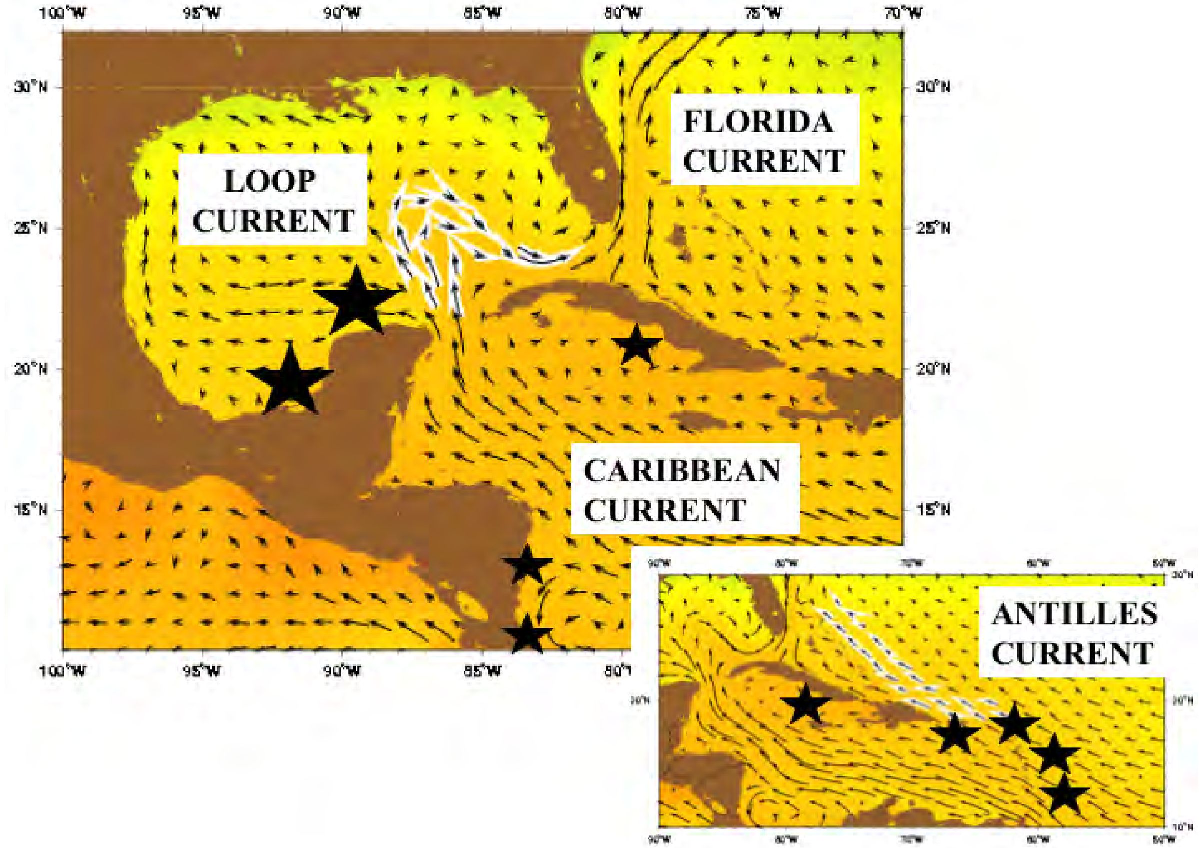

Figure 5-8. Average ocean current patterns relevant to the dispersal of hatchling hawksbill turtles (*Eretmochelys imbricata*) leaving nesting beaches in the Gulf of Mexico and Caribbean Sea, as determined by average ship-drift derived velocities (Loop Current) and Mariano Global Surface Velocity Analysis (Antilles and Caribbean currents). The locations of important hawksbill nesting beaches in the region are indicated with stars. Current data modified from Joanna Gyory, Arthur J. Mariano, and Edward H. Ryan. "The Loop Current." Ocean Surface Currents (http://oceancurrents.rsmas.miami.edu/caribbean/loop-current.html) and Elizabeth Rowe, Arthur J. Mariano, and Edward H. Ryan. "The Antilles Current." Ocean Surface Currents (http://oceancurrents.rsmas.miami.edu/atlantic/antilles.html).

Although post-hatchlings are likely to remain in the Florida Current (which is the beginning of the Gulf Stream system) and travel north along the east coast of Florida, the current moves farther offshore as it proceeds north, which would perhaps explain why sightings and strandings of hawksbills are less common in northeastern Florida (Fig. 5-6). Distribution records given in Table 5-1, such as that of the live, 26.0 cm SCL hawksbill dip-netted 46 km off Port Canaveral, and the strandings of hawksbills less than 22 cm SCL in almost all the counties along Florida's east coast, except for Nassau County, suggest that at least some post-hatchlings continue to travel north. The hypothesis of northward dispersal in the Gulf Stream is also consistent with observations of pelagic-sized hawksbills off Sapelo Island, Georgia, and off North Carolina (Parker, 1996; NMFS Sea Turtle Stranding and Salvage Network database). Other routes of dispersal are possible, and even likely, and will perhaps be better known when knowledge of marine turtle distributions within the Bahamas and the Caribbean expands.

Benthic-feeding (post-pelagic) juvenile and subadult hawksbills are present and likely resident in Florida waters in several areas. Foremost among these areas are the Florida Keys and the waters along the southeastern coast of the peninsula. The distribution of hawksbills in the state corresponds closely to the location of the Florida Reef Tract, the only shallow-water tropical coral reef ecosystem on the continental shelf of North America, and to the other hard-bottom communities in the Florida Keys and along the southeastern coast of peninsular Florida (Fig. 5-9). The considerable extent of reef habitat in Florida is not widely recognized. The reefs in Florida are most developed in the area south of Cape Florida (Miami-Dade County), from Soldier Key to Dry Tortugas, but representatives of the tropical reef biota are found as far north as St. Lucie Inlet (Martin County) (Jaap and Hallock, 1990). Coral reefs also extend into the Gulf of Mexico from Key West and Smith Shoal to the Content Keys (Jaap and Hallock, 1990). The distribution of reefs and other hard-bottom habitats along Florida's east coast was partially mapped and described by Perkins et al. (1997) and SEAMAP-SA (2001). Although coral reefs are the primary habitat of hawksbills after they leave the pelagic environment, there has been no systematic or sustained effort to document marine turtle distribution and abundance in the Keys other than the newly initiated project in the Key West National Wildlife Refuge mentioned above. Thus, it is likely that hawksbills are more abundant in this area than has been reported in the literature.

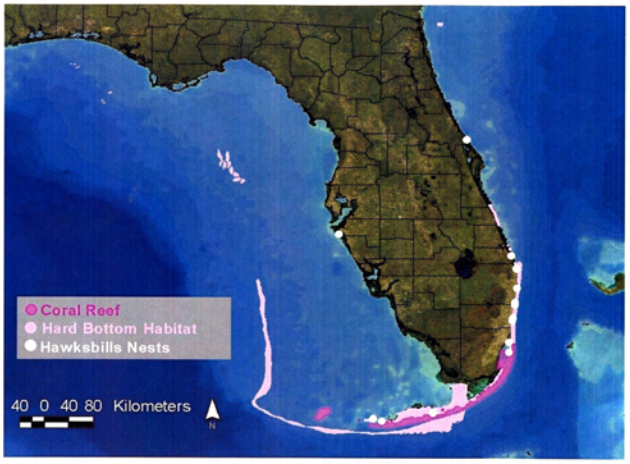

Figure 5-9. Distribution of coral reefs (dark pink) and other hardbottom habitats (light pink) in Florida, indicating the location of potential feeding habitat for juvenile and adult hawksbill turtles (*Eretmochelys imbricata*). White dots indicate known nesting sites of hawksbills (for exact localities see Table 5-3; *n* = 31 nests). Sources of habitat data: Florida Fish and Wildlife Conservation Commission, Fish & Wildlife Research Institute, Center for Spatial Analysis, St. Petersburg; NOAA Coastal Services Center. Extents of these habitats have been buffered (amplified) to allow visualization.

Residency by hawksbills on the reefs off Broward and Palm Beach counties is suggested by the observations of Wershoven (*pers. comm.*), who recaptured two of five tagged hawksbills (one recaptured seven times over a 526-day interval), and Norine Rouse (*pers. comm.*), who recorded multiple sightings of individual hawksbills of various sizes over periods as long as ten years (see Home Range). No hawksbills captured in the intake canal of the St. Lucie Nuclear Plant have been recaptured, but captures have occurred in all months of the year except January and February, which would be consistent with a year-round presence (M. Bresette, *pers. comm.*).

The size distribution of the 39 hawksbills captured in the intake canal of the St. Lucie Nuclear Plant from 1976 through 2003 is shown in Fig. 5-10. This is perhaps the largest sample currently available of live, free-ranging hawksbills measured in Florida. No pelagic-sized individuals have been taken at this site; the majority have been in the 40-to-50 cm size category (M. Bresette, *pers. comm.*). The intake canal draws water from the nearshore Atlantic in a region where shore-parallel, hard-bottom reef tracts are common. The distribution is typical of benthic developmental habitats for hawksbills elsewhere in the Caribbean. The largest animal captured was an 83.4 cm SCL_{min} female that weighed 86.8 kg. A second female, 74.6 cm (52 kg), and a 70.0 cm animal may also have been mature, but this was not confirmed by examination of the gonads via laparoscopy. Nearly all the other hawksbills captured at the plant through 2003 were also probably immature, based on their size.

As discussed above, there is some evidence that juvenile and subadult hawksbills may be resident off the central west coast of Florida. This evidence includes the larger number of strandings in this area than have occurred along the rest of the west coast (Fig. 5-4), the predominance of size classes that are associated with neritic environments (Fig. 5-7), and the series of apparent cold-related strandings in 2001. If hawksbills are resident in this area, it is likely that they inhabit hard-bottom areas offshore. These areas are not as thoroughly mapped as those off the east coast but are known to be extensive (Jaap and Hallock, 1990). On the west Florida shelf, in waters 12 to 30 m, there are numerous limestone outcroppings that form table-like structures that jut upwards 0.5–2 m above the bottom (Jaap and Hallock, 1990). These provide extensive ledges and cavernous vertical faces covered with plant and animal life. Another potential feeding habitat for hawksbills is southern Pulley Ridge, a recently discovered deep-water (60–75 m) coral reef extending ca. 32 km along the southwest Florida platform (Jarrett et al., 2005; Fig. 5-9). The reef may be too deep for hawksbills to use routinely, but it is within their known diving depth range (see Activity). The reef is bathed with clear waters from various gyres and the Loop Current and has a rich coral community.

Other potential hawksbill foraging habitat is the Florida Middle Ground reef complex (29˚10’ to 28˚45’N and 84°00’ and 84°25’W) which is the northernmost reef in the Gulf of Mexico and includes significant numbers of zooxanthellate stony corals (Jaap et al., 2003). Individual banks are 12 to 15 m in height and rise to 25 to 30 m below sea level; forty species of sponges have been documented there, including several species known to be eaten by hawksbills (Jaap et al., 2003). The extent to which these reefs and other live-bottom communities off Florida’s west coast provide habitat for marine turtles in general and hawksbills in particular remains unknown, but the presence of these reefs and other communities may help to explain the regular appearance of hawksbills along the west central coast.

There is no evidence that hawksbills use the major estuaries in southwest Florida, such as Tampa Bay and Charlotte Harbor, although they occasionally have stranded in the outer (seaward) periphery of these water bodies.

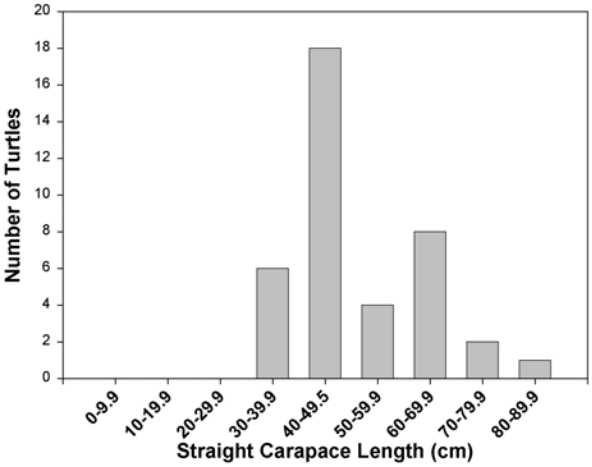

Figure 5-10. Size distribution of 39 hawksbill turtles (*Eretmochelys imbricata*) captured in the intake canal of the St. Lucie Nuclear Plant, Hutchinson Island, St. Lucie County, Florida, 1976–2003. Straight carapace length is SCL_{min}. (Source: M. Bresette, Quantum Resources, unnpubl. data).

Meylan et al. (2003) reported that ten immature hawksbills (27.3–54.6 cm CCL_{n-t}, *n* = 9) stranded in the outer portions of Tampa Bay from 1980 to 2002. The only other evidence of the possible use of inshore waters by hawksbills in Florida is that of a hawksbill carcass found in Brevard County on the shore of the Mosquito Lagoon (Ehrhart, 1983) and 16 strandings documented in Biscayne Bay (Miami-Dade County) from 1980 to 2002. It is possible that the turtles found in Biscayne Bay were transported inside the relatively open bay system by currents. Ten of the 16 were smaller than 22 cm SCL. Interestingly, one 25.7 cm SCL_{n-t} animal was captured alive 2.6 km up the Miami River. Extensive negative evidence from long-term netting studies on the central east coast suggests that hawksbills rarely enter the Indian River Lagoon system (see Distribution).

Adult hawksbills have rarely been documented in Florida waters, although nesting females occasionally visit beaches along the southeastern coast and the Florida Keys; one, possibly two, adult females have been captured at the St. Lucie Nuclear Plant. Recently initiated studies in the Florida Keys and the Marquesas Keys and on the reefs off Palm Beach County are likely to fill gaps in our knowledge of adult distribution patterns. There have been 12 strandings statewide of hawksbills greater than 75 cm SCL from 1980 to 2003. Nearly all have been in the Keys and along the lower southern Florida coast (FL STSSN).

The habitat preferences of juvenile and adult hawksbills in the Atlantic were poorly known until the late 1960s. Carr (1952) described the habitat of Atlantic hawksbills in very general terms as shallow coastal waters and commented that the species showed less habitat specificity than the green turtle, and showed a greater tolerance for shallow bays and lagoons with muddy bottoms, without rock holes, and with little or no submarine vegetation. Later, Carr et al. (1966) refined this description of the habitat preference of Atlantic hawksbills to “rocky places” and noted that the hawksbill was the sea turtle most frequently seen on coral reefs. Later studies confirmed the preeminence of the coral reef association but also supported the importance of other rocky, high-energy environments such as cliff walls, shoals, and limestone or volcanic rock outcrops (Carr et al., 1966; Carr and Stancyk, 1975; Nietschmann, 1981; Carr et al., 1982; van Dam and Diez, 1996, 1997a; Leon and Diez, 1999). The habitat preferences of hawksbills are tied closely to their highly spongivorous feeding habits, sponges typically requiring hard substrate for attachment and well-aerated water for nutrition.

Figure 5-11. Immature hawksbill turtle (*Eretmochelys imbricata*) on Juno Ledges, Palm Beach County, Florida. Approximate depth 21 m. Photo by Walter Jaap, Selena Kupfner and Tim MacIntosh.

In Florida, habitats where hawksbills were observed in Key West National Wildlife Refuge were described as sponge gardens, shallow sponge/hard-bottom flats, and areas with loggerhead and vase sponges (M. Bresette, *pers. comm.*). In Broward County, hawksbills were captured only 75–150 m offshore in habitat characterized by scattered hard and soft corals with 1-m ledges throughout. The reefs off Palm Beach County consist of a chain of barrier reefs that run parallel to the coastline with water depths of 5–30 m. This area receives warm, clear tropical waters from the Florida Current and although it is no longer an area of active reef development, the old reef provides complex bottom structure and a tropical reef flora and fauna (Fig. 5-11).

HABITAT RELATIONS

Activity. — Activity patterns of hawksbills have not been investigated in Florida waters, but data from studies elsewhere in the region suggest a strongly diurnal pattern for hawksbills living in nearshore environments. Immature hawksbills (27–53.4 cm SCL) living along cliff walls at Mona Island, Puerto Rico, spent an average of 8.4 hrs per day foraging, whereas those foraging in coral reef habitats spent 11.4 hrs per day. At both sites, hawksbills foraged primarily during daylight hours (van Dam and Diez, 1996, 1997a). Diving patterns, as revealed by time depth recorders, suggested that they rested > 96% of the time between dusk and dawn. Only a small amount (1.8–4%) of time was spent at the surface during either the day or night. Van Dam and Diez (1997b) concluded from surfacing profiles that immature hawksbills in both environments at Mona Island did not linger at the surface, coming there only to breathe. Average surface intervals were 50.5 sec in coral reef habitat and 32.9 sec in cliff-wall habitat. Foraging dives tended to be shorter (19–26 min) than resting dives (35–47 min) in the coral reef environment, although the dives were approximately equal in depth (foraging, 8–10 m, resting, 7–10 m). In the cliff-wall habitat, foraging dives tended to be shorter and shallower (8.6–14 min, 4.7 m) than were resting dives (30.4–37.1 min, 6.8 m) (van Dam and Diez, 1996, 1997a).

Although these data document routine use of shallow (< 10 m) waters, hawksbills are capable of diving to considerably greater depths. A 53.4 cm hawksbill at Mona Island was recorded diving deeper than 50 m three times within a 6-hr period; prolonged surfacing intervals before each dive suggested that the turtle anticipated the extent of the dives (van Dam and Diez, 1996). The maximum dive depth of a hawksbill recorded at Mona Island was 72 m. Hawksbills in Florida have been sighted at a wide range of depths, including shallow (< 8 m) nearshore waters off Broward County (Wershoven and Wershoven, 1988) and deeper (23–27 m) reef areas off Palm Beach County (Lund 1985; N. Rouse, *pers. comm.*; L. Wood, *pers. comm.*; W. Jaap, *pers. comm.*).

Hawksbills are known to use caves, crevices, and ledges for resting (Hirth et al., 1992; Limpus, 1992; T. Carr, 1977; A. Meylan, *pers. obs.*).

Like pelagic loggerheads and green turtles, pelagic hawksbills are believed to spend most of their time at the surface. They are often found associated with *Sargassum* algae, which provide both shelter and food (Hornell, 1927; Vaughan, 1981; Carr, 1987a; Meylan, 1984a, 1988).

Benthic-stage hawksbills appear to be solitary, unlike green turtles, which are sometimes seen feeding in small groups (Witzell, 1983). All sightings in a long-term study of hawksbills on the southern Great Barrier Reef in Australia were of solitary animals (Limpus, 1992).

Hawksbills sometimes assume a vertical posture in the water column, particularly when feeding. This posture may be maintained for at least several minutes, sometimes with the rear flippers planted on the substrate or with a front flipper resting on a structure within the reef (A. Meylan, *pers. obs.*).

Seasonality. — Hawksbills have been captured in the St. Lucie Nuclear Plant in St. Lucie County in all months except January and February. Strandings of hawksbills around the state occur in every month, with the highest numbers in March through June. The peak hatching season in Mexico, which is the largest rookery in the region and the presumed source for many of the post-hatchling hawksbills passing through Florida waters, is July and August (Guzman et al., 1995, inferred from Garduño-Andrade, 1999), but these hatchlings are likely to enter the sea over several months and to spend varying amounts of time in the Gulf of Mexico before entering the Florida Current, which takes them past southeastern Florida. There are pronounced differences in the timing of the nesting season in the western and eastern Caribbean, with hatching occurring several months later in the latter (see Nesting Season). These factors may mask patterns in the seasonality of occurrence of pelagic-sized animals in Florida. The majority of these smaller hawksbills that strand in Florida are larger than 10 cm SCL (Fig. 5-5), which would suggest that some may have traveled great distances from where they hatched, circling in eddies that delayed their arrival in Florida or lingered along the edge of the currents along the way.

Movements. — Few hawksbills have been tagged in Florida, and there has been little effort dedicated to documenting tagged turtles in the foraging areas where hawksbills are most likely to occur. Meylan (1999b) reviewed movements of hawksbill turtles in the Caribbean Sea, Gulf of Mexico, and western Atlantic Ocean based on published tag returns; none of these tag returns were from Florida. However, we are now aware of two long-distance tag returns that involve hawksbills from Florida. The single hawksbill (24.8 cm SCL_{n-t}) captured to date on the worm reefs off Sebastian Inlet (Indian River County) was recaptured nearly 7 yrs later at Walker's Cay, Bahamas (L. Ehrhart, *pers. comm.*). This represented a minimum straight-line distance of 203 km. The second documented movement involved a 9.2 cm SCL_{n-t} hawksbill that stranded at Mustang Island State Park, Texas. The animal was tagged and released 10 mo later in the Gulf of Mexico (27˚76'N, 96˚78'W), and then recovered a second time 5 mo later on the eastern coast of Florida at Hutchinson Island (Martin County) (TX & FL STSSN). Although the animal was in good condition, it had become entangled in a piece of netting. This turtle's multiple-recapture record provides support for the hypothesis suggested by stranding distributions and incidental sightings that some post-hatchling hawksbills from the western Gulf of Mexico are dispersing into the Atlantic, most likely through the Straits of Florida, and moving northward along Florida's eastern coast.

Home Range. — There is limited information about the home range of hawksbills in Florida waters. Wershoven and Wershoven (1988) captured one immature hawksbill seven times within a 526-day interval off Broward County. All captures were within two adjacent zones (≤ 6 km) of the study area. A second hawksbill was captured within the same distance after 15 days. Data on home range of hawksbills are also available from scuba diving observations on reefs approximately 2.4 km off Lake Worth Inlet, Palm Beach County, as follows: one individual seen 86 times over a 10-yr, 2-mo period; another individual seen 62 times over a 4-yr, 1-mo period; and a third individual seen 75 times over a 3-yr, 9-mo period (N. Rouse, *pers. comm.*).

Formal studies conducted in the Caribbean and elsewhere also suggest that hawksbills maintain limited home ranges and may remain resident in the same area for periods of at least several years. Immature (20.0–56.7 cm SCL_{n-t}) hawksbills at Mona and Monito islands, Puerto Rico, showed an average net displacement of only 0.45 km (SD = 0.66, range 0.00–5.22) after a mean intercapture interval of 465 days (van Dam and Diez, 1998a). Three immatures tracked 11–16 days via sonic transmitters used areas of 0.07–0.14 km^2 (van Dam and Diez, 1998a). Immature (19.5–69.7 cm SCL_{n-t}) hawksbills at a feeding ground in Jaragua National Park, Dominican Republic, showed an average displacement between subsequent capture sites of 0.36 km (SD = 0.32, range 0.06–1.55) over a mean intercapture interval of 204.4 days (Leon and Diez, 1999). In Bermuda, a 42.8 cm SCL_{min} hawksbill was hand-captured at the same resting spot after an interval of 1316 days (Meylan, Meylan, and Gray, unpubl. data).

Temperature Relationships. — Hawksbills are considered to be the most tropical of the sea turtles. In Florida, they are most common in the southern areas of the state, including the Florida Keys and along the southeast coast of the peninsula, where the warm Gulf Stream passes close to shore. A series of strandings on the west central coast of Florida in 2001 appeared to be related to unusually cold water temperatures, but the strandings happened over several months and could not be described as a cold-stunning event.

The sex of hawksbills is determined by temperature at which the eggs incubate, with warmer temperatures producing females and cooler temperatures producing males (Dalrymple et al., 1985; Godfrey et al., 1999). Pivotal temperatures of 29.2˚C and 29.6 ˚C were recorded at Antigua (Mrosovsky et al., 1992) and Brazil (Godfrey et al., 1999). Temperature also affects the duration of incubation (Godfrey et al., 1999). A late-season nest at Soldier Key, Miami-Dade County, Florida, hatched after 91 days (Dalrymple et al., 1985).

GROWTH AND REPRODUCTION

Growth. — There are few growth rates available for hawksbills in Florida. Lund (1985) measured a nesting female at Jupiter Island in July 1974, July 1977, and mid-1979 and recorded growth in carapace length from 80 to 81 to 81.5 cm SCL_{min}. That almost negligible growth is typical of adult hawksbills studied elsewhere (Chaloupka and Limpus, 1997). One of the five hawksbills captured on a reef off Broward County by Wershoven (see Distribution) was observed eight times and measured five times over a 526-day interval. The turtle grew from 34 to 48.7 cm CCL, yielding an average annual growth rate of 10.2 cm/yr (Wershoven and Wershoven, 1988, *pers. comm.*). Three hawksbills (initial CCL's of 48.3, 66.0, and 78.9 cm) observed by scuba divers on reefs off Lake Worth Inlet, Palm Beach County, over 21-, 40-, and 25-month intervals had average growth rates of 13.1, 5.2, and 3.1 cm/yr (N. Rouse, *pers. comm.*).

The growth rates recorded in Florida are comparable to those reported for post-pelagic hawksbills in the Caribbean (Bjorndal and Bolten, 1988; Boulon, 1994; Leon and Diez, 1999; Diez and van Dam, 2002). Growth rates of hawksbills vary ontogenetically, and some studies have shown sex-specific (Chaloupka and Limpus, 1997) and habitat-related differences (Leon and Diez, 1999; Diez and van Dam, 2002), the latter were presumably due to differences in prey abundance. Growth rates of hawksbills recorded in the Caribbean are much faster than those of hawksbills in Australia (Limpus, 1992; Chaloupka and Limpus, 1997; Whiting and Guinea, 1998) or in the Chagos Archipelago in the Indian Ocean (Mortimer et al., 2002).

Size at Maturity and Sexual Dimorphism. — As has been demonstrated in some other species of sea turtles (Limpus and Reed, 1985), sexual maturity in hawksbills occurs over a range of sizes (Limpus, 1992). Moncada et al. (1999) reported nesting female hawksbills in Cuba as small as 58.5 cm SCL, but minimum sizes of nesting females around the Caribbean are typically much larger. Nesting females in the Pearl Cays, Nicaragua, averaged 79.8 cm SCL_{min} (70.5–85.3 cm, SD = 3.2, *n* = 21) (Lagueux et al., 2003); 82 cm SCL_{max} (72.4–94.0 cm, SD = 3.9, *n* = 180) at Tortuguero, Costa Rica (Bjorndal et al., 1985); 83.1 cm $SCL_{n\text{-}t}$ at Mona Island (Diez and van Dam, 2002); and 83.5 cm $SCL_{n\text{-}t}$ (81.3–88.9 cm, SD = 2.04, *n* = 12) in Guyana (Pritchard, 1969).

Data on the average size of adult male hawksbills are not available. In the few studies in which hawksbills have been studied on the feeding grounds (where both sexes are potentially available), either few or no adult males were captured or maturity status was not definitively determined by examination of the gonads. Although some histological data are available on the gonads of animals killed in a directed fishery in Cuba, the sample was limited to 13 males, of which 8 showed evidence of spermatogenesis; the smallest males with spermatogenesis were 65–67 cm SCL (Moncada et al., 1999). It is possible that hawksbills in the Caribbean are sexually dimorphic with respect to size at maturity, as has been postulated for hawksbills in Australia on the basis of sex-specific growth patterns (Chaloupka and Limpus, 1997).

Van Dam and Diez (1998b) observed a sexually dimorphic pattern in tail length for Mona hawksbills larger than 68.2 cm SCL, with tails of males being longer than those of females. They inferred that 68.2 cm SCL was the minimum size of sexual maturity for adult males at Mona, although the animals were not examined laparoscopically nor was there confirmation of maturity based on histology. A practical consideration of the hawksbill's maturity being reached over a range of sizes is that males larger than the minimum size at maturity may still have undifferentiated tails and thus be externally indistinguishable from females (Limpus, 1992).

Hawksbills in the Caribbean have been recorded to attain a maximum weight of 127 kg (Lewis, 1940), but average weights for adults are typically much less. Mean weight of nesting females at Tortuguero, Costa Rica, was 59.0 kg (*n* = 16, range 46–69 kg, SD = 7.7) (Bjorndal et al., 1985); a sample of nesting females at Shell Beach, Guyana averaged 60.7 kg (SD = 7.87) (Pritchard, 1969).

Age at sexual maturity for hawksbills is not precisely known, partly because of the lack of knowledge of the duration of time spent as post-hatchlings in the pelagic environment. Current age-at-maturity estimates are typically given as the number of years required to reach maturity *after* recruiting to neritic environments. In the U.S. Virgin Islands, this age was 16.5–19.3 years (Boulon, 1994), whereas around Mona Island, Puerto Rico, it was 14.7 yr after recruitment (Diez and van Dam, 2002). These estimated ages are much younger than in Australia, where it is estimated that most hawsksbills are decades old at first breeding (Limpus, 1992; Chaloupka and Limpus, 1997).

Longevity. — A minimum estimate of longevity of hawksbills of 45 years can be calculated from the age at sexual maturity plus reproductive longevity. Meylan and Donnelly (1999) estimated the average age at which hawksbills are sexually mature to be 25 years, based on data from the Caribbean Sea (Boulon, 1983, 1994; Diez and van Dam, 2002), the Indian Ocean, (Mortimer, 1998) and the Pacific Ocean (Limpus, 1992, *pers. comm.*; Chaloupka and Limpus, 1997). Reproductive longevity has been estimated (Meylan and Donnelly, 1999) to be at least 20 years on the basis of observations of individual nesting hawksbills spanning 17–20 years (Mortimer and Bresson, 1999) and the likelihood that the reproductive longevity of hawksbills is comparable to that of other marine turtles within the family Cheloniidae, which is at least 20–30 years (Carr et al., 1978; FitzSimmons et al., 1995).

Estimates of longevity are difficult to make due to the confounding effects of factors such as tag retention, study-period limitations, and the existence of outliers in the data.

Male Reproductive Cycle. — The reproductive cycle of the male loggerhead turtle (*Caretta caretta*) was described by Wibbels et al. (1990), and it is likely that the prenuptial cycle they observed is the general pattern for sea turtles (Owens, 1997). This cycle entails spermatogenesis and highest testosterone levels in the winter and early spring and dropping testosterone levels as the mating season progresses. Laparoscopic examinations in Panama of male hawksbills that were observed to have been mating with females have revealed enlarged testes and epididymides, supporting the hypothesis that male hawksbills also have a prenuptial cycle (Meylan and Meylan, unpubl. data).

Female Reproductive Cycle. — The endocrinology of reproductive female sea turtles was described by Owens (1997). Hawksbills rarely nest in successive years, the more typical cycles reported being 2 to 4 years (Hirth, 1980; Meylan, 1984b; Miller, 1997), but intervals as long as 10 years have been suggested (Mortimer and Bresson, 1999). The mean remigration interval for hawksbills nesting at Jumby Bay, Antigua, where saturation tagging has been carried out for more than a decade, is 2.69 years; no 1-year remigrations were recorded in this study; 2- and 3-year migrations were the most common (Richardson et al., 1999). In Florida, the only hawksbill remigration data we are aware of are those of Lund (1985), who observed the same female hawksbill nesting at Jupiter Island during 3 seasons, with remigration intervals between nesting seasons of 3 years and 2 years.

The average number of nests per season per female is difficult to determine for any of the sea turtles because of the logistic challenge involved in attaining complete coverage of the nesting beach. This is particularly true for hawksbills, because nesting may occur over a six-month period or even longer (see Nesting season). Meylan and Donnelly (1999) adopted a range of 3 to 5 nests/female/season based on data from all ocean basins (Richardson et al., 1989; Hillis, 1995; Guzman et al., 1995; Dobbs et al., 1999; Mortimer and Bresson, 1999; Pilcher and Ali, 1999), but it is possible that this range is an underestimate. The average is 4.5 nests/female/season at Jumby Bay, Antigua, where coverage of the nesting beach is extremely thorough; a pronounced mode of 5 nests/female/season was recorded there (Richardson et al., 1999).

Miller (1997) reported the average internesting interval for hawksbills around the world to be 14.5 days but it was slightly longer at Tortuguero, Costa Rica (16.4 days; SD = 2.1, *n* = 28; Bjorndal et al., 1985). The most common intervals at Rio Lagartos, Mexico, were 14, 15, and 16 days (Garduño-Andrade, 1999).

Courtship / Mating Season / Mating Behavior. — Miller (1997) described the general pattern of courtship and mating for marine turtles. We are not aware of any detailed accounts for hawksbills. The timing and location of courtship and mating by hawksbills in Florida waters is unknown but could be predicted to be spring through early fall along the southeast coast and in the Florida Keys. Turtle fishermen in Caribbean Panama report that mating in this species occasionally takes place plastron-to-plastron. Hornell (1927) described the vulnerability, caused by the turtles' distraction, of mating pairs of hawksbills to harpooners in the Seychelles Islands. This vulnerability is also seen in Caribbean Panama, where harpooners specifically target mating pairs.

Nesting Season / Nest Sites / Nesting Behavior. — The hawksbill nests only rarely in Florida, with a maximum of four nests recorded in any year from 1979–2003 (Meylan et al., 1995, FWC Statewide Nesting Beach Survey database*)*. The only other nesting by hawksbills within the continental U.S. that we are aware of involved a single nest in Texas (Mays and Shaver, 1998). Based on a total of 31 nests recorded statewide through 2003, one can infer that hawksbill nesting in Florida occurs primarily from June through December. Most nests have been documented in August through October (Table 5-3). However, in the Marquesas Islands (Monroe County), a fresh track was observed on the beach on 23 November 1997 and relatively recent nests were found in late December (T. and E. Wilmers, *pers. comm*.). A single nest genetically confirmed to be that of a hawksbill was constructed in the Marquesas around 1 April 1999 and is the only hawksbill nest in the state recorded in the spring. This female had a mtDNA haplotype of Q (T. Wilmers, *pers. comm*.), which has been reported only for hawksbills nesting in Mexico, where springtime nesting is typical.

Although the sample size of nests is small, the nesting season in Florida appears to be more similar to that in the eastern Caribbean (Antigua, Puerto Rico, U.S. Virgin Islands) than to that of the large hawksbill population in the Yucatan, which peaks in May and June (Corliss et al., 1989; Richardson, 1990; Hillis, 1990; Garduño-Andrade, 1999). Curiously, the Florida nesting season differs somewhat from that of Cuba, where it occurs in the fall and continues until February (Moncada et al., 1999).

Nesting by hawksbills in Florida has been reported from Cape Canaveral National Seashore (Volusia County) south to Boca Grande Key and the Marquesas Islands (Monroe County) and at a single locality (Longboat Key, Manatee County) on the west coast (Figs. 5-9, Table 5-3, County Map, p. 32). Table 5-3 includes all hawksbill nests in the FWC Statewide Nesting Beach Survey database along with some older published and unpublished records that we consider to be valid. Only in rare cases was genetic testing carried out, however, and we now realize that considerable hybridization with other species is occurring, making such testing highly desirable (see Threats). We are aware of several nests resulting from hybrid crosses (usually between hawksbills and loggerheads), and in at least one case, the nesting female was genetically confirmed to be a hybrid (L. Ehrhart and D. Bagley, *pers. comm*.). We have excluded the nests of known or suspected hybrids from Table 5-3.

The extent of hawksbill nesting in Florida is likely to be underestimated for a number of reasons, including the following: incomplete surveillance of beaches in areas known

Table 5-3. Reported nesting activity of the hawksbill turtle, *Eretmochelys imbricata*, in Florida. Unless otherwise indicated, Date is the date on which the nest was constructed; CS = clutch size; HS = hatching success (%); IP = incubation period (days). *SNBS = Statewide Nesting Beach Survey program, Florida Fish & Wildlife Conservation Commission.

Location	Date	CS	HS	IP	Source
VOLUSIA COUNTY					
Canaveral National Seashore					
	8/16/82	125	0		McMurtray & Richardson, 1985
MARTIN COUNTY					
Jupiter Island	7/2/74	100	67	57	Lund, 1985
	8/13/74				Lund, 1985
	7/23/77	123	70.1	58	Lund, 1985
	6/10/79	118			Lund, 1985
	8/9/79				Lund, 1985
PALM BEACH COUNTY					
Juno Beach	8/1/59	172	29.1		Carr et al., 1966
Boca Raton	hatched 8/28/92	121	68.6		J. Wyneken, *pers. comm.*
	found 9/9/92				J. Wyneken, *pers. comm.*
Lantana	1985				SNBS* database
BROWARD COUNTY					
Ft. Lauderdale	9/14/94				SNBS database
	6/25/97	167	62.3	48	L. Fisher, *pers. comm.*
Port Everglades	8/21/86	76	61.8		Wyneken & Hicklin, 1988
MIAMI-DADE COUNTY					
Soldier Key	10/25/81	141		91	Dalrymple et al., 1985
	9/8/90	170	91.2	64	W. Teas, *pers. comm.*
	10/31/90				W. Teas, *pers. comm.*
Virginia Key	1995				SNBS database
MONROE COUNTY					
Bahia Honda State Park					
	hatched 10/10/00	90	58.9		M. Markey, *pers. comm.*
	9/14/00	137	38.7	58	M. Markey, *pers. comm.*
	9/12/00	135	68.9	72	M. Markey, *pers. comm.*
	hatched 9/22-29/02	138	34.1		M. Markey, *pers. comm.*
	ca. 9/1/02	105	28.6		M. Markey, *pers. comm.*
	9/19/02	95	65.3		M. Markey, *pers. comm.*
Boca Grande Key					
	excavated 9/1/89				P. Wells, *pers. comm.*
Marquesas Keys					
	found 12/22/95	146	4.1		Wilmers & Wilmers, 1998
	found 12/22/95	168	0		T. & E. Wilmers, *pers. comm.*
	found 11/23/97				T. & E. Wilmers, *pers. comm.*
	found 12/25/97				T. & E. Wilmers, *pers. comm.*
	found 4/10/99	187	0		T. & E. Wilmers, *pers. comm.*
	found 12/3/00				T. Wilmers, *pers. comm.*
MANATEE COUNTY					
Longboat Key	5/19/80	120	34.2	57	O. Clayton, *pers. comm.*

to be used by hawksbills, such as the Florida Keys; the greatly reduced level of beach surveys occurring in the fall months (statewide surveys primarily target the loggerhead turtle, which typically finishes nesting in August); the similarity of hawksbill and loggerhead tracks (both of similar size and with alternating gaits); the tendency for hawksbills to nest in or under vegetation, sometimes on narrow beaches leaving little or no track; and the similarity of loggerhead and hawksbill hatchlings, making detection less likely when nest inventories are carried out. Some of the nests at Bahia Honda State Park have been detected only by the presence of dead vegetation several days after the nest was constructed, and in one case, after hatchlings were found in a parking lot (M. Markey, *pers. comm.*).

It is possible that there is undetected hawksbill nesting in the Dry Tortugas. There is a museum specimen (USNM 7702) of a hatchling hawksbill from Garden Key (Dry Tortugas) that was catalogued in 1872 without any collecting information. The animal measures 4.84 cm SCL_{min} and still bears a distinct yolk sac scar and egg tooth. Although it conceivably hatched on Garden Key, it is slightly larger than most newborn hatchlings, so it is possible that it washed up on Garden Key after having hatched elsewhere. Hawksbill nesting has not been documented in the Dry Tortugas since regular monitoring began in 1995, but neither spatial nor temporal coverage of the various keys is complete.

Very little information about the historical nesting distribution of hawksbills in Florida is available. True (1884) stated that hawksbills occurred on the southern coasts of Florida and nested from late April to the first of July, preferring gravelly beaches to sandy ones. Audubon (1926) briefly mentioned that hawksbills nested in the outer Florida Keys in July and August. DeSola (1935) reported nesting by *Eretmochelys* at Soldier Key, Miami-Dade County; no details were given, but hawksbill nesting has been reported at this tiny mangrove key in Biscayne National Park three times in recent decades (see Table 5-3). The two nests recorded in 1990 were attributed to different individuals on the basis of photographs (W. Teas, *pers. comm.*). There is a report of a hawksbill nest in the late 1970s or early 1980s at nearby Cape Florida (C. LeBuff, *pers. comm.*). It is possible that this area in Miami-Dade County was historically a more important nesting site for hawksbills.

Nesting by hawksbills takes place primarily at night, but occasional daytime nesting is observed in the Caribbean region. Hawksbills traverse the beach with alternating front flipper movements, leaving a track that is similar to that of the loggerhead in this respect; the tracks are also similar in size. However, a few characters distinguish hawksbill tracks from loggerheads: the front flipper marks of hawksbills are longer and more prominent, like those of a green turtle; the hind flippers do not leave comma-shaped marks; and there is usually a weaving tail drag. There is a strong tendency for hawksbills to nest near or under vegetation, but their nests may be placed in any zone of the beach.

The nesting process takes approximately 1 to 1.5 hrs. A detailed description of nesting behavior was given by Carr et al. (1966). Hawksbills have been documented to show philopatry to a specific nesting beach, and they have a tendency to nest in the same general area of that beach (Carr et al., 1966; Carr and Stancyk, 1975; Diamond, 1976; Bjorndal et al., 1985). However, the extent to which the nest-site fidelity occurs within a population has not been quantified. All five nests of the turtle observed at Jupiter Island, Florida (Table 5-3), were within a stretch of 2.8 km, and two were less than 100 m apart (Lund, 1985).

Eggs. — Hawksbill eggs are white, approximately spherical, and have flexible calcareous shells. Egg diameters are approximately 38 mm in the Caribbean region (Van Buskirk and Crowder, 1994); a variable number of small, yolkless eggs may also be laid.

Clutch Size. — Most of the clutch counts available for Florida hawksbills were obtained by examining the contents of the nests after hatching, a method that is not as accurate as counts made at the time the eggs are deposited. The mean clutch size for 20 hawksbill nests recorded at various locations around Florida is 131.7 (SD = 30.39; Table 5-3). This compares with a mean of 130 (SE = 6.8) recorded for 17 hawksbill populations around the world and a mean of 150.7 (SD = 8.54) for seven localities in the Caribbean and Atlantic region (Van Buskirk and Crowder, 1994). Few data are available on egg volumes for Caribbean hawksbills; worldwide, egg volumes average 28.7 cc (SE = 1.3) (Van Buskirk and Crowder, 1994).

Reproductive Potential. — A female hawksbill laying 130 eggs per nest 3 to 5 times per reproductive season would produce from 390 to 650 eggs annually. Realized reproductive output would, of course, depend on hatching and emergence success. Based on estimates of reproductive longevity of 20 years (see Longevity), an individual hawksbill may be expected to produce for at least 6 reproductive seasons.

Incubation and Hatching. — Incubation periods for eight hawksbill nests in Florida varied from 48 to 91 days (mean = 63.1; SD = 13.2, Table 5-3), the longest period having been recorded for a nest constructed October 25. Van Buskirk and Crowder (1994) reported a mean incubation period of 60.2 days for four hawksbill populations in the Caribbean and Atlantic regions. Hatching success for 18 Florida nests varied widely (0 to 91.2%) and averaged 43.5% (Table 5-3).

Hatchling Size. — Hawksbill hatchlings averaged 42.1 mm in carapace length at four localities in the Caribbean and Atlantic region (Van Buskirk and Crowder, 1994). We are not aware of any Florida data on hatchling size. A hatchling from Bahia Honda State Park in the Florida Keys is shown in Fig. 5-3.

POPULATION BIOLOGY

Density and Biomass. — Density and biomass estimates are not available for hawksbills in Florida habitats. However, they do exist for the hawksbill foraging aggregation at Jaragua National Park in the Dominican Republic. Leon and Diez (1999) reported densities of 5.6, 6.6, and 8.2 turtles/km^2 at three study sites characterized by sparse hardbottom and of 58.3 and 96.8 turtles/km^2 in two coral reef areas. Corresponding biomass estimates were 35.8, 40.0, and 58.8 kg/km^2 on sparse hardbottom and 161.6 and 568.1 kg/km^2 on coral reef.

Population Structure. — The hawksbill population at Jaragua National Park in the Dominican Republic was shown to consist principally of juveniles and subadults, leading the authors to describe the site as developmental habitat (Leon and Diez, 1999). Other areas, such as Mona Island, Puerto Rico, and Las Coloradas, Mexico, are known to have a broader range of sizes represented, but it is likely that these are cases in which nesting and internesting habitats, or adult foraging areas, happen to overlap with developmental habitats. The size distribution of hawksbills entrapped at the St. Lucie Nuclear Plant is shown in Fig. 5-10. Nearly all animals can be considered immature.

The sex ratio of a sample of dead hawksbill hatchlings from a nest at Soldier Key, Florida, was heavily male-biased, presumably due to the cool incubation environment late in the nesting season (Dalrymple et al., 1985). Hawksbill nests from seven seasons in Brazil were predicted to be more than 90% female based on incubation duration (Godfrey et al., 1999). The sex ratios of immature hawksbill populations foraging at Jaragua National Park in the Dominican Republic and at Buck Island Reef National Monument in the U.S. Virgin Islands were also predicted to be skewed towards females on the basis of serum testosterone levels (Leon and Diez, 1999; Geis et al., 2003). This contrasts with a similar study at Mona Island, Puerto Rico that predicted a sex ratio not significantly different from 1:1 (Diez and van Dam, 2003).

INTERSPECIFIC INTERACTIONS

Diet and Feeding. — Post-hatchling hawksbills in the pelagic environment in the Caribbean and western Atlantic feed at the surface on pelagic species of *Sargassum* algae and other items associated with weed lines (Meylan, 1984a, 1988; Carr, 1987a). The gut contents of four post-hatchlings 14.0 to 21.3 cm SCL that stranded in Florida are listed in Table 5-2. The presence of several items that float, such as styrofoam, plastic beads, and tar droplets, suggests surface-feeding. Hawksbills that have left the pelagic environment and have begun to feed on the bottom consume principally demosponges (Meylan, 1984a, 1988; Anderes and Uchida, 1994; van Dam and Diez, 1997c; Leon and Bjorndal, 2002). However, at Buck Island Reef National Monument, U.S. Virgin Islands, sponges are very scarce, and the hawksbills have been documented to feed extensively on the zooanthid *Zoanthus sociatus* (Mayor et al., 1998; Pemberton et al., 2002). At study sites in the Dominican Republic, the corallimorpharian *Ricordea florida* was an important part of the diet, although sponges were still the most frequent diet item (Leon and Bjorndal, 2002). Diet studies have shown a high degree of selectivity with respect to prey items (Meylan, 1984a, 1988; Leon and Bjorndal, 2002). A description of foraging behavior of hawksbills is given by van Dam and Diez (1997c).

Predation. — Witzell (1983) reviewed the known predators of hawksbill turtles of various life history stages. In Florida, an immature female hawksbill (66.8 cm SCL_{min}) that stranded on Boca Chica Key, Monroe County, appeared to have died from a massive infection where the peritoneum had been punctured by a shark bite (Estep, 1998). Another documented predator of hawksbills in Florida is the fire ant (*Solenopsis invicta*) which killed emerged hatchlings at Bahia Honda State Park in the Florida Keys (M. Markey, *pers. comm.*). One of the hawksbill nests in Palm Beach County was partially preyed upon by either foxes or raccoons (J. Wyneken, *pers. comm.*), and the single nest in Volusia County was preyed upon by raccoons (McMurtray and Richardson, 1985).

Parasites and Disease. — Witzell (1983) reviewed known parasites and commensals of hawksbills. Diseases of hawksbills are poorly studied. Fibropapillomatosis (FP) has

Figure 5-12. Suspected hawksbill hybrid with fibropapillomatosis. Turtle was captured in Florida Bay, Monroe County, Florida (B. Schroeder, *pers. comm.*). Photo by the Turtle Hospital, Marathon, Florida.

Table 5-4. Carcass anomalies of hawksbill turtles (*Eretmochelys imbricata*) recovered by the Florida Sea Turtle Stranding and Salvage Network, 1980–2002. % *E.i.* = percent of all hawksbills; % All = percentage occurrence of each anomaly in strandings of all other species of sea turtles in Florida.

Anomaly	SCL$_{n-t}$ < 22 cm	SCL$_{n-t}$ ≥ 22 cm	% *E.i.* $n = 379$	% All $n = 19{,}388$
Boat-related injuries	1	17	4.7	13.7
Emaciated	12	13	6.6	3.2
Fibropapilloma tumors	0	0	0	5.8
Entangled in monofilament line and/or hooked	3	15	4.7	3.2
Entangled in net, trap line, or other debris	12	7	5.0	1.6
Shark bite wounds	0	7	1.8	2.9
Mutilated (e.g., bullet wounds, knife cuts)	0	5	1.3	2.4
Covered in tar or oil	35	10	11.9	1.1

rarely been reported to occur in hawksbills. D'Amato and Moraes-Neto (2000) reported two cases in Brazil that were histopathologically confirmed to be fibropapillomatosis. Both were captive animals, and the authors suggested that perhaps stressed immune systems made the animals more susceptible to FP. They also noted that a relatively high level of hybridization occurred between Brazilian hawksbills and loggerheads (Bass et al., 1996) and suggested that this may have been a factor, although they did not know whether the two animals they examined were hybrids. No FP was reported in any of the 379 hawksbills retrieved by the Florida STSSN from 1980 to 2002, but we are aware of three animals—two definitive and one suspected hawksbill/loggerhead hybrids captured in the Florida Keys with FP tumors (R. Moretti and S. Shaf, *pers. comm.*; B. Schroeder, *pers. comm.*; Fig. 5-12). We are aware of only one other report of FP in hawksbills, involving a captive turtle in Queensland, Australia (J. Miller, *pers. comm.*). No genetic data on this animal were available.

THREATS

Documented Threats. — Hawksbills in Florida waters face numerous threats, as evidenced by some of the carcass anomalies of animals recovered by the FL STSSN from 1980 to 2002 (Table 5-4). These anomalies were noted by stranding personnel at the time of recovery of the animals. Anomalies are not always observed or recorded, so these are minimum estimates of the number of animals affected by these factors. The anomalies may or may not be related to the cause of death. For example, turtles may be struck by boats after death. Also, multiple anomalies may be recorded for a single animal, and it is not always clear what was the initial one contributing to the stranding, e.g., fibropapillomas or entanglement in marine debris. Some mortality factors, such as drowning in shrimp trawls, may leave no obvious signs.

By far the most frequently recorded anomaly for hawksbill carcasses in Florida is fouling by oil or tar (Fig. 5-13). Fouling may be external, internal, or both. Some carcasses were described as being 'encased' in tar. Nearly 12% of stranded hawksbills showed this anomaly (Table 5-4), which compares with only 1.1 % of strandings of all other species combined. The geographic distribution of stranded hawksbills with evidence of oil or tar from 1980 to 2002 is shown in Fig. 5-14. Nearly all oil-affected turtles have stranded along the southeastern coast and in the Keys; there are no records from the west coast. All but 6 of 45 oiled hawksbills with carapace measurements were < 22 cm SCL$_{n-t}$ (Fig. 5-15) and thus were most likely living in the pelagic habitat when they were oiled. In some cases, *Sargassum* algae were found in the digestive tract. Table 5-4 compares the number of hawksbills less than and greater than 22 cm SCL$_{n-t}$ that were observed to have the various anomalies, including oil or tar.

Figure 5-13. Juvenile hawksbill turtle (*Eretmochelys imbricata*) 21.5 cm CCL$_{n-t}$ that stranded at Pompano Beach, Broward County, Florida, with tar on the shell, tongue, and oral mucosa. Photo by Susan Reed.

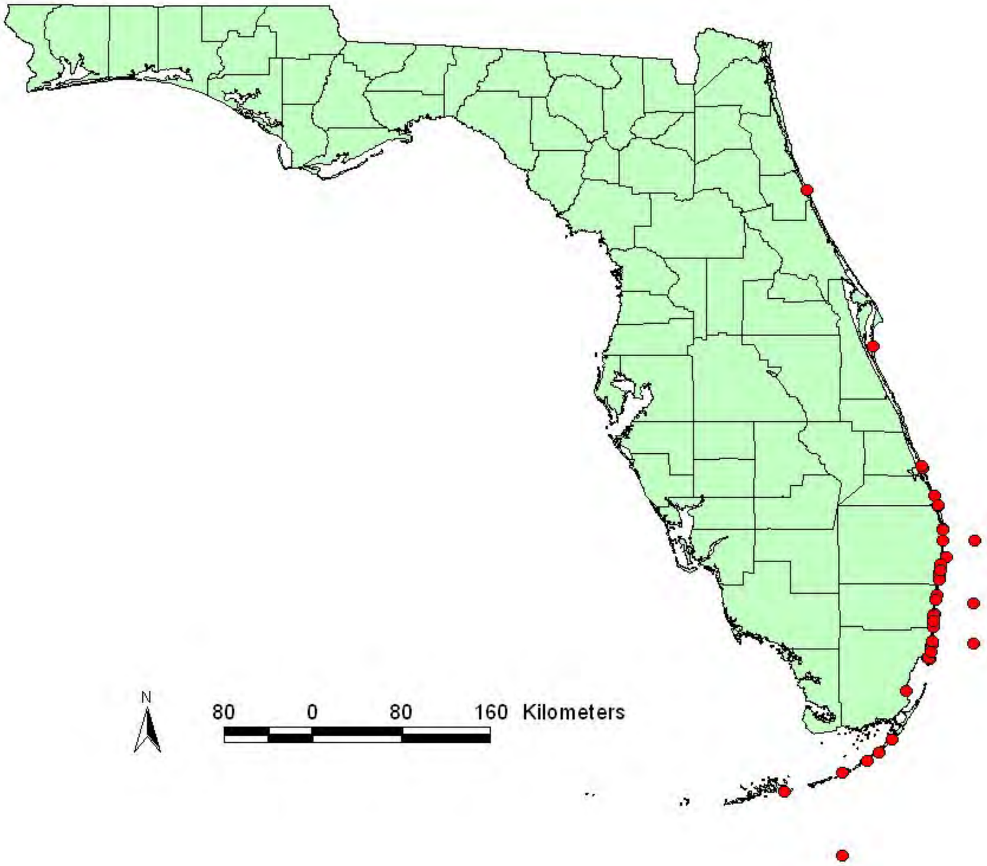

Figure 5-14. Geographic distribution of stranded hawksbill turtles (*Eretmochelys imbricata*) recorded in Florida with evidence of tar or oil, 1980–2002. Source: Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, Sea Turtle Stranding and Salvage Network; *n* = 48.

An episode of tarring of hawksbills occurred from mid-May to mid-July 1993 on the southeastern coast in Palm Beach, Broward, and Miami-Dade counties, with nine animals recovered with evidence of tar (FL STSSN). Tar analyses of two of the animals performed with a high-resolution gas chromatograph suggested that both animals had been affected by the same tar and that it was most likely fresh crude oil (T. Van Vleet, *pers. comm.*).

Hawksbills recovered by the FL STSSN have a higher incidence of entanglement in monofilament, net, trap line, and other debris than other species of marine turtles (Table 5-4). This may be due, at least in part, to the preponderance of small turtles in the sample. Carr (1987b) predicted a higher threat of entanglement by and ingestion of marine debris for young turtles inhabiting driftlines in the open ocean, due to the concentration of persistent plastic materials in these downwelling zones. Entanglement may lead to flipper loss in those animals that are rehabilitated (Redfoot et al., 1985; L. Wood, *pers. comm.*).

Boat-related injuries are much more common in hawksbills greater than 22 cm SCL than in those less than 22 cm SCL, presumably a consequence of differences in habitat occupation. On the nesting beaches, misorientation due to artificial lights in a parking lot in Bahia Honda State Park resulted in hatchling mortalities (M. Markey, *pers. comm.*). Other threats listed in the recovery plan for hawksbills in the U.S. Caribbean, Atlantic, and Gulf of Mexico (NMFS and USFWS, 1993) that are relevant to Florida include habitat loss or degradation due to beach erosion and erosion control methods, landscaping, vehicular traffic, siltation, agricultural and industrial pollution, sewage, anchoring and vessel groundings. The National Marine Fisheries Service's STSSN

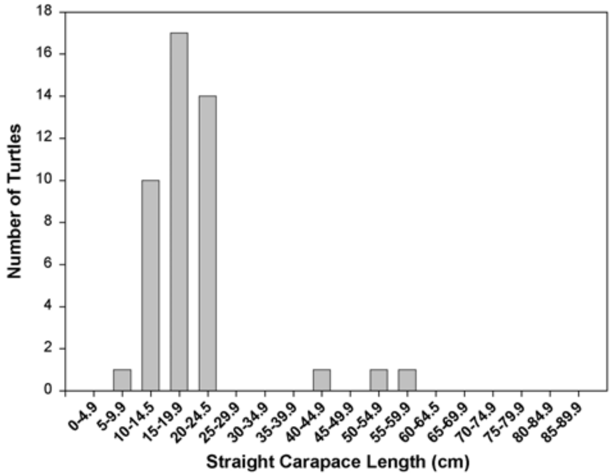

Figure 5-15. Size distribution of hawksbill turtles (*Eretmochelys imbricata*) that stranded in Florida with evidence of tar or oil, 1980–2002. Size is given as $\text{SCL}_{\text{n-t}}$. Source: Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, Sea Turtle Stranding and Salvage Network; *n* = 45.

Figure 5-16. (a) Removal of epidermal scutes (tortoiseshell) from the carapace of a hawksbill turtle (*Eretmochelys imbricata*) in Caribbean Panama, 1987. Photo by Anne Meylan. **(b)** Tortoiseshell hair ornaments, early Meiji period (ca. 1870s), Japan. Photo by Florida Museum of Natural History, Ethnographic Collection. **(c)** Hawksbill turtles, loggerhead turtles (*Caretta caretta*), and green turtles (*Chelonia mydas*) being dried for souvenirs, Guadeloupe, 1979. Photo by Anne Meylan.

has documented strandings and mortalities of hawksbills in the U.S. along the Gulf of Mexico and eastern seaboard caused by incidental capture in gill nets, shrimp trawls, pound nets, and flounder trawls, as well as entrapment in cooling-water intakes of power plants.

At the international level, the hawksbill has endured intense and sustained exploitation for its beautiful tortoiseshell (Fig. 5-16a,b) for thousands of years (Meylan and Donnelly, 1999). Traffic in products derived from hawksbills peaked in the latter half of the 20th century, when from 1970 to 1986 Japan imported shell from more than 50 countries, representing more than 600,000 adult hawksbills and 577,000 juveniles (Milliken and Tokunaga, 1987). International trade bans under the Convention on International Trade in Endangered Species (CITES), and focused conservation programs have averted the species' extinction in recent decades, although the local and tourist trade in tortoiseshell and hawksbill souvenirs (Fig. 5-16c) continues, often at high levels, in areas of Asia, Africa, and the Americas (Meylan and Donnelly, 1999; Arauz, 2000; Fleming, 2001; Chacon, 2002).

Figure 5-17. Hawksbill turtle (*Eretmochelys imbricata*) (right) and loggerhead turtle (*Caretta caretta*) (left) mating off Carysfort Lighthouse (Monroe County), Florida. Photo by Al Catalano, provided courtesy of NOAA, National Marine Fisheries Service, Pelagic Observer Program.

In Florida, the hawksbill and other sea turtles are protected by the Endangered Species Act. We are aware of only one case of the intentional killing of a hawksbill in Florida which took place north of Key West (Traffic North America, 1998a). Poaching of eggs is not a threat due to the low number of nests. The U.S. Fish and Wildlife Service has prosecuted individuals who were caught importing turtle eggs and meat from Central America into Florida and other states (Traffic USA, 1995; Traffic North America 1998b, 2000); hawksbill carapaces have been seized at Florida airports by wildlife authorities.

Potential Threats. — Hawksbills are known to use artificial reefs for resting sites. A few recent cases in Florida in which sea turtles of other species were fatally entrapped in artificial reef structures suggest that this is a potential threat to hawksbills.

As mentioned above (Growth and Reproduction, Interspecific Interactions), numerous incidences of hybridization involving hawksbills have been observed in Florida. The mating of a male hawksbill with a female loggerhead off Carysfort Lighthouse on the east coast is shown in Fig. 5-17. Other records of hybrids involve hatchlings from nests, adult female hybrids seen on the nesting beach, and immature hybrids captured on foraging grounds. Some turtles have been confirmed genetically to be hybrids (Witzell and Schmid, 2003; L. Ehrhart and D. Bagley, *pers. comm.*; A. and P. Meylan, unpubl. data; T. Wilmers, *pers. comm.*), but others are only suspected to be hybrids on the basis of morphological characteristics. We are not aware of any data that could be used to evaluate whether this is a new or continuing phenomenon. Cases of hybridization involving hawksbills have also been observed elsewhere in the region, including Panama (P. and A. Meylan, unpubl. data), Bermuda (P. Meylan, A. Meylan, and J. Gray, unpubl. data), the Cayman Islands (C. Bell and J. Blumenthal, *pers. comm.*), Puerto Rico (C. Diez, *pers. comm.*), Brazil (Bass et al., 1996), and Nicaragua (Lagueux et al., 2003). We suggest that hybridization represents a potential threat to hawksbills. Rhymer and Simberloff (1996) discussed the processes by which species can risk extinction due to hybridization and introgression; they pointed out that hybrids are more susceptible to disease. D'Amato and Moraes-Neto (2000) mentioned a possible link between hybridization and FP in hawksbills. We have seen some support for this idea in Florida, with one suspected and two confirmed hybrids with the disease (Fig. 5-12).

STATUS

The hawksbill is listed as Endangered in the U.S. under the Endangered Species Act and as Critically Endangered worldwide by IUCN (Baillie and Groombridge, 1996). Only five regional populations that have more than 1000 females nesting annually remain (Meylan and Donnelly, 1999). The status of the hawksbill in 35 countries in the Caribbean region was reviewed by Meylan (1999a) who reported widespread population declines. Lund (1978) and Meylan (1992) reviewed the status of the species in Florida where it is listed as Endangered. Threats identified in those reviews, including oil pollution and entanglement in marine debris, do not appear to have abated, judging from the evidence examined for this account. No apparent change in nesting level in Florida has occurred since statewide monitoring began in 1979 (FWC Statewide Nesting Beach Survey database). Population trends of hawksbills in Florida waters are unknown, although newly initiated in-water research projects may provide these data in the future.

CONSERVATION OPTIONS AND SOLUTIONS

Florida serves as a dispersal corridor for hawksbill turtles hatched at nesting beaches throughout the Caribbean region, so it is urgent that the issue of marine pollution in Florida waters be addressed. Tar, presumably from unintentional oil spills and ballast washings of tankers, and persistent anthropogenic debris threaten the survival of pelagic-stage hawksbills on a wide scale. State, national, and international efforts are necessary to address this issue.

Florida provides important foraging habitat for hawksbills, particularly in the Florida Keys and along the southeastern coast in Palm Beach, Broward, and Miami-Dade counties. Protection of coral reef and other hardbottom communities in these areas is vital to the future of hawksbills in Florida.

The continued closure of international markets for tortoiseshell and other products derived from hawksbills is critical for the long-term survival of this species. Exploitation in countries in the Caribbean region adversely affects recruitment of hawksbills to Florida waters.

Florida and the U.S. should play an active role in the Interamerican Convention on Sea Turtles and other regional efforts to promote research and regional management of hawksbill and other sea turtles.

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LITERATURE CITED

Amos, A.F. 1989. In: Eckert, S.A., Eckert, K.L., and Richardson, T.H. (Compilers). Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology. NOAA Technical Memorandum NMFS-SEFC-232, pp. 9-11.

Anderes, B.L., and Uchida, I. 1994. Study of hawksbill turtle (*Eretmochelys imbricata*) stomach contents in Cuban waters. In: Study of the hawksbill turtle in Cuba (1). Ministry of Fishing Industry, La Habana, Cuba, pp. 27-40.

Arauz, R. 2000. Can we save our sea turtles? WWF Central America 3(1).

Audubon, J.J. 1926. The turtlers. In: Delineations of American Scenery and Character. New York: G.A. Baker, pp. 194-202.

Baillie, J., and Groombridge, B. 1996. IUCN Red List of Threatened Animals. Gland, Switzerland: IUCN, 368 pp.

Bass, A.L., Good, D.A., Bjorndal, K.A., Richardson, J.I., Hillis, Z.M., Horrocks, J.A., and Bowen, B.W., 1996. Testing models of female reproductive migratory behavior and population structure in the Caribbean turtle, *Eretmochelys imbricata*, with mtDNA sequences. Molecular Ecology 5:321-328.

Bjorndal, K.A., and Bolten, A.B. 1988. Growth rates of immature green turtles, *Chelonia mydas*, on feeding grounds in the southern Bahamas. Copeia 1988(3):555-564.

Bjorndal, K. A., Carr, A., Meylan, A. B., and Mortimer, J. A. 1985. Reproductive biology of the hawksbill *Eretmochelys imbricata* at Tortuguero, Costa Rica, with notes on the ecology of the species in the Caribbean. Biological Conservation 34:353-368.

Bolten, A.B. 1999. Techniques for measuring sea turtles. In: Eckert, K.L., Bjorndal, K.A., Abreu-Grobois, F.A., and Donnelly, M. (Eds.). Reseach and Management Techniques for the Conservation of Sea Turtles. IUCN/SSC Marine Turtle Specialist Group Publication No. 4: 110-114.

Boulon, R., Jr. 1983. Some notes on the population biology of green *Chelonia mydas* and hawksbill *Eretmochelys imbricata* turtles in the northern U.S. Virgin Islands; 1981-1983. Rept. to NMFS, Grant No. NA82-GA-A-00044, 18 pp.

Boulon, R., Jr. 1994. Growth rates of wild juvenile hawksbill turtles, *Eretmochelys imbricata*, in St. Thomas, United States Virgin Islands. Copeia 1994(3):811-814.

Bresette, M., Gorham, J., and Peery, B. 1998. Site fidelity and size frequencies of juvenile green turtles (*Chelonia mydas*) utilizing near shore reefs in St. Lucie County, Florida. Marine Turtle Newsletter 82:5-7.

Brongersma, L.D., 1972. European Atlantic Turtles. Zoologische Verhandelingen No. 121. Leiden: E. J. Brill, 318 pp.

Carr, A.F. 1940. A contribution to the herpetology of Florida. University of Florida Publication, Biological Science Series 3(1):1-118.

Carr, A. 1952. Handbook of Turtles: The Turtles of the United States, Canada, and Baja California. New York: Cornell University Press, 535 pp.

Carr, A. 1986. Rips, FADS, and little loggerheads: years of research have told us much about the behavioral ecology of sea turtles, but mysteries remain. BioScience 36(2):92-100.

Carr, A. 1987a. New perspectives on the pelagic stage of sea turtle development. Conservation Biology 1(2):103-121.

Carr, A. 1987b. Impact of nondegradable marine debris on the ecology and survival outlook of sea turtles. Marine Pollution Bulletin 18(6B):352-356.

Carr, A.F., and Stancyk, S. 1975. Observations on the ecology and survival outlook of the hawksbill turtle. Biological Conservation 8:161-172.

Carr, A., Hirth, H., and Ogren, L. 1966. The ecology and migrations of sea turtles, the hawksbill turtle in the Caribbean Sea. American Museum Novitates 2248:1-29.

Carr, A.F., Carr, M.H., and Meylan, A.B. 1978. The ecology and migrations of sea turtles, 7. The west Caribbean green turtle colony. Bull. Amer. Mus. Nat. Hist. 162:1-46.

Carr, A.F., Meylan, A.B., Mortimer, J.A., Bjorndal, K.A., and Carr, T. 1982. Preliminary survey of marine turtle populations and habitats in the western Atlantic. NOAA Tech. Memo. NMFS-SEFC-91, 91 pp.

Carr, T. 1977. The marine turtles and terrestrial reptiles of Culebra Island. Report to US Fish and Wildlife Service, contract #14-16-0008-2089, 28 pp.

Chacón, D. 2002. Diagnóstico sobre el commercio de las tortugas marinas y sus derividados en el istmo centroamericano. Red Regional para la Conservación de las Tortugas Marinas en Centroamérica (RCA). San José, Costa Rica, 247 pp.

Chaloupka, M.Y., and Limpus, C.J. 1997. Robust statistical modeling of hawksbill sea turtle growth rates (southern Great Barrier Reef). Marine Ecology Progress Series 146:1-8.

Corliss, L.A., Richardson, J.I., Ryder, C., and Bell, R. 1989. The hawksbills of Jumby Bay, Antigua, West Indies. In: Eckert, S. A., Eckert, K. L., and Richardson, T. H. (Compilers). Proc. of the 9th Annual Workshop on Sea Turtle Conservation and Biology. NOAA Tech. Memo. NMFS-SEFC-232, pp. 33-35.

D'Amota, A.F., and Moraes-Neto, M. 2000. First documentation of fibropapillomas verified by histopathology in *Eretmochelys imbricata*. Marine Turtle Newsletter 89:12-13.

Dalrymple, G.H., Hampp, J.C., and Wellings, D.J. 1985. Male-biased sex ratio in a cold nest of a hawksbill sea turtle (*Eretmochelys imbricata*). Journal of Herpetology 19(1):158-159.

De Sola, C.R. 1931. The turtles of the Northeastern States. New York Zoological Society 34(5):131-160.

De Sola, C.R. 1935. Herpetological notes from southeastern Florida. Copeia 1935(1):44-45.

Diamond, W. 1976. Breeding biology and conservation of hawksbill turtles, *Eretmochelys imbricata* L., on Cousin Island, Seychelles. Biological Conservation 9:199-215.

Diez, C.E., and van Dam, R.P. 2002. Habitat effect on hawksbill turtle growth rates on feeding grounds at Mona and Monito Islands, Puerto Rico. Marine Ecology Progress Series 234:301-309.

Diez, C.E., and van Dam, R.P. 2003. Sex ratio of an immature hawksbill seaturtle aggregation at Mona Island, Puerto Rico. Journal of Herpetology 37(3):533-537.

Dobbs, K.A., Miller, J.D., Limpus, C.J., and Landry, A.M., Jr. 1999. Hawksbill turtle (*Eretmochelys imbricata*) nesting at Milman Island, Northern Great Barrier Reef, Australia. Chelonian Conservation and Biology 3(2):344-361.

Duellman, W.E., and Schwartz, A. 1958. Amphibians and reptiles of southern Florida. Biological Sciences 3(5):221-223.

Ehrhart, L.M. 1983. Marine turtles of the Indian River Lagoon system. Florida Scientist 46(3/4):337-346.

Estep, L.K. 1998. *Eretmochelys imbricata* (hawksbill). Predation. Herpetological Review 26(4):235.

Fitzinger, L.J.F.J. 1843. Systema Reptilium. Fasciculus primus. Amblyglossae. Vindobonae, Braumüller and Seidel. 106 pp.

FitzSimmons, N.N., Tucker, A.D., and Limpus, C.J. 1995. Long-term breeding histories of male green turtles and fidelity to a breeding ground. Mar. Turtle Newsletter 68:2-4.

Fleming, E. H. 2001. Swimming against the tide: recent surveys of exploitation, trade and management of marine turtles in the Northern Caribbean. Washington, DC: TRAFFIC North America, 162 pp.

Fretey, J. 1998. Marine turtles of the Atlantic Coast of Africa.

Convention on the Conservation of Migratory Species of Wild Animals. UNEP/CMS Technical Publications No. 1, 254 pp.

Fretey, J., Meylan, A., and Tiwari, M. 2000. Occurrence of the hawksbill turtle (*Eretmochelys imbricata*) in West Africa. In: Mosier, A., Foley, A., and Brost, B. (Compilers) Proceedings of the Twentieth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-477, pp. 95-96.

Garduño-Andrade, M. 1999. Nesting of the hawksbill turtle, *Eretmochelys imbricata*, at Rio Lagartos, Yucatan, Mexico, 1990–1997. Chelonian Conservation and Biology 3(2):281-285.

Geis, A., Wibbels, T., Phillips, B., Hillis-Starr, Z., Meylan, A., Meylan, P., Diez, C., and van Dam, R. 2003. Predicted sex ratio of juvenile hawksbill seaturtles inhabiting Buck Island Reef National Monument, U.S. Virgin Islands. Journal of Herpetology 37(2):400-404.

Godfrey, M.H., D'Amato, A.F., Marcovaldi, M.Â., and Mrosovsky, N. 1999. Pivotal temperature and predicted sex ratios for hatchling hawksbill turtles from Brazil. Canadian Journal of Zoology 77:1465-1473.

Groombridge, B. 1990. Marine turtles in the Mediterranean: distribution, population status, conservation. Strasbourg: Council of Europe Nature and Environment Series No. 48. 98 pp.

Guzmán Hernández, V., Rejón Puch, J.C., Gómez Gómez, R., and Silva Sanchez, J. 1995. Informe final del programa de investigacíon y protección de las Tortugas marinas del estado de Campeche, México, temporada 1994. Situación actual. Secretaria de Pesca, Instituto Nacional de la Pesca, Centro Regional de Investigación Pesquera Carmen.

Gunter, G. 1981. Status of turtles on the Mississippi coast. Gulf Research Reports 7(1):89-92.

Hillis, Z. 1990. Buck Island Reef National Sea Turtle Research Program: 1989 – the year of hawksbills and hurricanes. In: Richardson, T. H., J. I. Richardson, and Donnelly, M (Compilers). Proc. of the Tenth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS/SEFC-278, pp. 15-17.

Hillis, Z.M. 1995. Buck Island Reef National Monument sea turtle research program, 1991. In: Richardson, J. I., and Richardson, T. H. (Compilers). Proc. of the 12th Annual Workshop on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-361, pp. 47-56.

Hirth, H.F. 1980. Some aspects of the nesting behavior and reproductive biology of sea turtles. Amer. Zool. 20:507-523.

Hirth, H., Huber, M., Frohm, T., and Mala, T. 1992. A natural assemblage of immature green (*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) turtles on the fringing reef of Wuvulu Island, Papua New Guinea. Micronesica 25(2):145-153.

Hornell, J. 1927. The turtle fisheries of the Seychelles Islands. H.M. Stationery Office. Government of Madras, 55 pp.

Jaap, W.C., and Hallock, P. 1990. Coral reefs. In: Myers, R.L., and Ewel, J.J. (Eds.) Ecosystems of Florida. Orlando: University of Central Florida, pp. 574-616.

Jaap, W.C., Beaver, C., Callahan, M., Coleman, F., Dardeau, M., Horn, L., Kidney, J., McCarthy, A., Reed, S., and Schmahl, G. 2003. Florida Middle Ground Benthic Habitat Evaluation. Report to the Gulf of Mexico Fisheries Management Council, 14 pp.

Jarrett, B.D., Hine, A.C., Halley, R.B., Naar, D.F., Locker, S.D., Neumann, A.C., Twichell. D., Hu, C., Donahue, B.T., Jaap, W.C., Palandro, D., and Ciembronowiez, K. 2005. Strange bedfellows – a deep-water hermatypic coral reef superimposed on a drowned barrier island: southern Pulley Ridge, SW Florida platform margin. Marine Geology 214(4):295-307.

Lagueux, C., Campbell, C.L., and McCoy, W.A. 2003. Nesting and conservation of the hawksbill turtle, *Eretmochelys imbricata*, in the Pearl Cays, Nicaragua. Chelonian Conservation and Biology 4(3):588-602.

León, Y.M., and Bjorndal, K.A. 2002. Selective feeding in the hawksbill turtle, an important predator in coral reef ecosystems. Marine Ecology Progress Series 245:249-258.

León, Y.M., and Diez, C.E. 1999. Population structure of hawksbill turtles on a foraging ground in the Dominican Republic. Chelonian Conservation and Biology 3(2):230-236.

Lewis, C.B. 1940. The Cayman Islands and marine turtle. In: Grant, C. Herpetology of the Cayman Islands. Bull. Inst. Jamaica Science Series 2, pp. 56-65.

Limpus, C.J. 1992. The hawksbill turtle, *Eretmochelys imbricata*, in Queensland: population structure within a southern Great Barrier Reef feeding ground. Wildl. Res. 19:489-506.

Limpus, C.J., and Reed, P.C. 1985. The green turtle (*Chelonia mydas*) in Queensland: a preliminary description of the population structure in a coral reef feeding ground. In: Grigg, G., Shine, R., and Ehmann, H. (Eds.). Biology of Australasian Frogs and Reptiles. Sydney: Royal Zool. Soc. of New South Wales, pp. 47-52.

Linnaeus, C. 1766. Systema Naturae per Regna tria Naturae secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Stockholm. Ed. 12, Vol. 1., 532 pp.

Lund, F. 1978. Atlantic Hawksbill. In: McDiarmid, R.W. (Ed.) Rare and Endangered Biota of Florida. Vol. 3. Amphibians and Reptiles. University Press of Florida, pp. 24-25.

Lund, P.F. 1985. Hawksbill turtle (*Eretmochelys imbricata*) nesting on the east coast of Florida. Journal of Herpetology 19(1):164-166.

Mayor, P.A., Phillips, B., and Hillis-Starr, Z. M. 1998. Results of the stomach content analysis on the juvenile hawksbill turtles of Buck Island Reef National Monument, U.S.V.I. NOAA Technical Memorandum NMFS-SEFSC-415, pp. 230-232.

Mays, J. L., and Shaver, D. J. 1998. Nesting trends of sea turtles in national seashores along Atlantic and Gulf Coast waters of the United States. Final Report for Natural Resources Preservation Program, Project Number 95-15, 61 pp.

McMurtray, J. D., and Richardson, J. I. 1985. A northern nesting record for the hawksbill turtle. Herpetological Review 16(1):16-17.

Meylan, A.B. 1984a. Feeding ecology of the hawksbill turtle (*Eretmochelys imbricata*): Spongivory as a feeding niche in the coral reef community. Ph.D. Thesis, University of Florida, Gainesville.

Meylan A. 1984b. Biological synopsis of the hawksbill turtle (*Eretmochelys imbricata*). In: Bacon, P., Berry, F., Bjorndal, K., Hirth, H., Ogren, L., and Weber, M. (Eds.). Proceedings of the Western Atlantic Turtle Symposium. Vol. 1. Miami, FL: RSMAS Printing, pp. 112-117.

Meylan, A.B. 1988. Spongivory in hawksbill turtles: a diet of glass. Science 239:393-395.

Meylan, A. 1992. Hawksbill turtle. In: Moler, P.E. (Ed.). Amphibians and Reptiles. Rare and Endangered Biota of Florida. Gainesville, Florida: University of Florida Press, pp. 95-99.

Meylan, A.B. 1999a. The status of the hawksbill turtle (*Eretmochelys imbricata*) in the Caribbean Region. Chelonian Conservation and Biology 3(2):177-184.

Meylan, A.B. 1999b. International movements of immature and adult hawksbill turtles (*Eretmochelys imbricata*) in the Caribbean Region. Chelonian Conservation and Biology 3(2):189-194.

Meylan, A.B., and Donnelly, M. 1999. Status justification for listing the hawksbill turtle (*Eretmochelys imbricata*) as Critically Endangered on the 1996 *IUCN Red List of Threatened Animals*. Chelonian Conservation and Biology 3(2):200-224.

Meylan, A., Redlow, A., Mosier, A., Moody, K., Foley, A., and

Brost, B. 2003. Sea turtles in Tampa Bay, Florida. In: Pribble, J.R., Janicki, A.J., and Greening, H. (Eds.). Baywide Environmental Monitoring Report, Tampa Bay, 1998-2001. Tampa Bay Estuary Program. Technical Publication #06-02.

Meylan, A., Schroeder, B., and Mosier, A. 1995. Sea turtle nesting activity in the state of Florida, 1979-1992. Florida Marine Research Publications. Technical Report 52:1-51.

Meylan, P., Meylan, A., Gray, J., and Ward, J. 2003. The hawksbill turtle in Bermuda. In: Seminoff, J.A. (Compiler). Proceedings of the Twenty-Second Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-503, p. 26.

Miller, J.D. 1997. Reproduction in sea turtles. In: Lutz, P.L. and Musick, J.A. (Eds.). The Biology of Sea Turtles. Boca Raton: CRC Press, pp. 51-81.

Milliken, T., and Tokunaga, H. 1987. The Japanese Sea Turtle Trade 1970-1986. A Special Report prepared by TRAFFIC (Japan). Washington, DC: Center for Environmental Education, 171 pp.

Moncada, F., Carrillo, E., Saenz, A., and Nodarse, G. 1999. Reproduction and nesting of the hawksbill turtle, *Eretmochelys imbricata*, in the Cuban Archipelago. Chelonian Conservation and Biology 3(2):257-263.

Mortimer, J.A. 1998. Turtle and Tortoise Conservation Project J1. Environmental Management Plan of the Seychelles. Final report submitted to the Seychelles Ministry of the Environment and the Global Environment Facility. Vol. 1, 82 pp.

Mortimer, J.A., and Bresson, R. 1999. Temporal distribution and periodicity in hawksbill turtles (*Eretmochelys imbricata*) nesting in Cousin Island, Republic of Seychelles, 1971-1997. Chelonian Conservation and Biology 3(2):318-325.

Mortimer, J.A., Day, M., and Broderick, D. 2002. Sea turtle populations of the Chagos Archipelago, British Indian Ocean Territory. In Mosier, A., Foley, A., and Brost, B. (Compilers), Proceedings of the Twentieth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-477, pp. 47-49.

Mrosovsky, N., Bass, A., Corliss, L.A., Richardson, J.I., and Richardson, T.H. 1992. Pivotal and beach temperatures for hawksbill turtles nesting in Antigua. Canadian Journal of Zoology 70:1920-1925.

National Marine Fisheries Service and U.S. Fish and Wildlife Service. 1993. Recovery Plan for Hawksbill Turtles in the U. S. Caribbean, Atlantic Ocean, and Gulf of Mexico. National Marine Fisheries Service, St. Petersburg, FL, 52 pp.

National Marine Fisheries Service and U.S. Fish and Wildlife Service. 1998. Recovery Plan for U.S. Pacific Populations of the Hawksbill Turtle (*Eretmochelys imbricata*). National Marine Fisheries Service, Silver Springs, MD, 82 pp.

Nelson, D.A. 1999. Sea turtle relative abundance and seasonal movements in Tampa Bay Entrance Channel. Rept. to U.S. Army Corps of Engineers, Jacksonville, FL, 30 pp.

Nietschmann, B. 1981. Following the underwater trail of a vanishing species – the hawksbill turtle. National Geographic Society Research Reports 13:459-480.

Owens, D.W. 1997. Hormones in the life history of sea turtles. In: Lutz, P.L., and Musick, J.A. (Eds.). The Biology of Sea Turtles. Boca Raton: CRC Press, pp. 315-341.

Ordoñez, C., Troëng, S., Ruiz, A., Possardt, E., Godfrey, D., Meylan, P., and Meylan, A. In Press. Investigation and restoration of the nesting population of the hawksbill turtle (*Eretmochelys imbricata*) at Comarca Ngöbe-Buglé Chiriquí Beach, Escudo de Veraguas, and Bastimentos Island National Marine Park, Panamá. Proc. 24th Ann. Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC.

Parker, L.G. 1996. Encounter with a juvenile hawksbill turtle offshore Sapelo Island, Georgia. In: Keinath, J.A., Barnard, D.E., Musick, J.A., and Bell, B.A. (Compilers). Proceedings of the Fifteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-287, pp. 237-240.

Pemberton, R., Coyne, M., Musick, J.A., Phillips, B., and Hillis-Starr, Z. 2002. Habitat utilization of hawksbill sea turtles at Buck Island Reef National Monument: the zoanthid question. In: Mosier, A., Foley, A., and Brost, B. (Eds.). Proc. 20th Ann. Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-477, pp. 69-70.

Perkins, T.H., Norris, H.A., Wilder, D.T., Kaiser, S.D. Camp, D.K., Matheson, R.E., Jr., Sargent, F.J., Colby, M.M., Lyons, W.G., Gilmore, R.G., Reed, J.K., Zarillo, G.A., Connell, K., Fillingfin, M., and Idris, F.M. 1997. Distribution of hard-bottom habitats on the continental shelf off the northern and central east coast of Florida. Final report submitted to the Southeast Area Monitoring and Assessment Program Bottom Mapping Workgroup and National Marine Fisheries Service pursuant to NOAA Award No. NA47FS0036, 54 pp.

Pilcher, N.J., and Ali, L. 1999. Reproductive biology of the hawksbill turtle, *Eretmochelys imbricata*, in Sabah, Malaysia. Chelonian Conservation and Biology 3(2):330-336.

Pritchard, P.C.H. 1969. Sea turtles of the Guianas. Bull. Florida State Museum 13(2):85-140.

Pritchard, P.C. H., and Trebbau, P. 1984. The Turtles of Venezuela. Society for the Study of Amphibians and Reptiles, Contributions to Herpetology No. 2, 401 pp.

Redfoot, W.E., Ehrhart, L.M., and Raymond, P.W. 1985. A juvenile Atlantic hawksbill turtle, *Eretmochelys imbricata*, from Brevard County, Florida. Florida Scientist 48(4):193-196.

Rhymer, J.M., and Simberloff, D. 1996. Extinction by hybridization and introgression. Ann. Rev. Ecol. Syst. 27:83-109.

Richardson, J.I. 1990. Estimation of sea turtle abundance and nesting success on Mona Island, Puerto Rico. Final Report, U. S. Fish and Wildlife Service, Unit Coop. Agreement 14-16-0009-1551, Work Order #10, 42 pp.

Richardson, J.I., Corliss, L.A., Ryder, C., and Bell, R. 1989. Demographic patterns of Caribbean hawksbills, Jumby Bay, Antigua. In: Eckert, S.A., Eckert, K.L., and Richardson, T.H. (Compilers). Proc. of the 9th Annual Workshop on Sea Turtle Conservation and Biology. NOAA Tech. Memo. NMFS-SEFC-232, pp. 253-256.

Richardson, J.I., Bell, R., and Richardson, T.H. 1999. Population ecology and demographic implications drawn from an 11-year study of nesting hawksbill turtles, *Eretmochelys imbricata*, at Jumby Bay, Long Island, Antigua, West Indies. Chelonian Conservation and Biology 3(2):224-250.

Schmid, J.R. 1995. Marine turtle populations on the east-central coast of Florida: results of tagging studies at Cape Canaveral, Florida, 1986-1991. Fishery Bulletin 93:139-151.

Schmid, J.R. 1998. Marine turtle populations on the west-central coast of Florida: results of tagging studies at the Cedar Keys, Florida. Fishery Bulletin 96:589-602.

Shaver, D.J. 1998. Sea turtle strandings along the Texas Coast, 1980-94. In: Zimmerman, R. (Ed.). Characteristics and causes of Texas marine strandings. U.S. Dep. Commer. NOAA Technical Report NMFS 143, pp. 57-72.

Smith, H.M., and Smith, R.B. 1979. Synopsis of the Herpetofauna of Mexico. Vol. VI. Vermont: John Johnson, 1044 pp.

Southeast Area Monitoring and Assessment Program – South Atlantic (SEAMAP-SA). 2001. Distribution of bottom habitats on the continental shelf from North Carolina through the Florida Keys. SEAMAP-SA Bottom Mapping Workgroup, Atlantic States Marine Fisheries Commission, Washington, DC, 166 pp.

Summers, T., Redlow, A., Foley, A., Singel, K., and Blackwelder, J. 2004. Mass marine turtle stranding due to cold stress in St. Joseph Bay, Florida. In: Coyne, M.S. and Clark, R.D. (Compilers). Proceedings of the 21st Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-528, pp. 334-335.

TRAFFIC North America. 1998a. Sea turtle butcher jailed. TRAFFIC North America 1(3):9.

TRAFFIC North America. 1998b. N.Y. sea turtle sting. TRAFFIC North America 1(3):9.

TRAFFIC North America. 2000. One egg thief jailed—another pleads guilty. TRAFFIC North America 3(1):9.

TRAFFIC USA. 1995. Turtle smuggler locked up. TRAFFIC USA 14 (2):8.

True, F.W. 1884. The useful aquatic reptiles and batrachians of the United States. In: Goode, G.B. (Ed.). The Fisheries and Fishery Industries of the United States. Washington, DC: Government Printing Office, pp. 137-162.

Van Buskirk, J., and Crowder, L.B. 1994. Life-history variation in marine turtles. Copeia 1994(1):66-81.

van Dam, R.P., and Diez, C.E. 1996. Diving behavior of immature hawksbills (*Eretmochelys imbricata*) in a Caribbean cliff-wall habitat. Marine Biology 127:171-178.

van Dam, R.P., and Diez, C.E. 1997a. Diving behavior of immature hawksbill turtles (*Eretmochelys imbricata*) in a Caribbean reef habitat. Coral Reefs 16:133-138.

van Dam, R.P., and Diez, C.E. 1997b. Surfacing behavior of the marine turtle *Eretmochelys imbricata*. Journal of Herpetology 31(2):313-316.

van Dam, R.P., and Diez, C.E. 1997c. Predation by hawksbill turtles on sponges at Mona Island, Puerto Rico. Proceedings of the Eighth International Coral Reef Symposium 2:1421-1426.

van Dam, R.P., and Diez, C.E. 1998a. Home range of immature hawksbill turtles (*Eretmochelys imbricata* (Linnaeus)) at two Caribbean islands. Journal of Experimental Marine Biology and Ecology 220:15-24.

van Dam, R.P., and Diez, C.E. 1998b. Caribbean hawksbill turtle morphometrics. Bulletin of Marine Science 62(1):145-155.

Vaughan, P. 1981. Marine turtles: a review of their status and management in the Solomon Islands. Report to World Wildlife Fund, Project No. 1452, 70 pp.

Wershoven, R., and Wershoven, J. 1988. A survey of juvenile green turtles and their resting and foraging habitats off Broward County, Florida 3/1/86-12/13/87. Rept. to the Florida Department of Natural Resources, Division of Marine Resources, 35 pp.

Whiting, S.D., and Guinea, M.L. 1998. A large population of slow growing hawksbills: preliminary results from a wild foraging population in Fog Bay, Northern Territory. In: Epperly, S.P., and Braun, J. (Compilers). Proceedings of the Seventeenth Annual Sea Turtle Symposium. NOAA Technical Memorandum NMFS-SEFSC-415, pp. 104-107.

Wibbels, T., Owens, D.W., Limpus, C.J., Reed, P., and Amoss, M. 1990. Seasonal changes in serum gonadal steroids associated with migration, mating and nesting in the loggerhead sea turtle (*Caretta caretta*). General and Comparative Endocrinology 79:154-164.

Wilcox, J.R., Bouska, G., Gorham, J., Peery, B. and Bresette, M. 1998. Knee deep in green turtles: recent trends in capture rates at the St. Lucie Nuclear Power Plant. In: Byles, R. and Fernandez, Y. (Compilers). Proceedings of the Sixteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-412, pp. 147-148.

Wilmers, T.J., and Wilmers, E.M. 1998. *Eretmochelys imbricata* (Hawksbill). Herpetological Review 29(1):50.

Witherington, B.E. 2002. Ecology of neonate loggerhead turtles inhabiting lines of downwelling near a Gulf Stream front. Marine Biology 140:843-853.

Witherington, B.E., and Ehrhart, L.M. 1989. Hypothermic stunning and mortality of marine turtles in the Indian River Lagoon System, Florida. Copeia 1989(3):696-703.

Witzell, W.N. 1983. Synopsis of biological data on the hawksbill turtle, *Eretmochelys imbricata* (Linnaeus, 1766). FAO Fisheries Synopsis No. 137, 78 pp.

Witzell, W.N., and Schmid, J.R. 2002. Investigation of immature sea turtles in the coastal waters of southwest Florida In: Mosier, A., Foley, A. and Brost, B. (Compilers). Proceedings of the Twentieth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-477, pp. 276-277.

Witzell, W.N., and Schmid, J.R. 2003. Multiple recaptures of a hybrid hawksbill-loggerhead turtle in the Ten Thousand Islands, southwest Florida. Herpetological Review 34(4):323-325.

Wyneken, J., and Hicklin, J.A. 1988. Confirmed hawksbill, *Eretmochelys imbricata*, nesting in Broward County, Florida. Marine Turtle Newsletter 42:6.

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Lepidochelys kempii – Kemp's Ridley

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SUMMARY. – Kemp's ridley, *Lepidochelys kempii*, is a critically endangered species of sea turtle that is common in Florida waters. It is the smallest sea turtle species and is recognizable by its circular carapace, olive gray coloration, and relatively large head with a parrot-like beak. Kemp's ridleys are distributed throughout the Gulf of Mexico and western North Atlantic Ocean. A few nesting females of this species have been observed on Florida beaches; however, the primary nesting beach is along the Gulf coast of Tamaulipas, Mexico. Historic records, incidental captures, and tagging data were compiled to provide a detailed distribution of live, wild Kemp's ridleys inhabiting coastal waters of Florida. Seagrass beds and mud bottom have been identified as the benthic habitats used by subadult turtles, but quantitative analyses of habitat associations have determined that live bottom is also an important developmental habitat. The near-shore waters of Florida's west coast provide important summer foraging grounds, while the offshore waters of the east coast are an important overwintering area. Seasonal north-south migrations have been documented on both coasts. Kemp's ridleys establish restricted foraging ranges along the Florida Gulf coast and may return to these areas for at least 4 years. Kemp's ridleys feed primarily on decapod crustaceans and a possible ontogenetic shift in prey and habitat has been suggested for subadult turtles in northwestern Florida. Egg harvest and capture in shrimp trawls were identified as the primary causes for the rapid decline of the Kemp's ridley population. However, protection of the nesting beaches and regulations imposed on the shrimp fishery (primarily use of turtle excluder devices [TEDs]) has presumably led to the increasing number of nests over the past 20 years. Florida's coastal waters provide essential developmental habitat for Kemp's ridleys and these areas must be conserved to ensure the viability of the species.

CONSERVATION STATUS. – FNAI Global - G1 (Critically Imperiled), State - S1 (Critically Imperiled); ESA Federal - LE (Endangered); State - E (Endangered); CITES - Appendix I; IUCN Red List - CR (Critically Endangered).

Species Recognition. — Kemp's ridley, *Lepidochelys kempii*, is the smallest of the sea turtle species and is distinguishable by its shell morphology and color (Fig. 6-1). The carapace is circular to semicircular, and the width is greater than 90% of the length. By comparison, the carapaces of loggerheads (*Caretta caretta*), hawksbills (*Eretmochelys imbricata*), and green turtles (*Chelonia mydas*) are more elongated with widths 75–85 % of the length. The carapace of Kemp's ridley typically has five vertebral scutes, a single nuchal, five pairs of costals, 12 pairs of marginals, and two supracaudals. Smaller specimens have strongly keeled vertebral scutes. The bridge of the plastron has four pairs of inframarginal scutes, each of which has a small pore located on the posterior margin. The presence of these pores is diagnostic for the genus *Lepidochelys*. Hatchling *L. kempii* are dark gray or black in color. As they grow, the plastron and other ventral surfaces become white. The dorsal coloration later changes to olive gray and the ventral surfaces become yellow as the turtle approaches maturity (Figs. 6-2, 6-3). In contrast, loggerhead turtles are dark brown as hatchlings and become orange to reddish brown as adults. Green turtle hatchlings have a black carapace and white ventral surfaces becoming brown dorsally and yellow ventrally with age. Kemp's ridley has a relatively large head and a parrot-like beak which has resulted in its Spanish name "*lora*".

Taxonomic History. — The taxonomic history of Kemp's ridley is confusing. This is due in part to the fact that its nesting origin was unknown prior to 1960, and in part to the common belief that it was a hybrid of loggerhead, hawksbill, and green turtles; in fact, an early vernacular name for the species was the "bastard" turtle. Garman (1880) described the species from a pair of turtles sent by Richard M. Kemp from Key West, Florida. He established the species name *kempii*, which was placed in the former loggerhead genus *Thalassochelys*. Garman (1880) also applied the subgeneric name *Colpochelys* to *kempii* and indicated that this name might acquire generic status. Coker (1906) acknowledged the generic and subgeneric classifications of *kempii*, elaborated on the coloration and distinguishing characters of specimens from North Carolina, and published the first photographs of this species. Baur (1890) was the first to suggest *kempii* be included in the genus *Lepidochelys*, but this designation was not supported until Carr (1942) revised

Figure 6-1. Subadult Kemp's ridley, *Lepidochelys kempii*, from Florida Bay, Monroe Co., Florida. Photo by Blair Witherington.

the genera of cheloniid turtles. During this interim, some authors gave *Colpochelys* full generic status and used the species name *kempi* rather than *kempii* (Hay, 1908; Schmidt and Dunn, 1917; Deraniyagala, 1939).

There has been considerable debate over the past forty years on the correct spelling of species names ending in -i and -ii (see review by Pritchard, 1996). Carr (1942, 1952) initially used the specific name *kempii*, though he switched to *kempi* in later publications (Carr, 1957; Carr and Caldwell, 1956, 1958; Carr and Goin, 1959). At the 1990 meeting of the International Commission of Zoological Nomenclature, a proposal was submitted in which either spelling would be admissible regardless of the original spelling (Savage, 1990). However, the Commission (1999) recently ruled that species names ending in -i and -ii are homonyms when the taxa they denote are included in the same genus (Article 58.14), and, when two or more names are homonyms, only the senior may be used as the valid name as determined by the Principle of Priority (Article 23). Accordingly, the form *kempii* (Garman, 1880) is the appropriate specific name for the Kemp's ridley (J. Savage, *pers. comm.*).

DISTRIBUTION

Geographic Distribution. — Kemp's ridleys are distributed throughout the Gulf of Mexico and western North Atlantic Ocean. Almost the entire population of adult female Kemp's ridleys nests along the western Gulf coast from Padre Island, Texas, to Isla Aguada, Campeche (Márquez-M., 1994; Márquez-M. et al., 2005). The primary rookery for this species is located at Rancho Nuevo, Tamaulipas, where nesting aggregations known as "*arribadas*" (Spanish for arrival) or "*arribazones*" come ashore during daylight hours. Since 1989, however, sporadic and solitary nesting turtles have also been reported from the coasts of Florida and the Carolinas (Johnson et al., 1999 and references therein). The results of tagging and telemetry studies at Rancho Nuevo indicate that post-nesting females migrate northward to

Figure 6-2. Subadult Kemp's ridleys, *Lepidochelys kempii*, from Collier Co., Florida, showing variation in carapacial color. Photo by Jill Schmid.

Figure 6-3. Subadult Kemp's ridleys, *Lepidochelys kempii*, from Levy Co., Florida, in ventral view showing variation in plastron color. Photo by Jeff Schmid.

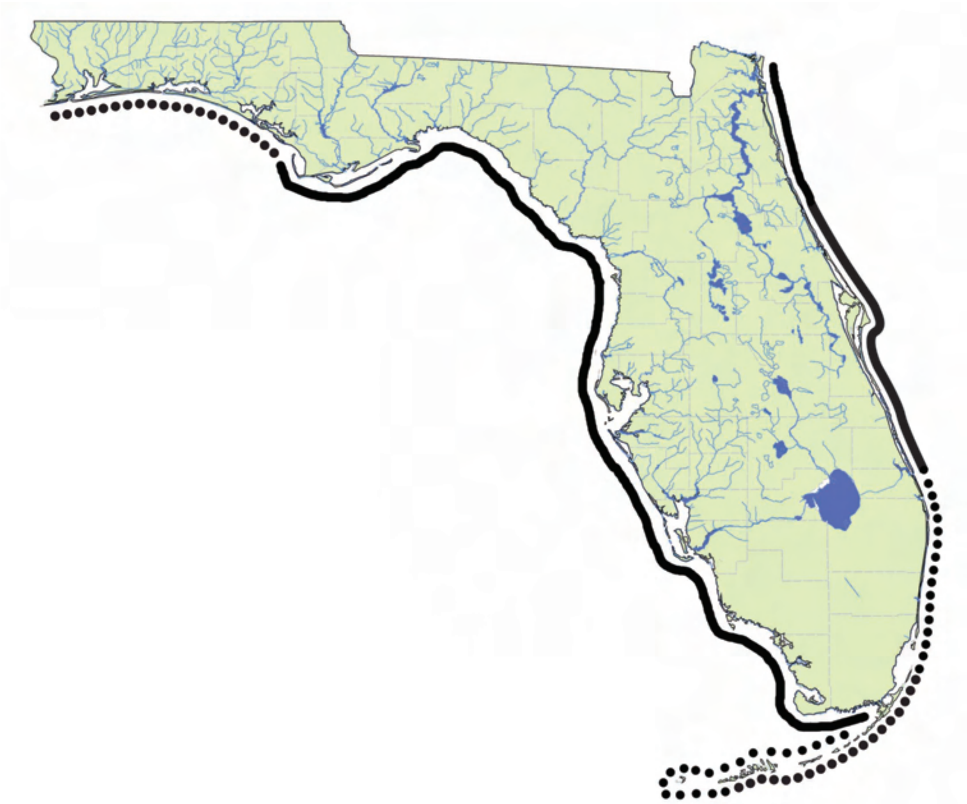

Figure 6-4. Map of foraging range distribution of *Lepidochelys kempii* in nearshore waters of Florida. The solid line shows known foraging areas and the dotted line shows possible discontinuities in their nearshore occurrence (western panhandle, Keys, and southeast coast).

feeding grounds offshore of Texas and Louisiana or southward to the Bay of Campeche in the Mexican states of Campeche and Tabasco (Pritchard and Márquez-M., 1973; Byles, 1989). Hatchling Kemp's ridleys leave the nesting beach by orienting toward the open ocean and actively swimming offshore for a period of time. Once the swimming frenzy has subsided, the juveniles become passive migrants in the epipelagic environment. The dispersion of pelagic juveniles has been correlated with major oceanic currents in the Gulf and Atlantic (Collard and Ogren, 1990; Márquez-M., 1994). Some turtles are transported across the North Atlantic Ocean to the coasts of the Azores and Europe (Brongersma, 1972, 1982; Pritchard and Márquez-M., 1973; Bolten and Martins, 1990), although there has been considerable debate as to whether these individuals are able to survive and return to the Gulf of Mexico breeding population (Carr, 1980; Ogren, 1989, 1992; Collard and Ogren, 1990). Post-pelagic Kemp's ridleys recruit to inshore waters from Texas to Massachusetts and begin a coastal-benthic stage of development that continues through adulthood (Ogren, 1989; Landry et al. 2005; Morreale and Standora, 2005; Schmid and Barichivich, 2005).

The remainder of this section focuses on distribution records for live, wild Kemp's ridleys inhabiting the nearshore coastal waters of Florida (Fig. 6-4). Dead turtles that strand on shorelines could be transported from other areas by coastal currents, and their occurrence may not reflect the actual in-water distribution of this species. Furthermore, the coverage of the Sea Turtle Stranding and Salvage Network is unequal and ranges from systematic surveys in some areas to opportunistic sampling in remote areas (Teas, 1992). Therefore, stranding records were not included in the present discussion and attempts were made to identify such records in former accounts of this species' distribution in Florida.

Kemp's ridleys were numerous along the coasts of Florida and in Florida Bay prior to the 1950s (Carr, 1980). Carr (1942) first described Sand Key in Florida Bay as the center of abundance, based upon his inquiries with local residents. However, efforts to substantiate these reports only resulted in the capture of a single Kemp's ridley. Saint Marks (Wakulla Co.) and Cedar Key (Levy Co.) were later identified as localities where Kemp's ridleys were common (Carr, 1952). The occurrence of this species was well known among fishers along the Florida Gulf Coast from Cedar Key to Key West. In fact, commercial turtle fishing near the Withlacoochee and Crystal rivers (Citrus Co.) often yielded equal numbers of Kemp's ridleys and green turtles (Carr and Caldwell, 1956), prompting Carr (1957) to identify this region as a site of maximum abundance.

Commercial mullet fishers reported captures of Kemp's ridleys in the near-shore waters around Sanibel Island (Lee Co.) prior to the early 1970s (LeBuff, 1990). Occasional captures were also reported from the shrimp fishery in the waters off southwest Florida. Aerial surveys in this area have documented the occurrence of Kemp's ridleys up to 127 km offshore and at depths up to 50 m (Fritts et al., 1983). A female Kemp's ridley tagged at the nesting beach in the western Gulf was recaptured by a shrimp trawler between the Dry Tortugas and Marquesas Keys (Sweat, 1969). In Brevard Co. on the east-central coast of Florida, Kemp's ridleys have been captured in the vicinity of Cape Canaveral and the Port Canaveral shipping channel during trawling research projects (Henwood and Ogren, 1987) and commercial shrimp fishing operations (Schmid, 1995). A few captures have also been reported from the Indian River Lagoon system during fishery-independent netting surveys (Ehrhart, 1983).

In 1984, the National Marine Fisheries Service initiated long-term tagging studies to characterize the aggregations of Kemp's ridleys occurring in Apalachicola and western Apalachee Bays, Franklin and Wakulla counties (Ogren, 1989; Rudloe et al., 1991) and Waccasassa Bay, Levy Co. (Schmid and Ogren, 1990, 1992; Schmid, 1998). Other tagging studies have resulted in a small number of captures in Tampa Bay, Hillsborough Co., and Charlotte Harbor, Charlotte Co., in west-central Florida (Manire and Foote, 1995), and Florida Bay, Monroe Co., in southwestern Florida (B. Schroeder, *pers. comm.*). Furthermore, intensive netting efforts have identified previously unknown Kemp's ridley aggregations in Deadman Bay, Taylor Co., in the northeastern Gulf of Mexico (Barichivich, 1998; Schmid and Barichivich, 2005) and Gullivan Bay, Collier Co., south of Naples (Witzell and Schmid, 2004).

Although Kemp's ridleys may occur throughout the continental shelf waters of Florida, their distribution in near-shore waters is not continuous. Carr (1957) noted that they were "common on the eastern coast of the northern half of the peninsula of Florida, but there is an odd fall in the frequency of records from Melbourne southward to Miami". There are no published records of in-water captures or sightings of Kemp's ridleys between Martin Co. and the Atlantic side of the Florida Keys (Carr, 1942; Pritchard, 1969a; Brongersma, 1972; Ogren, 1992). Interestingly, Johnson (1952) identified a large Kemp's ridley skull from a Caloosa Indian burial mound in northern Palm Beach Co. Ashton and Ashton (1985) reported the occurrence of Kemp's ridley in Dade Co., but Iverson and Etchberger (1989) could not verify this claim. Strandings of small turtles (20–30 cm SCL [standard straight carapace length; nuchal notch to the tip of supracaudals]) have been reported in this area (Teas, 1992, *pers. comm.*), and it is likely that the record in question was a dead specimen (R. Ashton, Jr., *pers. comm.*).

Another discontinuity in the near-shore distribution of this species may occur in the Florida panhandle, extending from Cape San Blas westward to Gulf Shores, Alabama. However, Iverson and Etchberger (1989) identified the following records from four localities in this area. Carr (1940) included Escambia Co. in his distribution list of Kemp's ridleys, but gave no details of their occurrence. Caldwell (1962) reported captures of three "22–28 cm" Kemp's ridleys near Fort Walton Beach, Walton Co. A Kemp's ridley captured 1.6 km offshore Shell Island, Bay Co. in November was recaptured offshore Louisiana the following April (Ogren, 1989), and cold-stunned turtles have been observed in Saint Joseph Bay, Gulf Co. after the passage of strong winter cold fronts (L. Ogren, *pers. comm.*). Areas of aggregation occur to the east (Apalachicola and Apalachee Bays; Rudloe et al., 1991) and west of the western Florida panhandle (Big Gulley, Alabama, and Mississippi Sound; Ogren, 1989), and ridleys occurring in this central region may be moving between these two areas. A similar scenario may exist for the discontinuity on the southeast Florida coast.

Ecological Distribution. — Ogren (1989) characterized Kemp's ridley life history stages according to ontogenetic shifts in habitat use: epipelagic juvenile (< 20 cm SCL), near-shore coastal-benthic subadult (20–60 cm SCL), and offshore coastal-benthic adult (> 60 cm SCL). Adult Kemp's ridleys occur in the continental shelf waters of the northern and southern Gulf of Mexico (Hildebrand, 1982; Márquez-M., 1994), but data are lacking as to the benthic habitats used in these offshore areas. Use of the *Sargassum* community has been suggested for pelagic juvenile loggerhead and green turtles in the North Atlantic (Carr, 1986). Shaver (1991) noted that 2 juvenile (< 20 cm SCL) Kemp's ridleys stranded in south Texas had ingested *Sargassum* and invertebrates associated with this brown macroalgae, providing support that this species may also use the *Sargassum* community as epipelagic developmental habitat. Subadult Kemp's ridleys inhabit bays, coastal lagoons, and estuaries along the Gulf and Atlantic seaboards (Márquez-M., 1994). Subadults tracked via radio and sonic transmitters frequented shallow-water, seagrass shoals in Cape Cod Bay (Danton and Prescott, 1988) and Chesapeake Bay (Byles, 1988) on the Atlantic coast and in Matagorda Bay on the Texas Gulf coast (Renaud and Williams, 1997).

Determining the habitat requirements of Kemp's ridley has been identified as a priority task in the conservation plans for this endangered species (Thompson et al., 1990; USFWS and NMFS, 1992), and a number of authors have inferred habitat use by Kemp's ridleys in Florida waters. Carr (1942) first suggested that Kemp's ridleys utilized the red mangrove (*Rhizophora mangle*) coastline of southern Florida. Carr and Caldwell (1956) later observed that this species was also captured among seagrass meadows (*Thalassia testudinum*, turtle grass, and *Syringodium filiforme*, manatee grass) in the west Florida turtle fishery. Ogren (1989) identified shallow seagrass beds and mud bottom of coastal salt marshes as the benthic habitats of subadult turtles. Rudloe et al. (1991) compared the substrates (mud, sand, and seagrass) at the capture sites of subadult turtles in western Apalachee Bay and detected no significant difference in use of bottom type. Barichivich (1998) emphasized the importance of the shallow seagrass flats in Deadman Bay as developmental habitat for Kemp's ridleys. Schmid (1998) suggested that Kemp's ridleys in Waccasassa Bay were preferentially utilizing an oyster (*Crassostrea virginica*) reef complex and the mud bottom adjacent to the reefs. However, none of these studies have quantified habitat use and habitat availability, both of which are necessary to test for habitat preferences and subsequently determine essential developmental habitat for this species.

Telemetry monitoring and geographic information system (GIS) mapping have been employed to investigate the habitat preferences of Kemp's ridleys in western Florida. Turtles in Waccasassa Bay exhibited a preference for limestone outcroppings and the accompanying macroalgae and sessile invertebrates (i.e., live bottom) that surrounded the oyster reefs (Schmid, 2000; Schmid et al., 2003). Kemp's ridleys in Gullivan Bay also exhibited a preference for live bottom habitat, but tube-building polychaetes (plumed worms, *Diopatra cuprea*, and parchment worms, *Chaetopterus variopedatus*) provided the substrate for live bottom attachment in an otherwise muddy sand substrate (Schmid, 2004). Use of live bottom habitat has also been inferred for turtles on the east-central coast (Schmid, 2000; Schmid et al., 2003). A visual comparison of a satellite tracked turtle (Gitschlag, 1996) and benthic mapping data (Southeast Area Monitoring and Assessment Program, 1999) suggests Kemp's ridleys may use hard bottom areas located 20–30 km offshore the Atlantic seaboard of Florida. Similarly, offshore live bottom areas in the Gulf may be the benthic habitat used by subadults during winter migrations and adults between nesting seasons.

The aforementioned gaps in near-shore distribution in southeastern and northwestern Florida may be attributable to the limited availability, or absence, of habitats preferentially used by Kemp's ridleys. Estuarine habitats in these two areas (the Indian River Lagoon on the southeast coast and the bays of the west Florida panhandle) are essentially land-locked by barrier islands. Seagrass beds, oyster reefs, and live bottom habitat occur in these inland bays and lagoons, but access is restricted to narrow, often man-made, inlets. Sabellariid and coral reefs are the dominant hard-bottom features in the coastal waters of southeast Florida. Along the northwest Florida coast, quartz sand is the dominant bottom type to depths of 20 m from Cape San Blas to near Mobile Bay (Lyons and Collard, 1974). Artificial reefs and jetties provide the only hard substrate in this area, although scattered rock outcrops occur at 20 m depths offshore Panama City and Destin. The presence of other marine turtle species has been recorded in these two regions, but Kemp's ridleys do not appear to consistently use these inland embayments or the coastal hard-bottom habitats.

HABITAT RELATIONS

Activity. — Kemp's ridleys have been described as cryptic inhabitants of remote localities in coastal estuaries (Ogren, 1989). Marine turtles must surface to breathe, and therefore may be viewed via boat or aircraft. However, Kemp's ridleys exhibit surface durations less than 60 seconds and typically spend 90% of their time submerged (Byles, 1988; Renaud, 1995; Gitschlag, 1996; Morreale and Standora, 1998; Schmid et al., 2002). Thus, their relatively small size and infrequent surface intervals limit their chances of being seen by the casual observer. These characteristics also have important implications with regards to aerial surveys for Kemp's ridleys. Since these turtles are poikilotherms, activities on large spatial and temporal scales are dictated by water temperature, and, given its benthic-carnivore foraging strategy, small-scale activities are related to food acquisition and bioenergetics. Telemetry monitoring indicated that Kemp's ridleys and loggerheads oriented their movements to take advantage of prevailing tidal currents as an energy-efficient means of foraging in bays and estuaries (Byles, 1988; Schmid et al., 2002; Schmid, 2003). Furthermore, diel activity patterns were not observed for either species, indicating that these turtles are nocturnally active when inhabiting coastal waters.

Seasonality. — The near-shore waters of Florida serve as important foraging grounds for Kemp's ridleys, but there are differences in their seasonal occurrence on the Gulf and Atlantic coasts. Kemp's ridleys were captured in the former west Florida turtle fishery in April through November (Carr and Caldwell, 1956; Carr, 1980). Recent tagging studies have confirmed this pattern of seasonal occurrence (Schmid and Ogren, 1990, 1992) and have determined that turtles occur in these shallow waters when water temperatures are above 20ºC (Schmid, 1998). However, sightings and captures have also been reported in December and March during periods of unseasonably warm water temperatures (Barichivich, 1998; Schmid and Barichivich, 2005). Turtles were captured or sighted in the coastal waters of southwest Florida during all months of the year, but abundance decreased in winter months (December–February) and turtles were not observed during some of the colder winters (Witzell and Schmid, 2004). Conversely, the Atlantic coast of Florida is an important area for overwintering as indicated by the increasing numbers of Kemp's ridleys captured off Cape Canaveral from January to March (Henwood and Ogren, 1987; Schmid, 1995; Morreale and Standora, 2005).

Movements. — The results of tagging studies along the Atlantic coast indicate a seasonal north-south migration of Kemp's ridleys. Turtles tagged off the Florida east coast during the winter have been recaptured as far north as Chesapeake Bay during the summer, and turtles tagged in northern waters in summer have been recaptured off Florida in winter (Henwood and Ogren, 1987; Schmid, 1995; Morreale and Standora, 2005). In recent years, Kemp's ridleys tagged along the eastern seaboard have been observed nesting at Rancho Nuevo (Schmid, 1995; Chaloupka and Zug, 1997; Schmid and Witzell, 1997; Witzell, 1998), providing support that subadult turtles in the Atlantic recruit to the Gulf of Mexico breeding population. Tag-recapture data along the northern Gulf coast have demonstrated east-west movements of turtles between Florida and Louisiana (Carr, 1980; Ogren, 1989), but there are no recoveries that indicate a seasonal migration (Schmid, 1998; Schmid and Barichivich, 2005). Ogren (1989) proposed an offshore migration for Kemp's ridleys in the northeastern Gulf based upon the capture of turtles in deeper waters during the winter (Rudloe et al., 1991).

Satellite telemetry has been used extensively to document the seasonal north-south migration of Kemp's ridleys along the Atlantic coast (Morreale and Standora, 2005). Two separate studies have documented overwintering off east-central Florida and remigration northward the following spring. A subadult turtle (< 60 cm SCL; Renaud, 1995) and an adult-size turtle (60.7 cm SCL; Gitschlag, 1996) traveled southward from the coastal waters of Georgia and northern Florida in October and November, remained in coastal waters south of Cape Canaveral from December through February, moved northward in March and April, and resided off the South Carolina coast through July. Satellite telemetry has also been used to document a west to east migration in the Gulf of Mexico and a southerly winter migration in the eastern Gulf (Renaud, 1995; Renaud and Williams, 2005). Recent efforts in west Florida confirmed that subadult Kemp's ridleys emigrated from coastal foraging grounds in Waccasassa Bay during November, migrated southward and overwintered in offshore waters from Anclote Keys to Captiva Island, and returned to Waccasassa Bay by late March (Schmid and Witzell, in press).

Kemp's ridleys have also been recaptured at sites of initial capture within a relatively short period, suggesting localized movements within specific coastal areas of Florida. Short-term fidelity has been observed along the eastern seaboard in the Cape Canaveral area (Schmid, 1995), and on the Florida gulf coast in Apalachicola-Apalachee Bays (Rudloe et al., 1991), Deadman Bay (Barichivich, 1998; Schmid and Barichivich, 2005), Waccasassa Bay (Schmid, 1998), and Gullivan Bay (Witzell and Schmid, 2004). Radio and sonic telemetry studies determined that Kemp's ridleys confined their tidally-oriented movements to relatively small areas for up to 3–4 months in Waccasassa Bay (Schmid, 2000; Schmid et al., 2002, 2003) and Gullivan Bay (Schmid, 2003).

Homing and Home Range. — Carr and Caldwell (1956) noted that a Kemp's ridley released in the Cedar Keys traveled approximately 35 km to the original capture site near the Withlacoochee–Crystal Rivers within 43 days. The authors suggested that this turtle, as well as green turtles captured and released in the same areas, were exhibiting homing behavior and that both species may establish home ranges during their seasonal occurrence in the near-shore waters of western Florida. Multiple short-term recaptures at the site of initial capture suggest Kemp's ridleys may establish restricted home ranges in Deadman Bay (Barichivich, 1998; Schmid and Barichivich, 2005), Waccasassa Bay (Schmid and Ogren 1990, 1992; Schmid, 1998) and Gullivan Bay (Witzell and Schmid, 2004). Radio and sonic telemetry studies have confirmed that turtles establish restricted foraging ranges in the latter 2 localities (Schmid, 2000, 2003; Schmid et al., 2003). Long-term and multiannual recaptures of Kemp's ridleys in west Florida bays indicate that turtles return to capture sites between seasons and may do so for at least 4 years (Schmid, 1998; Schmid and Barichivich, 2005; Witzell and Schmid, 2004). Satellite telemetry has further demonstrated that turtles return to previously occupied foraging areas and may inhabit the same home range areas from year to year (Schmid and Witzell, in press).

Despite numerous telemetry studies in U.S. coastal waters, there have been only three home range analyses for subadult Kemp's ridleys. Renaud and Williams (1997) calculated a composite home range of 437 km^2 for six turtles tracked in Matagorda and Lavaca Bays, Texas. Furthermore, the authors detected high utilization of a small portion of the individual home ranges of two of the turtles (35–37 km^2). In west-central Florida, a composite home range of 46 km^2 was calculated for nine Kemp's ridleys tracked in Waccasassa Bay (Schmid, 2000; Schmid et al., 2003). Five of the turtles occupied small home ranges (5–13 km^2) peripheral to an oyster reef complex, while the remaining turtles occupied larger areas (18–30 km^2) due to movements around the reef. Kemp's ridleys in southwest Florida exhibited a similar pattern of home range stability and expansion, but the composite home range in Gullivan Bay was substantially smaller (16 km^2) as were the home ranges of individual turtles (Schmid, 2003, 2004). Four of the turtles occupied small home ranges (2–3 km^2) in passes between barrier islands of the Ten Thousand Islands, while the other turtles occupied slightly larger areas (4–8 km^2) due to movements offshore and between island passes. However, a number of turtles may have left the Gullivan Bay study area, possibly moving to the numerous island passes to the south, and therefore occupied larger home range areas. The difference in home range sizes between studies may also be due to dissimilarities in the geography of each area (open bay vs. island chain) and the availability of resources (food and habitat).

GROWTH AND REPRODUCTION

Growth. — Mark-recapture studies in Florida waters have provided valuable information on the age and growth of Kemp's ridleys (Schmid and Witzell, 1997). Mean annual growth rates were not significantly different among three Florida localities ($\chi^2 = 1.11$, $p = 0.58$; Table 6-1), but the comparison was confounded by significant differences in the variability of growth rates among sites (non-homogeneity of variances, $\chi^2 = 28.05$, $p = 0.0001$). This was due to a few exceptionally high growth rates at Cape Canaveral. Extrapolating annual growth rates from short-term recaptures will amplify errors associated with carapace measurements and will yield overestimates during periods of rapid growth. Measurement errors were minimized in western Florida studies as one person performed all measurements at each locality. Therefore, these data sets were combined to investigate growth rates of Kemp's ridleys in Florida coastal waters. Although growth rates did not differ significantly by size class ($\chi^2 = 2.29$, $p = 0.51$), there was a trend for slower growth in the 20–29.9 cm SCL size class and faster growth in the 40–49.9 cm size class (Table 6-2). By comparison, Witzell and Schmid (2004) calculated a mean growth rate of 6.5 ± 3.0 cm/yr for Kemp's ridleys in southwest Florida, and growth for turtles < 40 cm (8.0 ± 3.0 cm/yr) was significantly greater than turtles > 40 cm (5.6 ± 2.6 cm/yr). There may be regional variability in growth due

Table 6-1. Annual growth rates for Kemp's ridleys in Florida waters. Standard deviations given in parentheses.

Locality	n	Growth rate (cm/yr)	Range
Western Florida			
Deadman Bay	12	4.1 (± 2.3)	1.2–9.1 cm/yr
Waccasassa Bay	24	5.4 (± 3.3)	1.2–13.0 cm/yr
Eastern Florida			
Cape Canaveral	14	7.6 (± 9.2)	0.0–29.2 cm/yr

Table 6-2. Mean annual growth rates and estimated durations for size classes of Kemp's ridleys in western Florida. Turtles were assigned to size classes by the mean of the initial and recapture carapace measurements (Bjorndal and Bolten, 1988). Standard deviations given in parentheses.

Size class (cm)	*n*	Growth rate (cm/yr)	Duration (yrs)
20–29.9	6	3.6 (± 2.1)	2.8
30–39.9	12	4.7 (± 2.7)	2.1
40–49.9	14	6.0 (± 3.6)	1.7
50–59.9	4	4.5 (± 2.5)	2.2

to differences in seasonal occurrence and migration and the availability of resources in each region.

The calculated duration for the coastal-benthic immature stage in western Florida is 8–9 years (Table 6-2), which is in agreement with von Bertalanffy growth models computed from the Cape Canaveral and Cedar Key datasets (Schmid and Witzell, 1997). However, the von Bertalanffy model assumes a steadily decreasing growth rate during the succession of developmental stages. There is evidence of seasonal (Schmid, 1998) and ontogenetic variation (Zug et al., 1997) in the growth rates of Kemp's ridleys. Chaloupka and Zug (1997) proposed a polyphasic growth model for this species and, interestingly, the growth rates observed in west Florida size classes (Table 6-2) correspond to those of the growth cycles in the polyphasic model. The first growth phase of the Kemp's ridley coincides with the epipelagic developmental stage and growth slows after shifting to coastal-benthic habitats, as observed for post-pelagic turtles in the 20–29.9 cm size class. During the second growth phase, Chaloupka and Zug attributed a growth spurt at 46 cm SCL to a possible shift in developmental habitat prior to sexual maturation. The size for this proposed shift corresponds to the decreasing frequency of turtles > 40 cm SCL at Deadman Bay and their increasing frequency in Waccasassa Bay (Fig. 6-5). Furthermore, differences in the bottom types available in these two areas suggest a shift in habitat use. In addition to an ontogenetic habitat shift, we suggest the peak of the second growth phase may coincide with the onset of puberty in the 40–49.9 cm size class (Gregory and Schmid, 2001).

Reproductive Biology. — Nesting for by Kemp's ridley occurs almost exclusively in the western Gulf of Mexico. Sporadic nesting has been reported on the Florida coast (Johnson et al., 1999), though there has been speculation that these may have been captive-raised specimens (Bowen et al., 1994). Given the rarity of nesting in Florida, the present account provides a limited examination of the reproductive parameters for this species. Detailed descriptions of Kemp's ridley reproductive cycle are provided by Pritchard and Márquez-M. (1973), Márquez-M. (1994), and Rostal (2005). Carr and Caldwell (1958) first described the sexes of Kemp's ridley, although reproduction was still undocumented for the species at this time. The authors provided photographs of captive-reared specimens depicting the longer tail of a male turtle presumed to be mature. Since the discovery of the

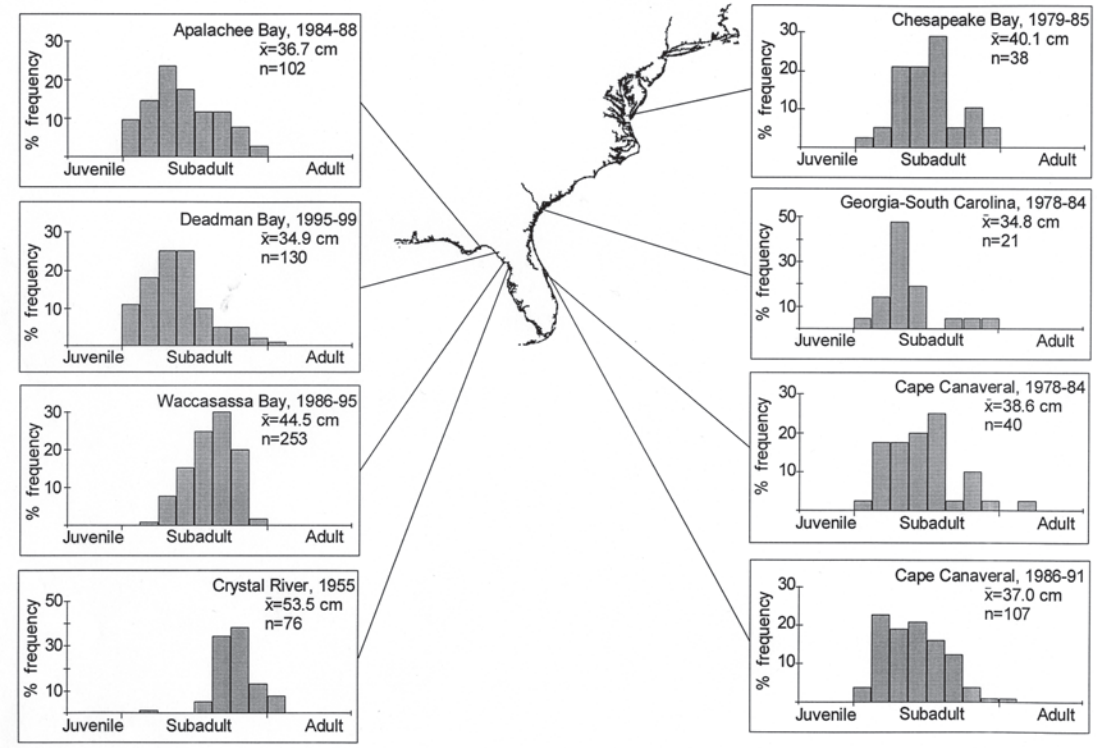

Figure 6-5. Relative size composition for Kemp's ridleys at seven sites in the western Atlantic Ocean and eastern Gulf of Mexico. Data for Chesapeake Bay are from Byles, 1988; Georgia/South Carolina from Henwood and Ogren, 1987; Cape Canaveral from Henwood and Ogren, 1987 and Schmid, 1995; Apalachee Bay from Rudloe et al., 1991; Deadman Bay from Barichivich, unpubl.; Waccasassa Bay from Schmid, 1998; and Crystal River from Carr and Caldwell, 1956 .

nesting beach in Tamaulipas, Mexico, in 1963, studies of Kemp's ridley have focused on females owing to their greater accessibility when coming ashore to nest. There does not appear to be a difference in size between sexes (Pritchard and Márquez-M., 1973), though nesting females may weigh 2–5 kg more owing to the egg mass (Márquez-M., 1994). Size at maturity has been estimated to be 58 cm (Márquez-M., 1994) to 60 cm SCL (Ogren, 1989; Schmid, 1995) based on minimum sizes of nesting females.

Marine turtles exhibit temperature-dependent sex determination, where the incubation temperature of the eggs determines the sex of the hatchlings. Long-term conservation efforts on the primary nesting beaches for Kemp's ridley involve excavating nests and relocating the eggs to protected hatcheries. This practice may have inadvertently produced a female-biased sex ratio and enhanced the recovery of this endangered species (Geis et al., 2005). All tagging studies of immature Kemp's ridleys along the west coast of Florida have reported female-biased sex ratios: 1.8F:1.0M at Waccasassa Bay (Gregory and Schmid, 2001), 1.9F:1.0M at Gullivan Bay (Witzell et al., 2005), and 3.7F:1.0M at Deadman Bay (Geis et al., 2005). However, there are a number of factors that can influence the observed sex ratio for immature turtles and, given these influences, this population parameter is subject to change over time (Ruckdeschel et al., 2005).

POPULATION BIOLOGY

Population Structure. — Ogren (1989) divided the in-water life history of Kemp's ridley into a pelagic juvenile stage (< 20 cm SCL), a coastal-benthic subadult stage (20–60 cm SCL), and a coastal-benthic adult stage (> 60 cm SCL). Observations from butchered specimens (Carr and Caldwell, 1956) and analyses of plasma hormones (Gregory and Schmid, 2001) suggest Kemp's ridleys may begin gonadal maturation at 40–50 cm SCL. Recent physiological data have prompted some authors to divide the coastal-benthic immature stage into pre-pubertal juvenile and pubertal subadult stages (Coyne and Landry, 2000; Gregory and Schmid, 2001). However, Ogren's (1989) size classes and corresponding life history stages will be used in the demographics described herein.

The aggregations of Kemp's ridleys on the U.S. Atlantic coast are primarily composed of early to mid-subadults (20–40 cm SCL; Fig. 6-5) with the exception of a few adult-size turtles captured in east-central Florida (Henwood and Ogren, 1987; Schmid, 1995). Carr (1980) and Ogren (1989) suggested an increasing size gradient from north to south for Kemp's ridleys along the U.S. Atlantic coast. Such a pattern is apparent when comparing the mean size of New England aggregations (mean = 30 cm SCL in Massachusetts [Ogren, 1989] and New York waters [Standora et al., 1992]) to that in Virginia (mean = 40 cm, Byles, 1988). However, an increasing gradient in mean size or size class composition is not observed when comparing collections of Kemp's ridleys from Virginia, South Carolina/Georgia, and Florida (Fig. 6-5). These size distributions and measures of central tendency are subject to error owing to small sample sizes and possible sampling bias, among others (Morreale and Standora, 2005). The comparison is further complicated by the fact that individuals move among these areas seasonally.

Spatial and temporal variation in size class composition have been observed for Kemp's ridleys along the Gulf coast of Florida (Schmid, 1998; Schmid and Barichivich, 2005). The aggregations at Apalachicola-Apalachee and Deadman Bays are dominated by early to mid-subadults, whereas the aggregation at Waccasassa Bay is predominately mid- to late subadults (Fig. 6-5). In fact, the size distribution for Kemp's ridleys captured at Deadman Bay is significantly smaller (Kolmogrov-Smirnov 2-sample test, $p = 0.0001$) than that of turtles captured at Waccasassa Bay. Schmid (1998) also noted that the seasonal mean carapace lengths for Kemp's ridleys in Waccasassa Bay were 5–10 cm smaller than those reported for the Withlacoochee-Crystal Rivers area over 30 years earlier (Carr and Caldwell, 1956). The relative absence of smaller size classes in the earlier study (Fig. 6-5) may be indicative of reduced subadult recruitment owing to egg harvesting at the nesting beach or may reflect a preference for landing larger turtles in the commercial turtle fishery.

INTERSPECIFIC INTERACTIONS

Community Structure. — Kemp's ridleys were captured with green turtles in the former west Florida turtle fishery (Carr and Caldwell, 1956), and were captured with both loggerhead and green turtles in Waccasassa Bay (Schmid, 1998), Deadman Bay (Barichivich, 1998), and Gullivan Bay (Witzell and Schmid, 2004); however, possible interactions among these species is unknown. Carr and Caldwell (1956) suggested that "setting nets across the channels among the flats results in an intercepting of the two forms as they move along the most favorable highway - perhaps towards very divergent goals". As indicated by the authors, green turtles are foraging on the extensive seagrass flats and Kemp's ridleys are possibly feeding on crabs and other invertebrates on the flats and in the channels. Therefore, the two species exhibit habitat partitioning based on their respective feeding strategies. Loggerheads also feed upon benthic invertebrates and the possibility of competition for food with Kemp's ridley could be investigated by comparing fecal samples collected from both species captured in the same location (Schmid, 1998, 2000).

Diet and Feeding. — Subadult and adult Kemp's ridleys feed primarily on decapod crustaceans (Hildebrand, 1982; Shaver, 1991; Ogren, 1992; Burke et al., 1993, 1994; Márquez-M., 1994; Seney and Musick, 2005). Carr and Caldwell (1956) postulated that Kemp's ridleys captured near the Withlacoochee-Crystal Rivers fed on crabs and other benthic invertebrates on the grass flats and in the channels. Schmid (1998) noted the occurrence of both stone crab (*Menippe* sp.) and blue crab (*Callinectes sapidus*) in fecal specimens collected from turtles captured near an oyster bar complex in Waccasassa Bay. Barichivich (1998) collected fecal samples from Kemp's ridleys captured among the shallow grass flats of Deadman Bay, and indicated that spider crabs (*Libinia* sp.) were present in all samples but blue and stone crabs occurred in only a few samples. Based on these observations and differences in length frequency distributions, Schmid and Barichivich (2005) suggested a possible ontogenetic shift in the utilization of benthic habitats and corresponding prey items by subadult turtles in western Florida. Morreale and Standora (1998) originally proposed that new recruits to the coastal waters of New England selected slower-moving prey (e.g., spider crabs) and switched to faster-moving prey (e.g., blue crabs) as they became more experienced at feeding in benthic habitats. However, Witzell and Schmid (2005) observed that the predominant food item for Kemp's ridleys in Gullivan Bay was a benthic tunicate (*Molgula occidentalis*), which has not been reported in any other dietary studies. The consumption of tunicates and polychaete worm tubes supported the supposition that turtles were using live bottom habitat in southwestern Florida.

Predation. — Predators of marine turtles can be classified according to the life history stages of their prey (Stancyk, 1982). Humans and coyotes (*Canis latrans*) were major predators on the eggs of Kemp's ridleys, and black vultures (*Coragyps atratus*) and ghost crabs (*Ocypode albicans*) molested hatchlings during their trek to the sea (Pritchard and Márquez-M., 1973). However, intensive efforts to protect the Mexican nesting beaches have essentially halted the predation of eggs and emerging hatchlings. Among the many predatory fishes occurring off the nesting beaches, jackfish (*Caranx hippos*) and redfish (*Sciaenops ocellatus*) are known to feed on hatchling Kemp's ridleys (Hildebrand, 1963). There is no published information on the specific predators of pelagic juveniles or coastal-benthic subadults and adults, although sharks have been implicated as the primary predator (Márquez-M., 1994).The tiger shark (*Galeocerdo cuvier*) preys extensively on large cheloniid turtles (Stancyk, 1982; Witzell, 1987) and its foraging habitat overlaps that of Kemp's ridley, but there are no records of predator-prey interactions between these two species. In August 1998, a shark identified as a great hammerhead (*Sphyrna mokarran*) was observed attacking a post-pelagic (21 cm SCL) Kemp's ridley in the shallow waters of Deadman Bay (Barichivich, *pers. obs.*). The turtle was recovered immediately after the shark released its prey, and subsequent inspection revealed abrasions on the carapace and plastron as a result of the attack. Another slightly larger turtle (33 cm SCL) was captured in the same area later that year and exhibited similar wounds. Many of the Kemp's ridleys captured in western Florida were missing the distal ends of the flippers, particularly the rear flippers (Schmid, *pers. obs.*), which may indicate frequent, non-lethal encounters with sharks or other large predatory fish.

THREATS

Since the early 1970s, incidental or accidental capture has been recognized as a major factor threatening the survival of Kemp's ridley (Pritchard and Márquez-M., 1973) and marine turtle populations worldwide (Carr et al., 1978; Hillestad et al, 1982). Most incidental captures of marine turtles occur in conjunction with commercial fishing activities directed at other species (Weber, 1989). Shrimp trawling has been identified as the primary source of capture and mortality. Other commercial fishing gear that incidentally captures marine turtles includes finfish trawls, drift and set gill nets, trammel nets, pound nets, beach seines, purse seines, longlines, and buoy ropes for crab and lobster traps. However, the mortality associated with these latter methods accounted for only one-tenth of that associated with shrimp trawling (Magnuson et al., 1990). Power plant intake pipes and channel dredging equipment have also been implicated in the capture of marine turtles, but mortality is believed to be low (Magnuson et al., 1990). With the exception of finfish trawls and pound nets, all of these methods of incidental capture occur in Florida waters.

The shrimp industry in the southeastern U.S. is the nation's most valuable commercial fishery (Conner, 1987; Ross et al., 1989; Magnuson et al., 1990). In addition to the large commercial fleet, a larger number of recreational vessels participate in the harvesting of several species of shrimp. The most commonly employed gear is the otter trawl, a heavy mesh net with wings on each side that funnel shrimp into the bag, or cod end, of the webbing. Subadult and adult marine turtles, particularly loggerheads and Kemp's ridleys, typically forage within the shrimping grounds and are incidentally taken as the trawl is dragged along the bottom. Some turtles are able to avoid capture by outswimming the trawl (Ogren et al., 1977) or altering their depth (Standora et al., 1994). Others, if not most, are unable to outdistance the trawl and either become entangled within the webbing or immobilized in the cod end. Turtles captured within a trawl are unable to surface to breathe and will drown if held submerged for an extended period. In Florida waters, trawlers fish for brown shrimp (*Penaeus aztecus*) primarily on the northwestern coast, pink shrimp (*Penaeus duorarum*) off the southwestern coast, and white shrimp (*Penaeus setiferus*) off the northeastern and east-central coast (Magnuson et al., 1990). Correspondingly, incidental captures of Kemp's ridleys have been recorded in northwestern (Rudloe et al., 1991), southwestern (Sweat, 1969; LeBuff, 1990), and east-central Florida (Schmid, 1995). Mass strandings of Kemp's ridleys on the northeastern coast have been correlated to the shrimping activities in this area (Schroeder and Maly, 1989). Efforts to mitigate marine turtle captures in the shrimp fisheries are discussed below.

Different types of gear and techniques have been employed in Florida's commercial entanglement net fisheries, but the two main types are gill and trammel nets. Gill nets consist of a single panel of webbing suspended from a float line and weighted by a lead line. Trammel nets consist of three panels of webbing, with the outer panels a larger mesh size than the inner panel, suspended from a common float line and attached to a common lead line. Anchored trammel nets have been used in the pompano fishery of eastern

Florida, and, if left unattended for a period of time, resulted in the drowning of green turtles and loggerheads (Ehrhart et al., 1990; Magnuson et al., 1990). Conversely, strike trammel nets used in the pompano fishery of western Florida were rapidly deployed upon sighting of fish and retrieved within 30 min of the strike. While this method did result in marine turtle captures, including Kemp's ridleys, entangled turtles did not drown due to the limited in-water time of the net (Schmid, *pers. obs*.). Mullet fishers of western Florida also reported captures of ridleys in gill nets (LeBuff, 1990). As with trammel nets, the mortality incurred with gill nets depends upon the fishing method (passive versus active). Legislation was enacted in 1996 that banned the use of entanglement nets in Florida State waters, thus eliminating incidental captures of marine turtles by these methods.

Pelagic longlines, used primarily for swordfish and tuna, consist of hundreds to thousands of baited hooks attached to leaders, or gangions, that hang vertically from a main fishing line. The main line may be up to 75 km long and is suspended from floats at various depths depending upon the target species. Marine turtles may either become entangled in the fishing lines or ingest the baited hooks. Leatherback (*Dermochelys coriacea*) and loggerhead captures have been recorded near the continental shelf edge off both coasts of Florida (Witzell, 1999). Bottom longlines are set for groupers and snappers in the outer shelf waters and for sharks in the inner shelf waters, but evidence of marine turtle take by this method is sparse (Oravetz, 1999). Nonetheless, this fishery may impact turtles during their seasonal migrations and overwintering in offshore waters. Recreational fishermen and fishing guides have reported Kemp's ridleys being caught on baited hooks in near-shore waters of western Florida. Similar reports from Texas indicate the majority of turtles caught by hook-and-line are released alive, though they may suffer from the effects of hook ingestion after release (Cannon et al., 1994).

Commercial crab fishermen in western Florida have reported looting of their traps by marine turtles. Loggerhead turtles crush wire traps to gain access to the captured crabs, while Kemp's ridleys remove the appendages of crabs through the wire. Entanglement in the buoy lines is possible, resulting in drowning if the turtle is unable to surface, and it is likely that mortality is also incurred through retribution by fishermen who are disgruntled with gear damage (Oravetz, 1999).

All five species of marine turtles inhabiting waters of the eastern U.S. have been entrained in the intake pipes at the St. Lucie power plant in southeast Florida (Ernest et al., 1989). However, nets are set in the intake canal to capture and remove turtles, primarily loggerhead and green turtles, thus minimizing mortality. Incidental captures have also been reported at four other power plants in eastern Florida (Magnuson et al., 1990). Additionally, there have been reports of entrainment and mortality at the Crystal River power plant in western Florida. This latter facility is of particular concern given its proximity to major foraging grounds for Kemp's ridleys and green turtles.

STATUS

The U.S. Fish and Wildlife Service and National Marine Fisheries Service (1992) established a recovery goal of 10,000 females/season in the nesting population to remove the Kemp's ridley from Endangered status and downlist to Threatened status. This goal equates to 15,000-30,000 nests/season depending upon the estimate of the number of nests laid by females each year. Despite recent increases in the number of nests, the species remains endangered as nesting intensity is still well below the recovery objective and is extremely low when compared to historical levels (Fig. 6-6). If the increasing trend in nesting continues, preliminary demographic models suggest that this intermediate recovery goal may be achieved by 2015–20, provided that the assumptions of these models are correct (Turtle Expert Working Group, 1998, 2000; Heppell et al., 2005).

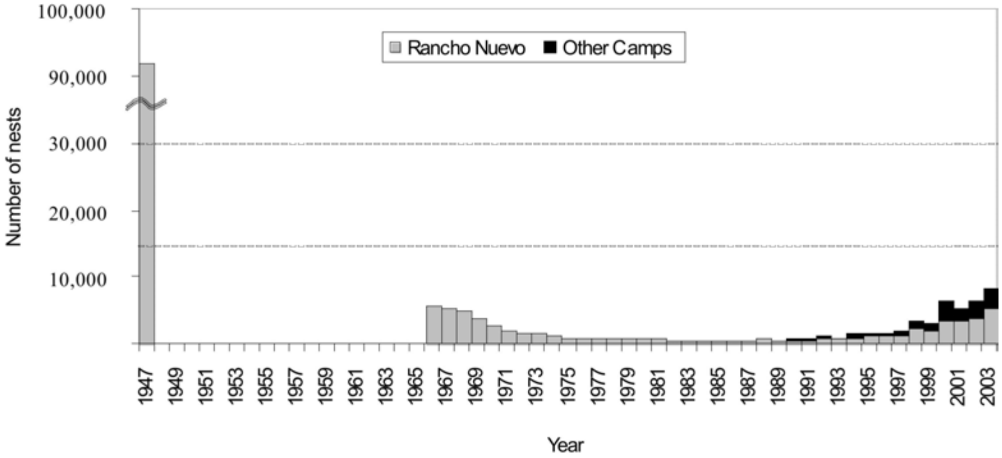

Figure 6-6. Annual number of nests laid by Kemp's ridley in Mexico. The estimate for 1947 is from Magnuson et al., 1990; data for 1966–88 from Turtle Expert Working Group, 1998; data for 1989–2002 from annual reports of conservation efforts; data for 2003 from Márquez-M. et al., 2005. Dashed lines indicate recovery goals of 15,000 or 30,000 nests per year. The lower goal assumes females deposit 1.5 clutches per season, the higher goal assumes that females lay 3.0 clutches per season. The ultimate goal of recovery is the existence of 10,000 females nesting annually.

CONSERVATION OPTIONS AND SOLUTIONS

Kemp's ridley is the most endangered species of marine turtle (Ross et al., 1989; Magnuson et al., 1990) and the IUCN classifies it as Critically Endangered on its Red List. Human impacts on the various life history stages of this species have resulted in its rapid population decline. Exploitation of eggs (Hildebrand, 1982), slaughter of nesting females (Pritchard, 1969b), commercial fisheries for subadults and adults (Pritchard and Márquez-M., 1973; Márquez-M., 1994), and incidental capture of subadults and adults in shrimp trawls (Ross et al., 1989; Magnuson et al., 1990) have been identified as causes for the population decline.

Prior to 1961, the location of Kemp's ridley nesting beach was unknown. A film of ridleys nesting at Rancho Nuevo, Tamaulipas made in 1947 was discovered by Hildebrand (1963) and reported by marine turtle biologists (Carr, 1963). In this film, an estimated 40,000 females nested during a single *arribada*. By 1966, when the Mexican government established the first protection camp at Rancho Nuevo, these *arribadas* included only 2000 turtles (Márquez-M., 1994). This rapid decrease in numbers was attributed to decades of heavy human exploitation of adult females and their eggs, coupled with the natural predation at the nesting beach, which resulted in virtually no recruitment to the aging adult population. Protection of the nesting beach by Mexican authorities essentially halted the exploitation of the females and their nests. The U.S. government listed the Kemp's ridley as Endangered in 1970 and federal protection of the species was initiated under the Endangered Species Act of 1973 and subsequent amendments (Magnuson et al., 1990).

Since 1978, Mexican and U.S. authorities have participated in a cooperative program for Kemp's ridley research and conservation. During each nesting season, biologists from both countries patrol the beaches of Rancho Nuevo, measure and tag nesting females, and relocate eggs to protected corrals. The hatchery program has been closely monitored and has resulted in the release of approximately 20,000 hatchlings annually from 1966–78 and over 50,000 thereafter (Márquez-M., 1994). The number of nesting females provides the best available index for the size of the Kemp's ridley population (Magnuson et al., 1990) and has been calculated from the total number of nests divided by the average number of nests deposited by females each year. However, this population parameter is particularly sensitive to the annual number of emergences by females and estimates have ranged from 1.5 to 3 nests/season (Rostal et al., 1997). Therefore, the total number of nests observed at Rancho Nuevo has been the standard used to assess the status of the species (U.S. Fish and Wildlife Service and National Marine Fisheries Service, 1992).

Despite intensive protection of the nesting beach, the reproductive output of the population steadily declined from a total of 954 nests in 1979 to a low of 702 nests in 1985 (U.S. Fish and Wildlife Service and National Marine Fisheries Service, 1992). Incidental capture of subadult and adult turtles in commercial fisheries, particularly shrimp trawling, was identified as the major source of mortality hindering the restoration of the species (Ross et al., 1989; Magnuson et al., 1990). In 1987, regulations were enacted requiring the seasonal use of turtle excluder devices (TEDs) in shrimp trawlers operating in the offshore waters from North Carolina to Texas. By 1994, legislation was passed requiring year-round use of TEDs in all shrimp trawlers operating in U.S. waters. In addition, the Mexican government announced in 1993 that offshore shrimp trawlers operating in the Gulf of Mexico and Caribbean Sea would be required to use TEDs.

There are indications that the binational conservation efforts of the past four decades are benefiting the highly endangered Kemp's ridley. The number of nests recorded at Rancho Nuevo has been steadily increasing since the mid-1980's. Newly established research camps to the north and south of Rancho Nuevo are also reporting increases in nest numbers (Márquez-M. et al., 1996, 1999, 2001, 2005). In 2003, researchers recorded 5373 nests at Rancho Nuevo (Márquez-M. et al., 2005), which was the highest observed level of nesting in 36 years. Increased nesting may be attributable to the reduced mortality of adults and subadults resulting from the restrictions placed on the shrimp fishery (Turtle Expert Working Group, 1998; Márquez et al., 1999, 2005). Protection of the nesting beach has presumably led to increased numbers of subadult turtles in U.S. coastal waters, but there are no quantitative data to substantiate this supposition (Ogren, 1989; Ross et al., 1990; Schmid, 1998). Nonetheless, human encroachment in critical habitats, such as nesting beaches and foraging grounds, continues to threaten the recovery of this species. The shallow coastal waters of Florida provide essential developmental habitat and these areas must be conserved to ensure the viability of Kemp's ridley.

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LITERATURE CITED

ASHTON, R.E., JR., AND ASHTON, P.S. 1985. Handbook of Reptiles and Amphibians of Florida. Part 2. Lizards, Turtles, and Crocodilians. Miami, FL: Windward Publications, Inc. 191 p.

BARICHIVICH, W.J. 1998. Feeding ecology and habitat affinities of Kemp's ridley sea turtles (*Lepidochelys kempi*) in the Big Bend, Florida. Annual report, December, 1998. Panama City, FL: National Marine Fisheries Service. 18 p.

Baur, G. 1890. The genera of Cheloniidae. American Naturalist 24:486-487.

Bjorndal, K.A., and Bolten, A.B. 1988. Growth rates of immature green turtles, *Chelonia mydas*, on feeding grounds in the southern Bahamas. Copeia 1988:555-564.

Bolten, A.B., and Martins, H.R. 1990. Kemp’s ridley captured in Azores. Marine Turtle Newsletter 48:23.

Bowen, B.W., Conant, T.A., and Hopkins-Murphy, S.R. 1994. Where are they now? The Kemp’s ridley headstart project. Conservation Biology 8:853-856.

Brongersma, L.D. 1972. European Atlantic turtles. Zoologishe Verhandlungen Museum Leiden. 121:1-318.

Brongersma, L.D. 1982. Marine turtles of the eastern Atlantic Ocean. In: Bjorndal, K.A. (Ed.). Biology and Conservation of Sea Turtles, Washington, D.C.: Smithsonian Institution Press. pp. 407-416.

Burke, V.J., Morreale, S.J., and Rhodin, A.G.J. 1993. Life history notes: *Lepidochelys kempii* (Kemp's ridley sea turtle) and *Caretta caretta* (loggerhead sea turtle). Diet. Herpetological Review 24:31-32.

Burke, V.J., Morreale, S.J., and Standora, E.A. 1994. Diet of the Kemp’s ridley, *Lepidochelys kempii*, in New York waters. Fisheries Bulletin 92:26-32.

Byles, R.A. 1988. Behavior and ecology of sea turtles from Chesapeake Bay, Virginia. Ph.D. Dissertation, Williamsburg, VA: Virginia Institute of Marine Science, College of William and Mary. 112 p.

Byles, R.A. 1989. Satellite telemetry of Kemp’s ridley sea turtle, *Lepidochelys kempi*, in the Gulf of Mexico. In: Eckert, S.A., Eckert, K.L., and Richardson, T.H. (Compilers). Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology. NOAA Tech. Memo. NMFS-SEFC-232:25-26.

Caldwell, D.K. 1962. Growth measurements of young captive Atlantic sea turtles in temperate waters. Contributions in Science Los Angeles County Museum 50:1-8.

Carr, A.F., Jr. 1940. A contribution to the herpetology of Florida. University of Florida. Publications, Biological Sciences Series, Vol. III, No. 1, 118 p.

Carr, A. F., Jr. 1942. Notes on sea turtles. Proceedings New England Zoology Club 21:1-16.

Carr, A. 1952. Handbook of turtles: the turtles of the United States, Canada, and Baja California. Ithaca, NY: Comstock Publishing Assoc. 542 p.

Carr, A. 1957. Notes on the zoogeography of the Atlantic sea turtles of the genus *Lepidochelys*. Revistas Biologico Tropical 5:45-61.

Carr, A. 1963. Panspecific reproductive convergence in *Lepidochelys kempi*. Ergebnesse Biol. 26:298-303.

Carr, A. 1980. Some problems of sea turtle ecology. American Zoologist 20:489-498.

Carr, A. 1986. New perspectives on the pelagic stage of sea turtle development. NOAA Tech. Memo. NMFS-SEFC-190, 36 p.

Carr, A.F., and Caldwell, D. K. 1956. The ecology and migrations of sea turtles: 1. Results of field work in Florida, 1955. American Museum of Natural History, Novitates 1793:1-23.

Carr, A., and Caldwell, D. K. 1958. The problem of the Atlantic ridley turtle (*Lepidochelys kempi*) in 1958. Revistas Biologico Tropical 6:245-262.

Carr, A., and Goin, C. J.1959. Guide to the Reptiles, Amphibians, and Fresh-water Fishes of Florida. Gainesville, FL: University of Florida Press. 341 p.

Carr, A., Carr, M. H., and Meylan, A. B. 1978. The ecology and migrations of sea turtles, 7. The west Caribbean green turtle colony. Bulletin of the American Museum of Natural History 162:1-46.

Cannon, A. C., Fontaine, C. T., Williams, T. D., Revera, D. B., and Caillouet, C.W., Jr. 1994. Incidental catch of Kemp’s ridley sea turtles (*Lepidochelys kempii*), by hook and line, along the Texas coast, 1980-1992. In: Schroeder, B.A., and Witherington, B.E. (Compilers). Proceedings of the Thirteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-341:40-42.

Chaloupka, M., and Zug, G. R. 1997. A polyphasic growth function for the endangered Kemp’s ridley sea turtle, *Lepidochelys kempii*. Fisheries Bulletin 95:849-856.

Coker, R.E. 1906. The natural history and cultivation of the diamond-back terrapin with notes on other forms of turtles. Other forms of turtles (Chelonia) at Beaufort, N.C. North Carolina Geological Survey 14:55-67.

Collard, S.B., and Ogren, L.H. 1990. Dispersal scenarios for pelagic post-hatchling sea turtles. Bulletin of Marine Science 47:233-243.

Conner, D.K. 1987. Turtles, trawlers, and TEDS: what happens when the Endangered Species Act conflicts with fishermen’s interests. Water Log 7:3-27.

Coyne, M.S., and Landry, A.M., Jr. 2000. Plasma testosterone dynamics in the Kemp’s ridley sea turtle. In: Abreu-Grobois, F.A., Briseno-Duenas, R., Marquez-Millan, R., and Sarti-Martinez, L. (Compilers). Proceedings of the Eighteenth International Sea Turtle Symposium. NOAA Technical Memorandum NMFS-SEFSC-436, p. 286.

Danton, C., and Prescott, R. 1988. Kemp’s ridley in Cape Cod Bay, Massachusetts - 1987 field research. In: Schroeder, B.A. (Ed.). Proceedings of the Eighth Annual Workshop on SeaTurtle Conservation and Biology. NOAA Technical Memorandum NMFS-SEFC-214, pp.17-18.

Deraniyagala, P. E. P. 1939. The distribution of the Mexican loggerhead turtle *Colpochelys kempi* Garman. Bulletin of the Institute of Oceanography., Monaco, 772:1-4.

Ehrhart, L. M. 1983. Marine turtles of the Indian River Lagoon system. Florida. Scientist 46:337-346.

Ehrhart, L. M., Raymond, P., Guseman, J. L., and Owen, R. 1990. A documented case of green turtles killed in an abandoned gill net: the need for better regulation of Florida’s gill net fisheries. In: Richardson, T.I., Richardson, J.I., and Donnelly, M. (Compilers). Proceedings of the Tenth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFC-278:55-58.

Ernest, R. G., Martin, R. E., Williams-Walls, N., and Wilcox, J. R. 1989. Population dynamics of sea turtles utilizing shallow coastal waters off Hutchinson Island, Florida. In: Eckert, S.A., Eckert, K.L., and Richardson, T.H. (Compilers). Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology. NOAA Tech. Memo. NMFS-SEFC-232:57-59.

Fritts, T. H., Irvine, A. B., Jennings, R. D., Collum, L. A., Hoffman, W., and McGehee, M. A. 1983. Turtles, Birds, and Mammals in the Northern Gulf of Mexico and Nearby Atlantic Waters: An Overview Based on Aerial Surveys of OCS Areas, with Emphasis on Oil and Gas Effects. U.S. Fish and Wildlife Service, Division of Biological Services, Washington, D.C. FWS/OBS-82/65. 455 p.

Garman, S. 1880. On certain species of Chelonioid.. Bulletin of the Museum of Comparative Zoology 6:123-126.

Geis, A. A., Barichivich, W. J., Wibbels, T., Coyne, M., Landry Jr., A. M., and Owens, D. 2005. Predicted sex ratio of juvenile Kemp’s ridley turtles captured near Steinhatchee, Florida. Copeia 2005:393-398.

Gitschlag, G. R. 1996. Migration and diving behavior of Kemp’s ridley (Garman) sea turtles along the U.S. southeastern Atlantic coast. Journal of Experimental Marine Biology and Ecology 205:115-135.

Gregory, L. F., and Schmid, J. R. 2001. Stress responses and sex ratio of wild Kemp’s ridleys *(Lepidochelys kempi)* in the northeastern Gulf of Mexico. General and Comparative Endocrinology 124:66-74.

Hay, O. P. 1908. On three existing species of sea-turtles, one of them (*Caretta remivaga*) new. Proceedings of the U.S. National Museum 34:183-198.

Henwood, T. A., and Ogren, L. H. 1987. Distribution and migrations of immature Kemp's ridleys (*Lepidochelys kempi*) and green turtles (*Chelonia mydas*) off Florida, Georgia, and South Carolina. Northeast Gulf Science 9:153-159.

Heppell, S.S., Crouse, D.T., Crowder, L.B., Epperly, S.P., Gabriel, W., Henwood, T., Márquez, R., and Thompson, N.B. 2005. A population model to estimate recovery time, population size, and management impacts on Kemp's ridley sea turtles. Chelonian Conservation and Biology 4:767-773.

Hildebrand, H.H. 1963. Hallazgo del area de anidacion de la tortuga marina "lora" *Lepidochelys kempi* (Garman) en la costa occidental del Golfo de Mexico. Cienca 22:105-112.

Hildebrand, H.H. 1982. A historical review of the status of sea turtle populations in the western Gulf of Mexico. In: Bjorndal, K.A. (Ed). Biology and Conservation of Sea Turtles, Washington, D. C.: Smithsonian Institution Press. pp. 447-453.

Hillestad, H.O., Richardson, J.I., McVea, C., Jr., and Watson, J.M., Jr. 1982. Worldwide incidental capture of sea turtles. In: Bjorndal, K.A. (Ed). Biology and Conservation of Sea Turtles, Washington, D. C.: Smithsonian Institution Press. pp. 489-495.

International Commission Of Zoological Nomenclature. 1999. International Code of Zoological Nomenclature. Fourth edition. London: The International Trust for Zoological Nomenclature. 306 p.

Iverson, J.B., and Etchberger, C. R. 1989. The distributions of turtles in Florida. Florida Scientist 52:119-144.

Johnson, S.A., Bass, A.L., Libert, B., Marshall, M., and Fulk, D. 1999. Kemp's ridley (*Lepidochelys kempi*) nesting in Florida. Florida Scientist. 3/4:194-204.

Johnson, W.R., Jr. 1952. *Lepidochelys kempii* and *Caretta c. caretta* from a south Florida Indian mound. Herpetologica 8:36.

Landry, A.M., Jr., Costa, D.T., Kenyon, F.L., and Coyne, M.S. 2005. Population characteristics of Kemp's ridley sea turtles in nearshore waters of the upper Texas and Louisiana coasts. Chelonian Conservation and Biology 4:801-807.

LeBuff, C.R., Jr. 1990. The Loggerhead Turtle in the Eastern Gulf of Mexico. Sanibel, FL: Caretta Research, Inc., 216 pp.

Lyons, W.G. and Collard, S.B. 1974. Benthic invertebrate communities of the eastern Gulf of Mexico. In: Smith, R.E. (Ed.). Proceedings of Marine Environmental Implications of Offshore Drilling in the Eastern Gulf of Mexico. State University System of Florida, Institute of Oceanography, St. Petersburg, FL, pp. 157-167.

Magnuson, J. J., Bjorndal, K. A., Dupaul, W. D., Graham, G. L., Owens, D. W., Peterson, C. H., Pritchard, P. C. H., Richardson, J. I., Saul, G. E., and West, C. W. 1990. Decline of the Sea Turtles: Causes and Prevention. Washington, D. C.: National Academy Press. 274 p.

Manire, C.A., and Foote, J.J. 1995. Capture and tag-and-release of juvenile turtles caught in gill nets in nearshore habitat of the eastern Gulf of Mexico during fishery-independent shark studies. In: Keinath, J. A., Barnard, D. E., Musick, J.A., and Bell, B.A. (Compilers). Proceedings of the Fifteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-387:182-186.

Márquez-M., R. 1994. Synopsis of the Biological Data on the Kemp's ridley, *Lepidochelys kempi* (Garman, 1880). NOAA Tech. Memo. NMFS-SEFSC-343, 91 p.

Márquez -M., R., Byles, R. A., Burchfield, P., Sanchez-P, M., Diaz-F, J., Carrasco-A, M.A., Leo-P, A. S., and Jimenez-Q, M.C. 1996. Good news! Rising numbers of Kemp's ridleys nest at Ranch Nuevo, Tamaulipas, Mexico. Marine Turtle Newsletter 73:2-5.

Márquez, R., Diaz, J., S Sanchez-, M., Burchfield, P., Leo, A., Carrasco, M., Pena, J., Jimenez, C., and Bravo, R. 1999. Results of the Kemp's ridley nesting beach conservation efforts in Mexico. Marine Turtle Newsletter 85:2-4.

Márquez-M., R., Burchfield, P., Carrasco, M., Jimenez, C., Diaz, J., Garduno, M., Leo, A., Pena, J., Bravo, R., and Gonzalez, E. 2001. Update on the Kemp's ridley nesting in México. Marine Turtle Newsletter 92:2-4.

Márquez-M., R., Burchfield, P., Diaz-F., J., Sanchez-P., M., Carrasco-A., M., Jimenez-Q., M., Leo-P., A., Bravo-G., R., and Pena-V., J. 2005. Status of the Kemp's ridley sea turtle, *Lepidochelys kempii*. Chelonian Conservation and Biology 4:761-766.

Morreale, S.J., and Standora, E. A. 1998. Early life stage ecology of sea turtles in northeastern U.S. waters. NOAA Tech. Memo. NMFS-SEFSC-413, 49 p.

Morreale, S.J., and Standora, E. A. 2005. Western North Atlantic waters: crucial developmental habitat for Kemp's ridley and loggerhead turtles. Chelonian Conservation and Biology 4:872-882.

Ogren, L.H. 1989. Distribution of juvenile and subadult Kemp's ridleys: preliminary results from the 1984-1987 surveys. In: Caillouet, C.W., Jr., and Landry, A.M., Jr. (Eds.). Proceedings of the First International Symposium on Kemp's Ridley Sea Turtle Biology, Conservation, and Management. Texas A & M University Sea Grant College Program, TAMU-SG-89-105:116-123.

Ogren, L.H. 1992. Atlantic ridley turtle, *Lepidochelys kempii* (Garman). In: Moler, P.E. (Ed). Rare and Endangered Biota of Florida, Vol. III. Amphibians and Reptiles, Gainesville: University Press of Florida, pp. 100-104.

Ogren, L.H., Watson, J.W., Jr., and Wickham, D.A. 1977. Loggerhead sea turtles, *Caretta caretta*, encountering shrimp trawls. Marine Fisheries Review 39:15-17.

Oravetz, C.A. 1999. Reducing incidental catch in fisheries. In: Eckert, K.L., Bjorndal, K.A., Abreu-Grobois, F.A., and Donnely, M. (Eds.). Research and Management Techniques for the Conservation of Sea Turtles. IUCN/SSC Marine Turtle Specialist Group Publication No. 4, pp. 189-193.

Pritchard, P.C.H. 1969a. Studies of the systematics and reproductive cycles of the genus *Lepidochelys*. Ph.D. Dissertation, Gainesville, FL: University of Florida. 226 p.

Pritchard, P.C.H. 1969b. The survival status of ridley sea turtles in American waters. Biological Conservation 2:13-17.

Pritchard, P.C.H. 1996. How many i's in kempi(i)? They're all wrong or all right. Marine Turtle Newsletter 72:10-13.

Pritchard, P.C.H., and Márquez-M., R. 1973. Kemp's ridley or Atlantic ridley. IUCN Monograph No. 2: Marine Turtle Series. 30 p.

Renaud, M.L. 1995. Movements and submergence patterns of Kemp's ridleys (*Lepidochelys kempii*). Journal of Herpetology 29:370-374.

Renaud, M.L., and Williams, J.A. 1997. Movements of Kemp's ridley (*Lepidochelys kempi*) and green (*Chelonia mydas*) sea turtles using Lavaca Bay and Matagorda Bay 1996-1997. Report to Environmental Protection Agency, Dallas, TX: Office of Planning and Coordination, Region 6, 54 pp.

Renaud, M.L., and Williams, J.A. 2005. Kemp's ridley sea turtle movements and migrations. Chelonian Conservation and Biology 4(4):808-816.

Ross, J.P., Beavers, S., Mundell, D., and Airth-Kindree, M. 1989. The Status of Kemp's Ridley. Washington, D. C.: Center for Marine Conservation. 51 p.

Rostal, D.C. 2005. Seasonal reproductive biology of the Kemp's ridley sea turtle (*Lepidochelys kempii*): comparison of captive and wild populations. Chelonian Conservation and Biology 4:788-800.

Rostal, D.C., Grumbles, J.S., Byles, R.A., Márquez-M., R., and Owens, D.W. 1997. Nesting physiology of Kemp's ridley sea turtles, *Lepidochelys kempi*, at Rancho Nuevo, Tamaulipas, Mexico, with observations on population estimates. Chelonian Conservation and Biology 2:538-547.

Ruckdeschel, C., Shoop, C. R., and Kenney, R. D. 2005. On the sex ratio of juvenile *Lepidochelys kempii* in Georgia. Chelonian Conservation and Biology 4:860-863.

Rudloe, A., Rudloe, J., and Ogren, L. 1991. Occurrence of immature Kemp's ridleys, *Lepidochelys kempi*, in coastal waters of northwest Florida. Northeast Gulf Sci. 12:49-53.

Savage, J.M. 1990. Meetings of the International Commission on Zoological Nomenclature. Herpetological Review 21:55-57.

Schmid, J.R. 1995. Marine turtle populations on the east-central coast of Florida: results of tagging studies at Cape Canaveral, Florida, 1986-1991. Fisheries Bulletin. 93:139-151.

Schmid, J.R. 1998. Marine turtle populations on the west-central coast of Florida: results of tagging studies at the Cedar Keys, Florida, 1986-1995. Fisheries Bulletin 96:589-602.

Schmid, J.R. 2000. Activity patterns and habitat associations of Kemp's ridleys, *Lepidochelys kempi*, in the coastal waters of the Cedar Keys, Florida. Ph.D. Dissertation, Gainesville, FL: University of Florida.

Schmid, J.R. 2003. Activity patterns of the Kemp's ridley turtle in the Ten Thousand Islands, Florida. Final Report to the Marine Turtle Grants Program. St Petersburg, FL: Florida Fish and Wildlife Conservation Commission, 25 pp.

Schmid, J.R. 2004. Determining essential habitat for the Kemp's ridley turtle in the Ten Thousand Islands, Florida. Final Report to the Marine Turtle Grants Program. Gainesville, FL: Caribbean Conservation Corporation, 31 pp.

Schmid, J.R., and Barichivich, W.J. 2005. Developmental biology and ecology of Kemp's ridleys, *Lepidochelys kempi*, in the eastern Gulf of Mexico. Chelonian Conservation and Biology 4:828-834.

Schmid, J.R., and Ogren, L.H. 1990. Results of a tagging study at Cedar Key, Florida, with comments on Kemp's ridley distribution in the southeastern U.S. In*:* Richardson, T.I., Richardson, J.I., and Donnelly, M. (Compilers). Proceedings of the Tenth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFC-278:129-130.

Schmid, J.R., and Ogren, L.H. 1992. Subadult Kemp's ridley sea turtles in the southeastern U.S.: results of long-term tagging studies. In*:* Salmon, M., and Wyneken, J. (Compilers). Proceedings of the Eleventh Annual Workshop on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-32:102-103.

Schmid, J.R., and Witzell, W.N. 1997. Age and growth of wild Kemp's ridleys *(Lepidochelys kempi)*: cumulative results of tagging studies in Florida. Chelonian Conservation and Biology 2:532-537.

Schmid, J.R., and Witzell, W.N. In Press. Seasonal migrations of immature Kemp's ridley turtles along the west coast of Florida. Gulf of Mexico Science.

Schmid, J.R., Bolten, A.B., Bjorndal, K.A., and Lindberg, W.J. 2002. Activity patterns of Kemp's ridleys, Lepidochelys kempii, in the coastal waters of the Cedar Keys, Florida. Marine Biology 140:215-228.

Schmid, J.R., Bolten, A.B., Bjorndal, K.A., and Lindberg, W.J., Percival, H.F., and Zwick, P.D. 2003. Home range and habitat use by Kemp's ridleys in west-central Florida. Journal of Wildlife Management 67:197-207.

Schmidt, K. P., and Dunn, E. R. 1917. Notes on *Colpochelys kempi* Garman. Copeia 44:50-52.

Schroeder, B.A., and Maly, C.A. 1989. 1988 fall/winter strandings of marine turtles along the northeast Florida and Georgia coasts. In: Eckert, S.A., Eckert, K.L., and Richardson, T.H. (Compilers). Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology. NOAA Tech. Memo. NMFS-SEFC-232:159-161.

Seney, E.E., and Musick, J.A. 2005. Diet analysis of Kemp's ridley sea turtles (*Lepidochelys kempii*) in Virginia. Chelonian Conservation and Biology 4(4):864-871.

Shaver, D. J. 1991. Feeding ecology of wild and head-started Kemp's ridleys in South Texas waters. Journal of Herpetology 25:327-334.

Southeast Area Monitoring And Assessment Program. 1999. South Atlantic Bight Hardbottom Mapping. South Atlantic Bottom Mapping Workgroup. CD-ROM Version 1.1.

Stancyk, S. E. 1982. Non-human predators of sea turtles and their control. In*:* Bjorndal, K.A. (Ed). Biology and Conservation of Sea Turtles, Washington, D. C.: Smithsonian Institution Press. pp. 139-152.

Standora, E.A., Morreale, S.J., and Burke, V.J. 1992. Application of recent advances in satellite transmitter microtechnology: integration with sonic and radio tracking of juvenile Kemp's ridleys from Long Island, NY. In: Salmon, M. and Wyneken, J. (Compilers). Proceedings of the Eleventh Annual Workshop on Sea Turtle Conservation and Biology. NOAA Technical Memorandum NMFS-SEFC-302, pp. 111-113.

Standora, E.A., Morreale, S.J., Bolten, A.B., Eberle, M.D., Edbauer, J.M., Ryder, T.S., and Williams, K.L. 1994. Diving behavior and vertical distribution of loggerheads, and a preliminary assessment of trawling efficiency for censusing. In: Schroeder, B.A., and Witherington, B.E. (Compilers). Proceedings of the Thirteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-341:174-177.

Sweat, D. E. 1969. Capture of a tagged ridley turtle. Quarterly Journal of the Florida Academy of Sciences 31:47-48.

Teas, W.G. 1992. 1991 annual report of the sea turtle stranding and salvage network: Atlantic and Gulf coasts of the United States, January-December 1991. NOAA-NMFS-SEFSC, Miami Laboratory, MIA-91/92-62. 48 p.

Thompson, N., Henwood, T., Epperly, S., Lohoefner, R., Gitschlag, G., Ogren, L., Mysing, J. and Renaud, M. 1990. Marine Turtle Habitat Plan. NOAA Technical Memorandum, NMFS-SEFC-255, 20 p.

Turtle Expert Working Group. 1998. An assessment of the Kemp's ridley (*Lepidochelys kempii*) and loggerhead (*Caretta caretta*) sea turtle populations in the western North Atlantic. NOAA Tech. Memo. NMFS-SEFSC-409. 96 p.

Turtle Expert Working Group. 2000. Assessment update for the Kemp's ridley and loggerhead sea turtle populations in the western North Atlantic. NOAA Tech. Memo. NMFS-SEFSC-444. 115 p.

U. S. Fish and Wildlife Service and National Marine Fisheries Service. 1992. Recovery Plan for the Kemp's Ridley Sea Turtle (*Lepidochelys kempii*). St. Petersburg, FL: National Marine Fisheries Service. 40 p.

Weber, M. 1989. Socioeconomic importance of sea turtles: incidental capture. In: Ogren, L., Berry, F., Bjorndal, K., Kumpf, H., Mast, R., Medina, G., Reichart, H., and Witham, R. (Eds.). Proceedings of the Second Western Atlantic Turtle Symposium. NOAA Tech. Memo. NMFS-SEFC-226:50-73.

Witzell, W.N. 1987. Selective predation on large cheloniid sea turtles by tiger sharks (*Galeocerdo cuvier*). Japanese Journal of Herpetology 12:22-29.

Witzell, W.N. 1998. Long-term tag returns from juvenile Kemp's ridleys. Marine Turtle Newsletter 79:20.

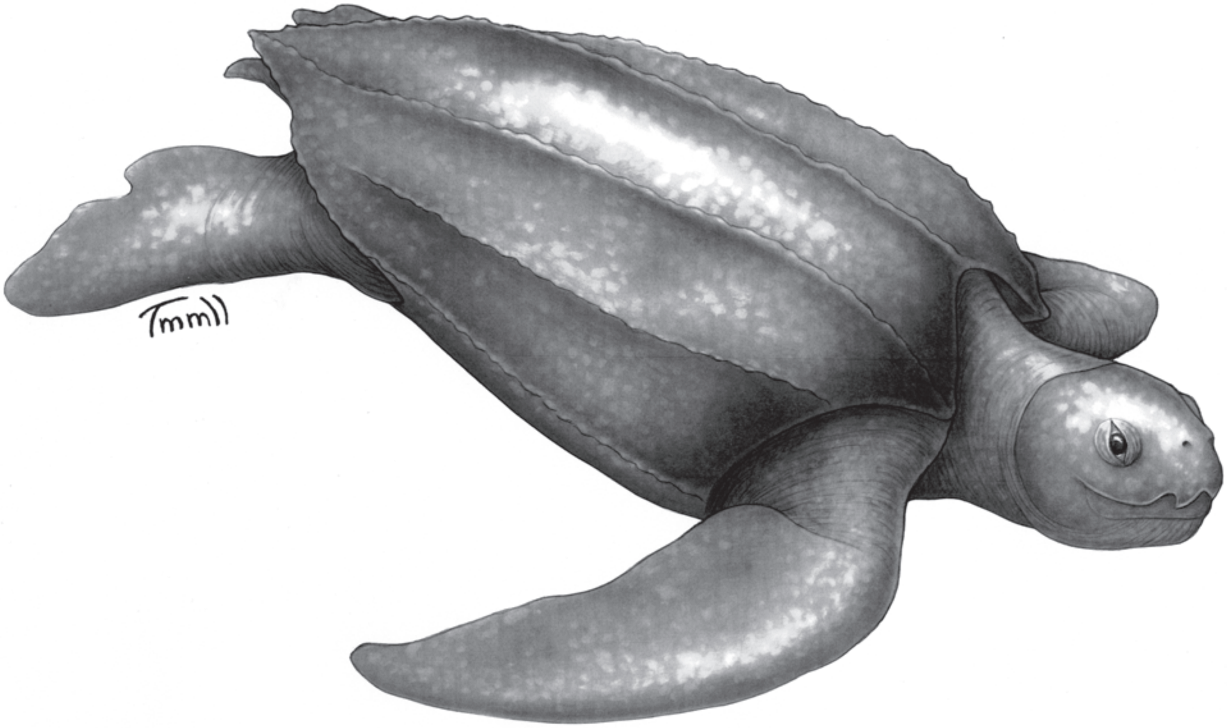
Witzell, W.N. 1999. Distribution and relative abundance of sea turtles caught incidentally by the U.S. pelagic longline fleet in the western North Atlantic Ocean, 1992-1995. Fisheries Bulletin 97:200-211.

Witzell, W.N., and Schmid, J.R. 2004. Immature sea turtles in Gullivan Bay, Ten Thousand Islands, southwest Florida. Gulf of Mexico Science 22:54-61.

Witzell, W. N., and Schmid, J. R. 2005. Diet of immature Kemp's ridley turtles (*Lepidochelys kempii*) from Gullivan Bay, Ten Thousand Islands, southwest Florida. Bulletin of Marine Science 77:191-199.

Witzell, W. N., Geis, A. A., Schmid, J. R., and Wibbels, T. 2005. Sex ratio of immature Kemp's ridley turtles (*Lepidochelys kempi*) from Gullivan Bay, Ten Thousand Islands, south-west Florida. Journal of the Marine Biological Association of the United Kingdom 85:205-208.

Zug, G. R., Kalb, H. J., and Luzar, S. J. 1997. Age and growth on wild Kemp's ridley sea turtles *Lepidochelys kempii* from skeletochronological data. Biological Conservation 80:261-268.



Leatherback Sea Turtle, *Dermochelys coriacea* (Dermochelyidae).
Drawing by Susan Trammell.

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Introduction to the Leatherback Turtles: Family Dermochelyidae

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Leathery-shelled sea turtles make up the family Dermochelyidae. There is only one living species of this distinctive group. It is easily recognized by its massive adult size and unique shell morphology. In members of this family, the deeper elements of the carapace, the vertebrae and ribs, are separate from the overlying dermal bone. In all other turtles these elements are united into a single bony carapace.

Content. — One genus and species is all that remains of a once diverse lineage (encompassing the Dermochelyidae and the closely-related Protostegidae) that blossomed during the Cretaceous and produced such giant forms as *Archelon* and *Protostega*. The one living species, *Dermochelys coriacea*, the leatherback, occurs in Florida as part of its global distribution. In fact, the numbers of nesting females that use Florida beaches for nesting appears to be on the increase. However, this species is clearly in decline worldwide (Spotilla et al., 1996, 2000) and requires serious conservation attention wherever it occurs.

Relationships. — Because of its soft and incomplete shell, the leatherback was at one time considered to be a species that was just becoming a turtle and it was classified separately from all other turtles. But now it is clear that leatherbacks have reduced their shell over evolutionary time (Wood et al., 1996; Hirayama and Hikida, 1998). Morphological and molecular data both indicate that they are actually very closely related to other living sea turtles (Gaffney and Meylan, 1988; Shaffer et al., 1997; Near et al., 2005) and are not some kind of primitive turtle. Although leatherbacks and hard-shelled sea turtles are each others' closest living relatives, they apparently started down separate evolutionary paths more than 110 million years ago. The evolutionary split between the two lineages is dated by *Santanachelys*, a fossil sea turtle of the family Protostegidae (Hirayama, 1998). It is possible that the leatherback represents the oldest family of living turtles that is reduced to one living species. If this one species disappears, the last representative of well over 100 million years of sea turtle evolution will be gone.

Geologic Distribution. — This family has a rich fossil record that dates back to the Cretaceous (Wood et al., 1996; Hirayama and Hikida, 1998). The genus *Dermochelys*, however, is not known until the Pleistocene. Wood et al. (1996) suggested that diversity in this family has slowly declined since the Eocene.

Geographic Distribution. — The single living species in this family occurs in all of the world's oceans from the Arctic Circle to southern coastal Chile. It appears to be rare in the Indian Ocean and declining significantly in the Pacific. The healthiest populations are those in the western Atlantic, including the population that nests in Florida. Nesting beaches are all located in tropical or subtropical regions (Spotilla et al., 1996).

Status. — The leatherback is considered critically endangered worldwide. A thorough consideration of the decline and demographic limitations of leatherbacks led Spotilla et al. (1996, 2000) to the conclusion that leatherbacks are "on the road to extinction". They cited a rapid state of decline since 1980, especially in the Pacific, and the continuing impact from the harvest of eggs as well as mortality from indigenous and commercial fisheries as reasons for this status.

LITERATURE CITED

Gaffney, E.S. and Meylan, P.A. 1988. A phylogeny of turtles. In: Benton, M.J. (Ed.). The Phylogeny and Classification of Tetrapods. Clarendon Press, Oxford, England, pp. 157-219.

Hirayama, R. 1998. Oldest known sea turtle. Nature 392:705-708.

Hirayama, R. and Hikida, Y. 1998. *Mesodermochelys* (Testudines; Chelonioidea; Dermochelyidae) from the Late Cretaceous of Nakagawa-cho, Hokkaido, North Japan. Bulletin of the Nakagawa Museum of Natural History 1:69-76.

Near, T.J., Meylan, P.A., and Shaffer, H.B. 2005. Assessing concordance of fossil calibration points in molecular clock studies: an example using turtles. American Naturalist 165:137-146.

Shaffer, H.B., Meylan, P.A., and McKnight, M. 1997. Tests of turtle phylogeny: molecular, morphological and combined approaches. Systematic Biology 46:235-268.

Spotila, J.R., Dunham, A.E., Leslie, A.J., Steyermark, A.C., Plotkin, P.T., and Paladino, F.V. 1996. Worldwide population decline of *Dermochelys coriacea*: are leatherback turtles going extinct? Chelonian Conservation and Biology 2:209-222.

Spotila, J.R., Reina, R.D., Steyermark, A.C., Plotkin, P.T., and Paladino, F.V. 2000. Pacific leatherbacks face extinction. Nature 405:529-530.

Wood, R.C., Johnson-Gove, J., Gaffney, E.S., and Maley, K.F. 1996. Evolution and phylogeny of leatherback turtles (Dermochelyidae), with descriptions of new fossil taxa. Chelonian Conservation and Biology 2:266-286.

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Dermochelys coriacea – Leatherback Sea Turtle

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Summary. – The leatherback, *Dermochelys coriacea*, is the largest living turtle and the most widely distributed reptile in the world. It is classified as Endangered in Florida (U.S. Fish and Wildlife Service) and Critically Endangered globally by the World Conservation Union (IUCN). The first leatherback nest in Florida was recorded in 1947, and since then nesting along the coast of Florida has been increasing significantly. Tagging studies show that there are more individuals nesting in Florida than previously thought. Leatherbacks are found in Florida waters year-round, but in higher densities during the nesting season, which runs from March through June. For the last 10 years, nest numbers have averaged 508 nests per year. The size of female leatherbacks nesting in Florida is 151.8 ± 6.63 cm curved carapace length, and each female lays on average 73 ± 18.26 eggs in each clutch. When choosing a nesting beach, Florida leatherbacks are not highly site-specific and each female may travel over 120 km either within or between seasons for subsequent nestings. Nests incubate for 66.9 ± 7.8 days and average hatching success is 67 ± 24.7%. Leatherbacks nesting in Florida spend a significant amount of time in US waters following the nesting season and may forage close to shore in the southeast US during the summer months. Major potential threats to leatherbacks in Florida include boat strikes and degradation of nesting habitat. Provided that nesting habitat continues to be well protected and mitigation for coastal development is undertaken, the conservation outlook for this species in Florida is encouraging.

Conservation Status. – FNAI Global - G2 (Imperiled), State - S2 (Imperiled); ESA Federal - LE (Endangered); State - E (Endangered); CITES - Appendix I; IUCN Red List - CR (Critically Endangered).

Species Recognition. — Leatherbacks are unique among reptiles. They are gigantic in size when compared to other turtles (carapace up to ca. 1.8 m in length) and are colored primarily black with irregular patches of white spots over their carapace, head and flippers. They are unique among turtles in having seven longitudinal ridges along their carapace, long front flippers almost as long as their bodies, and a carapace that tapers to a distinct posterior point (Fig. 7-1, see also book cover). Instead of having a solid bony carapace like other sea turtle species, their shell is composed of a thick layer of fibrous fatty tissue, overlaid with a mosaic of tiny bones (ossicles that are separate from the underlying ribs), and covered by a thin, fragile skin. The front flippers are proportionally longer than in any other sea turtle species. The jaws of the leatherback are specialized to consume gelatinous prey. They have two sharp cusps on the upper jaw interlocking with a single sharp cusp on the mandible (Fig. 7-2). Leatherbacks have a pink spot on the dorsal surface of the head, located dorsal to the pineal gland. The shape of this spot varies among individuals and has been used as a secondary method of female identification (McDonald et al., 1996). Leatherback hatchlings have long flippers and carapacial keels are evident (Fig. 7-3).

An excellent description of leatherback anatomy, nesting behavior, and a complete description of development can be found in Deraniyagala (1939). This reference describes the growth and morphological changes that take place in hatchlings up to 600 days of age.

Taxonomic History. — This species was first described by Vandelli in 1761 (Fretey and Bour, 1980; King and Burke, 1997) as *Testudo coriacea*. In 1816, Blainville proposed the genus *Dermochelys* but failed to name *D. coriacea* as the type species (Smith and Smith, 1979). This led to some confusion about the correct scientific name for the species but generally since the publication of Boulenger (1889), *Dermochelys coriacea* has been considered the correct name for the leatherback. The leatherback is the only living member of the family Dermochelyidae.

Relationships Among Populations. — Recent improvements in genetic analytical methods have allowed researchers to determine distinctiveness of stocks, delineate population boundaries, and define allelic diversity within populations of turtles including leatherbacks. Typically, genetic material derived from the maternal lineage (mitochondrial DNA or mtDNA) has been examined to provide evidence that the natal homing hypothesis is valid for this species and this method can be used to delineate maternal lines in populations. There is less genetic differentiation among female leatherback breeding stocks within oceanic basins than what is found for the cheloniid sea turtles (Dutton et al., 1999) although some populations are distinguishable from others. Nesting stocks can be strongly separated among the Indian,

Figure 7-1. Nesting adult female leatherback, *Dermochelys coriacea,* from Juno Beach, Palm Beach Co., Florida, showing carapacial ridges. Photo by Chris Johnson.

Atlantic, and Pacific Oceans (Dutton et al., 1999) based on mtDNA analysis. For the Atlantic basin, a recent study using mtDNA did not detect differences in genetic make-up between Florida and much larger nesting aggregations in Suriname, French Guiana, and South Africa (Dutton et al., 1999). This low diversity in haplotypes is hypothesized to be the result of leatherbacks having gone through a bottleneck and radiating out into all ocean basins from one location (and one maternal lineage) in the Indian and Pacific Oceans during the glaciation of the early Pleistocene (Dutton et al., 1999). Recent microsatellite data (nuclear DNA) revealed that all nesting aggregations within the Caribbean are genetically distinct except for Trinidad and Suriname/French Guiana (Dutton et al., 2003). However these two colonies were distinct according to mtDNA analyses; this indicates that natal homing is utilized by females from these two rookeries. Florida is of interest since there has been little historical nesting until recently when the number of nesting leatherbacks has increased dramatically. Whether these turtles are migrants from local Caribbean populations or the descendents of founding females may be elucidated through ongoing mtDNA and microsatellite genetic analyses.

Figure 7-2. Head of a stranded adult leatherback, *Dermochelys coriacea*, showing deep cusps on the upper jaw and extensive papillae throughout the mouth and throat. These features help the leatherback handle its prey. Photo by Scott Eckert.

DISTRIBUTION

Geographic Distribution. — The leatherback is the most widely distributed reptile in the world (Mrosovsky, 1987). It is found in the Pacific, Atlantic, and Indian Oceans

Figure 7-3. Hatchling leatherback, *Dermochelys coriacea,* at Juno Beach, Florida. Photo by Chris Johnson.

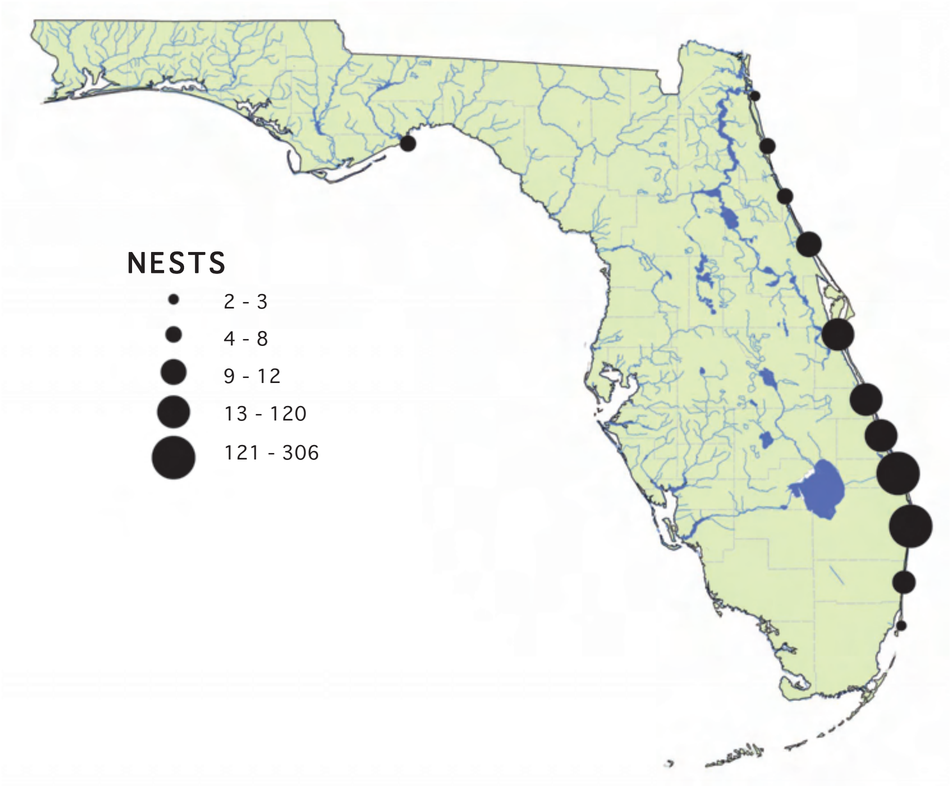

Figure 7-4. Distribution of Florida nesting records for *Dermochelys coriacea* from 2004.

from 71°N to 47°S (Pritchard and Trebbau, 1984). Following nesting on subtropical and tropical beaches from 30°N to 20°S (Starbird et al., 1993) the species travels to temperate and subarctic waters to forage. Adult leatherbacks are found as far north as Newfoundland and Labrador in the Atlantic (Goff and Lien, 1988; James et al., 2005b), and as far south as South Africa (Hughes et al., 1998) and Argentina (Pritchard and Trebbau, 1984).

Based on limited strandings and sightings, hatchlings and smaller juveniles (less than 100 cm CCL), appear to be limited to tropical waters where water temperatures are above 26°C (Eckert, 2002a). Once they reach 100 cm (CCL) they apparently develop the physiological mechanisms that allow them to move into colder waters (Eckert, 2002a). Juvenile leatherbacks have been captured near São Tomé and Príncipe, which is west of Gabon in western Africa (Fretey et al., 1999). This may be a juvenile feeding area (Fretey et al., 1999), and this finding merits further investigation.

There are numerous important nesting beaches worldwide; some are considered to be in decline, while a few appear to be increasing. Many Pacific leatherback populations are critically endangered with extinction in the foreseeable future (Spotila et al., 2000; Spotila, 2004). In particular, Eastern Pacific populations of the leatherback have declined precipitously in the last 15 years (Sarti et al., 1996; Sarti et al., 2000; Spotila et al., 2000; Spotila, 2004). In the Atlantic, significant nesting beaches are found in French Guiana (Girondot and Fretey, 1996) and Suriname (Pritchard and Trebbau, 1984; Hilterman and Goverse, 2005) in South America, along the eastern and northern coasts of Trinidad in the southern Caribbean (S. Eckert, pers. comm.; Cheong, 1990; Godley et al., 1993) and the western coast of Africa (Fretey, 2004), specifically in Gabon (Fretey and Girardin, 1989; Billes and Fretey, 2004). Other important nesting locations include Shell Beach in Guyana (Pritchard, 2004), La Playona, Colombia (Duque and Paez, 2000), Gandoca and Tortuguero in Costa Rica (Leslie et al., 1996; Chaverri, 1999; Troëng et al., 2004), Chiriquí Beach in Panama (Meylan et al., 1985), and several Caribbean islands, including Puerto Rico (Hall, 1993), Culebra (Tucker and Frazer, 1991), and St. Croix (Boulon et al., 1996; Dutton et al., 2005). In the Pacific, nesting beaches are found in Costa Rica (Chaves et al., 1996; Steyermark et al., 1996; Reina et al., 2002a), Malaysia (Chan and Liew, 1996), Mexico (Sarti et al., 2000), Indonesia (Suarez et al., 2000), and the Andaman and Nicobar Islands (Bhaskar, 1993; Andrews and Shanker, 2002). A modestly increasing nesting population also exists in South Africa (Hughes, 1996).

The first record of a leatherback nesting in Florida dates from 1947 (Carr, 1952), with additional reports coming after 1955 (Caldwell et al., 1955; Caldwell, 1959). The densest nesting in Florida now occurs along the Atlantic coast from Jensen Beach south to Palm Beach (FWRI, 2006). Approximately 250 km of Florida's coastline regularly receives leatherback nests, however, individual leatherbacks are not as site-specific as the hard-shelled turtles and may nest anywhere along this stretch of beach (Stewart et al., submitted B). Nesting has been recorded in many coastal counties in Florida (Fig. 7-4), although presently the heaviest nesting is found in Palm Beach County followed by Martin County (FWRI, 2006). Some nesting also occurs along the panhandle of Florida (FWRI, 2006), and sporadic nesting occurs in Georgia, South Carolina, and as far north as North Carolina (Rabon et al., 2003).

Ecological Distribution. — Generally, leatherbacks are pelagic, utilizing the open ocean and concentrating their foraging efforts near watermass boundaries (Collard, 1990), or on areas of high productivity where floating debris and organisms such as jellies and other gelatinous prey tend to aggregate. Leatherbacks are also found in coastal waters, where they feed on jellies (Leary, 1957; Grant et al., 1996). However, they are able to navigate through the open sea with few detectable oceanographic features such as currents (Hughes et al., 1988; Goff et al., 1994).

In Florida, leatherbacks have been recorded from both nearshore and offshore waters, although distribution and abundance vary throughout the year (Fritts et al., 1983; Schroeder and Thompson, 1987). Leatherbacks inhabit Florida waters extensively during the nesting season. They are generally found in higher densities close to shore rather than offshore, generally in water less than 40 m deep (Schroeder and Thompson, 1987). They may be in coastal waters to feed, or remain in the area during the internesting interval. It is likely that they are also feeding on jellyfish on the continental shelf and off points of land where currents meet (Fritts et al., 1983).

HABITAT RELATIONS

Activity. — Leatherbacks swim and dive constantly (Eckert et al., 1986, 1996; Eckert, 2002b). Using time-depth-recorders, Eckert et al. (1989b) found that leatherbacks in the Caribbean dove more frequently to shallower depths at night than during the day, which suggested that they were feeding at the deep scattering layer. Deepest dives were recorded at dawn, consistent with the deep-scattering layer hypothesis (Eckert et al., 1989b). Dive-depth profiles for leatherbacks are similar to those recorded for marine mammals with similar foraging behavior, such as pilot whales and spotted dolphins (Baird et al., 2001, 2002). Caribbean leatherbacks dive quickly to depth and then return to the surface, spending little, if any, time at the bottom. This is a different pattern than what is seen in cheloniid sea turtles, which spend a longer time on the bottom foraging on benthic invertebrates, or grazing on sea grasses. However, in the South China Sea, which is characterized by shallower depths relative to the Caribbean, leatherbacks spent more time at the bottom, although the overall behavioral pattern of diving was similar to that observed in the Caribbean (Eckert et al., 1996).

Seasonality. — Seasonal movements of leatherbacks are extensive, due to their ability to withstand cold water temperatures (Paladino et al., 1990; James and Mrosovsky, 2004), at least as adults. Turtles less than 100 cm CCL have never been found north of Cape Hatteras (NMFS-SEFSC, 2001; Eckert, 2002a). The greatest number of turtles sighted in Monterey Bay during summer months coincided with highest sea surface temperatures (Starbird et al., 1993).

Leatherbacks are found in Florida waters during all seasons; however, their abundance is higher during months that coincide with the nesting season (March–June) (Schroeder and Thompson, 1987). Off the Atlantic coast of Florida, leatherbacks were spotted in all seasons during aerial surveys in the early 1980s by the National Marine Fisheries Service (NMFS - Southeast Fisheries Science Center), however, concentrations were higher in the spring and summer, which agrees with satellite telemetry data collected in 2002 (S. Eckert, *pers. comm.*). Turtles may be using thermal cues (cooler water) at these locations, where food sources might be concentrated (Knowlton and Weigle, 1989; Thompson and Huang, 1993).

On the Gulf coast of Florida, leatherbacks have also been spotted during spring, summer, and winter months, but densities are not as high as Atlantic coastal waters (Fritts et al., 1983; NMFS-SEFSC, 2001).

In the northwest Atlantic, aerial surveys have been conducted for several years to examine leatherback distribution and densities. Northeastern US and Canadian waters serve as foraging grounds; leatherbacks are spotted there regularly from June to November (James and Herman, 2001; James et al., 2005a). Most turtles were seen shoreward of the 200 m isobath (James and Herman, 2001).

Shoop and Kenney (1992) summarized several years of aerial survey information and found that leatherbacks were distributed in increasing densities during the summer months from Georges Bank south to Cape Hatteras (shore to 2000 m isobath), with an aggregation of turtles south of Long Island, New York. Fewer turtles were seen during spring and fall, and none were seen in the winter. These results were similar to those found by NMFS (Northeast Fisheries Science Center), during the summer of 1995 and 1998 (no spring, fall, or winter surveys conducted). Florida nesting turtles travel north after completion of nesting (S. Eckert, *pers. comm.*) and turtles from remote nesting grounds in the Caribbean may pass through Florida waters on their way north to forage (Goff et al., 1994).

Movements. — Leatherbacks make both local and long-distance migrations (Eckert et al., 1989a; Morreale et al., 1996; James et al., 2005b). One turtle tagged while nesting in French Guiana was found 128 days later in Newfoundland (Goff et al., 1994). This represented a minimum directed movement of 39 km/day (Goff et al., 1994). During the internesting interval, leatherbacks remain in the general area of the nesting beach, however some do travel a significant distance (Eckert et al., 1989a; Eckert, 2002b; Eckert et al., in press).

Leatherbacks are not as site specific in their nest site selection as are hard-shelled sea turtles (Dutton et al., 1999) and may switch nesting beaches, sometimes relocating a hundred kilometers or more (Eckert et al., 1989a) for additional nests within the season. This is also the case in Florida where an individual turtle may lay subsequent nests up to 125 km from where she was first observed within one nesting season (Stewart et al., submitted B). Individuals may choose nesting sites up to 137 km apart between seasons (Stewart et al., submitted B). Since leatherbacks are known to lay up to 14 clutches per season (Boulon et al., 1996; Girondot and Fretey, 1996), and on average each individual in Florida is spotted 1.83 times per season (Stewart et al., submitted B) it is apparent that females are choosing adjacent non-surveyed beaches (sometimes at quite a distance) to lay subsequent nests after tagging.

Three leatherbacks which were satellite tagged while nesting at Juno Beach, Florida, moved to just north of Cape Canaveral for their internesting period in the summer of 2002 (Eckert et al., in press). Two of those turtles returned to Juno Beach for an additional nest near the end of the season, while one nested at Merritt Island National Wildlife Refuge instead of returning south to where she had been flipper-tagged originally (Eckert et al., in press).

Once leaving the nesting beach, females may travel thousands of kilometers (Morreale, 1996) and undertake trans-oceanic migrations (Ferraroli et al., 2004; Hays et al., 2004). One turtle that was tagged and fitted with a satellite transmitter at Juno Beach in May 2002, traveled nearly 5000 km before she was found dead on a New Jersey beach in October 2002 (S. Eckert, *pers. comm*.; Stewart and Johnson, unpubl. data). At the time she died, she had been moving steadily north, after spending a couple of months in nearshore waters off Cape Hatteras (S. Eckert, *pers. comm*.). She had wounds on her plastron, but the cause of the damage was not determined. Data received from this turtle did not indicate anything out of the ordinary for several weeks before she stopped transmitting and the battery pack had plenty of charge remaining. Depth data from this turtle showed that during her last day she spent a significant amount of time at depths deeper than she had been for the previous few weeks. This was a curious change in behavior and one that may suggest some sort of fishery interaction, although that is not definitely the case (S. Eckert, *pers. comm*.).

Two females tagged on a nesting beach in Trinidad made long migrations to the eastern Atlantic. One swam to the Bay of Biscay, France, and then headed to Mauritania off the African coast. The other turtle swam directly up the middle of the Atlantic, and then moved to Mauritanian waters (Eckert, 1998). Similarly, nesting females that were satellite tagged in French Guiana and Suriname dispersed widely throughout the Atlantic; their transmitters ceasing to function in the southeast US, the mid-Atlantic, and off the coast of Africa (Ferraroli et al., 2004). Hays et al. (2004) found similar results for leatherbacks satellite tagged on Grenada nesting beaches. Those turtles also dispersed widely throughout the Atlantic, following no particular route and swimming across, against, and within major oceanographic currents.

In contrast to the extensive pattern of post-nesting migrations seen in the Atlantic, leatherbacks satellite tagged in Pacific Costa Rica, took a fairly narrow corridor (ca. 500 km wide) to the southwest, and into open water of the Pacific (Morreale et al., 1996). This well defined migration corridor is now the basis of an international effort to protect and conserve leatherbacks during their migrations away from their natal beach complex (J. Spotila, *pers. comm*.) and may hold the key to the recovery of this species in the Pacific. It is clear that major international efforts must be undertaken to prevent the extinction of the leatherback in the Pacific (Crowder, 2000) as the situation there is dire.

Until recently, it was only possible to satellite tag and track female leatherbacks from the nesting beach. However, James et al. (2005c) successfully tracked 11 male turtles from the foraging grounds in Nova Scotia and Cape Breton. Analysis of the tracks revealed that male turtles swam southward to low-latitude waters adjacent to nesting beaches and remained there until the peak of the nesting season. This suggests that mating takes place immediately off nesting beaches (James et al., 2005c) in the Caribbean. Male leatherbacks then returned to coastal waters off Nova Scotia and New England. For two of the turtles with long-term tracks, James et al. (2005c) found that mating migrations were made two years in a row.

Home Range. — Leatherbacks are truly pelagic animals. In the Atlantic, they travel from nesting grounds to foraging areas and appear to move through waters with no appreciable landmarks, paying no attention to currents (Eckert, 1998; Hughes et al., 1998) or other oceanographic features, although they may sometimes associate with certain features such as the edge of the Gulf Stream (Hoffman and Fritts, 1982; S. Eckert, *pers. comm*.). In the Pacific, they migrate southwestward following nesting, and this corridor (Morreale et al., 1996) may have some appreciable features associated with it.

The home range for Florida leatherbacks during the internesting period is located 2–60 km offshore, centered east-southeast off the tip of Cape Canaveral. This area runs 215 km along the east coast (Eckert et al., in press).

Temperature Relationships. — Leatherbacks are capable of maintaining warmer internal body temperatures—up to 18°C higher than the cold waters in which they forage (Mrosovsky and Pritchard, 1971; Frair et al., 1972; James and Mrosovsky, 2004). There is a counter-current system of blood flow in leatherback flippers (Greer et al., 1973) similar to that found in sharks and tunas. Leatherbacks also possess a subepidermal layer of fat (Greer et al., 1973), which provides extra insulation. They are gigantotherms, defined by their large body size, low metabolic rates and ability to maintain warm body temperatures by insulating themselves against cold water temperatures (Paladino et al., 1990). Leatherbacks are also dependent on incubation temperatures for sex differentiation in the nest (Mrosovsky, 1980).

GROWTH AND REPRODUCTION

Growth. — Estimates of growth rates are based on skeletochronological analysis (Zug and Parham, 1996). From analysis of sclerotic ossicles (a ring of small bones in the eyes), Zug and Parham (1996), using a von Bertalanffy growth model, estimated that the average age of nesting females in a population might be 13–14 yrs, however, they estimated it would take a leatherback female 6–9 yrs to grow to maturity. Growth rate for juveniles was calculated at 34.9 cm/yr for very small turtles, and 8.6 cm/yr for nearly mature individuals (Zug and Parham, 1996). For conservation purposes, Zug and Parham (1996) advocated using 9 yrs as minimum time to maturity for these turtles. This means that leatherbacks have the ability to grow much faster and attain a greater body size than any of the cheloniid turtles.

Others (Deraniyagala, 1939; Birkenmeier, 1971; Rhodin, 1985; Bels et al., 1998) have estimated that hatchlings might reach sexual maturity in as few as 2–6 yrs. However, these growth rates were based on hatchling leatherbacks in captivity held only for short periods of time (maximum 1200 days). Leatherback bones and cartilage are highly vascularized, and demonstrate histologic features of very rapid growth—similar to what is seen in large, rapidly-growing marine mammals (Rhodin, 1985; Rhodin et al., 1996).

In any case, the growth of hatchling leatherbacks must be rapid, or they must be extremely cryptic, as few juvenile sized individuals are ever seen (Fretey et al., 1999; Eckert, 2002a). If leatherback turtles do indeed mature more quickly than hard-shelled sea turtles, positive effects of conservation measures on nesting beaches and in fisheries could be seen quite quickly, and populations may be able to rebound in relatively short time spans compared to other turtle species.

Size Dimorphism. — Differences in morphology between males and females are few. In males the tail extends well beyond the rear flippers, while in females, the tail rarely extends beyond the terminal end of the carapacial peduncle, and never beyond the rear flippers. Few morphometrics exist for adult male leatherbacks, but they are generally the same size as females, except for the length of the tail (Deraniyagala, 1939; Pritchard, 1971; M. James, *pers. comm*.).

Size at Maturity in Females. — The smallest female recorded nesting in Florida (2003) measured 125.0 cm CCL (Stewart et al., submitted A). The average size for female leatherbacks nesting at Juno Beach (*n* = 174) is 151.8 ± 6.63 cm CCL (Stewart et al., submitted A). The average curved carapace width for Florida turtles is 109.2 ± 5.03 cm (*n* = 174; Stewart et al., submitted A). Generally leatherbacks in Florida fall within the size range (130–180 cm) recorded for leatherbacks at other nesting beaches (Boulon et al., 1996; Chaves et al., 1996; Godfrey and Drif, 2002).

Size at Maturity in Males. — The largest male ever recorded weighed 916 kg and had a CCL of 159 cm, and a total length (nose to tip of tail) of 291 cm (Eckert and Luginbuhl, 1988; Morgan, 1989). On average, mature males are approximately the same size (length and width) as mature females (M. James, *pers. comm*.).

Longevity. — There are no estimates of the longevity of leatherbacks, however, if as suggested by Zug and Parham (1996), they grow to maturity in only 9 yrs, their life span may be considerably shorter than that of other sea turtles. At St. Croix, mother-daughter relationships have been established between nesting females using mitochondrial DNA analysis, providing evidence that longevity for adult leatherbacks is longer than time to maturity (Dutton et al., 2002). In terms of reproductive longevity, the longest tag returns to date are from females at 18 yrs (Hughes, 1996) and 19 yrs (Pritchard, 1996) from first tagging.

Male Reproductive Cycle. — Little information is known about male reproductive cycles, except that it appears that males make seasonal migrations to waters off nesting beaches for the purposes of mating (James et al., 2005c).

Female Reproductive Cycle. — Within the same nesting season, females in Florida return every 10.2 ± 1.01 days (*n* = 37) to nest (Stewart and Johnson, unpubl. data). This is similar to other published reports of 9 or 10 days (Pritchard, 1971; Hirth, 1980; Boulon et al., 1996; Girondot and Fretey, 1996). At Las Baulas National Park in Costa Rica, female leatherbacks had an internesting interval of 9.5 ± 0.04 days (Reina et al., 2002a).

Mating Season / Mating Behavior. — It is thought that mating in sea turtles takes place within the month before first nesting, however, this may not be the case for leatherbacks. The most recent evidence shows that Atlantic leatherbacks may mate just offshore from the nesting beaches (James et al., 2005c). It was previously thought that leatherbacks mated prior to migrating to nesting grounds (Eckert and Eckert, 1988), however, accounts of mating immediately off the nesting beach (Carr and Carr, 1986; Godfrey and Barreto, 1998; Reina et al., 2005; J. Spotila, *pers. comm*.) corroborates the evidence reported by James et al. (2005c). Leatherbacks may exhibit differences in courtship and mating at different locations.

Nesting Season / Nest Sites / Nesting Behavior. — Nesting begins in Florida in late February to early March, rises to a peak in May and then falls off quickly (FWRI, 2006), although some nests have been recorded as late as August (Stewart and Johnson, unpubl. data). Nesting behavior for leatherbacks is similar to other sea turtle species; a nest typically takes 1.5 hrs to complete.

Eggs. — Leatherbacks lay the largest eggs of all turtle species (Van Buskirk and Crowder, 1994); they measure 53.4 (± 0.5) mm in diameter and weigh 75.9 (± 4.2) g (Van Buskirk and Crowder, 1994). Leatherbacks also commonly lay spacers or shelled albumen gobs (SAGs; Wallace et al., 2004), which are albumen-filled eggshells. It is not clear what purpose, if any, these spacers serve. Nests relocated and buried without spacers did not affect hatching success at Sandy Point, St. Croix (Dutton and McDonald, 1995), nor did the mass of spacers affect the oxygen levels in leatherback nests as they incubated (Wallace et al., 2004). Spacers (or SAGs) may simply be a consequence of the physiology of egg-laying in leatherbacks (Dutton and McDonald, 1995).

Clutch Size. — Average clutch size for Florida leatherbacks is 73 ± 18.26 yolked eggs and 24.9 ± 12.6 spacers (*n* = 208 nests; Stewart and Johnson, unpubl. data). Mean clutch sizes from other locations are similar to Florida: St. Croix, 79.7 yolked, 36.4 spacers (Boulon et al., 1996), Costa Rica, 80–86 yolked, 33–53 spacers (Leslie et al., 1996) and Suriname, 86 yolked, 25 spacers (Pritchard, 1971). Mean clutch size from the Pacific was reported to be 64.7 ± 1.4 eggs and 38.5 ± 1.0 spacers (Reina et al., 2002a).

Reproductive Potential. — Florida turtles lay multiple clutches, but because they are less site-specific than turtles on other beaches, or because they are able to spread their reproductive effort over a wider area, it is difficult to determine an accurate number of nests that they are capable of laying in one season. We documented one turtle that laid 7 nests (Stewart and Johnson, unpubl. data), and several others that nested between 2 and 6 times in one season. We are sure that because leatherbacks choose nearby nesting beaches to lay additional clutches, our estimate of clutches laid per year is probably rather low.

Sex Ratio. — As with other sea turtles, sex determination is temperature dependent (TSD). Wibbels (2003) summarized several studies that examined sex ratios for hatchlings on worldwide nesting beaches. The proportion of female hatchlings in these studies ranged from 44% to nearly 100%. Using indirect methods (sand temperature), Leslie et al. (1996) estimated sex ratio throughout the season and found it to be generally female-biased, although variations were noted. Variation can be expected with changes in location, temperature and beach condition (such as sand grain size, sun exposure, etc.). Other authors (Mrosovsky et al., 1984; Dutton et al., 1992) agree that seasonal or yearly variation should exist.

Incubation and Hatching. — For south Florida nests, incubation duration is 66.9 ± 7.8 days (*n* = 177 nests), with an average hatch success of 67 ± 24.7% (*n* = 208 nests; Stewart and Johnson, unpubl. data). Average hatchling emergence from the nest is 46.1 ± 22.8 hatchlings (*n* = 208 nests; Stewart and Johnson, unpubl. data). For other populations in the Atlantic, incubation duration ranges from 52–74 days (Hirth, 1980; Boulon et al., 1996; Hilterman and Goverse, 2005).

Hatchling Size. — Hirth (1980) summarized many studies on leatherback reproductive biology and reported hatchling carapace lengths ranging from 55–62.8 mm CCL. Upon hatching, leatherbacks weigh approximately 39 g (Reina et al., 2002b). Hatchlings look like miniature adults, except that their front flippers are proportionally longer relative to those of adults, and extend along the entire length of their bodies. Hatchlings are covered with tiny black and white scales, which they lose after a few weeks of growth (Pritchard, 1971).

POPULATION BIOLOGY

The population structure for leatherbacks is unknown because hatchlings and sub-adults are oceanic and rarely seen. Males are often seen in northern waters or off nesting beaches with females (James et al., 2005c). Estimates are available for the number of adult females at some nesting beaches. By modeling nest numbers, it has been possible to determine that Florida has a significantly increasing leatherback population (Witherington and Koeppel, 2000). This trend seems evident over the past 10 years for which consistent survey data are available. St. Croix also has an exponentially growing population (13% per yr), based on two decades of data collection (Dutton et al., 2005).

From stranding information available for juveniles (classified as less than 145 cm CCL; *n* = 48) on the Gulf and Atlantic coasts of the US, a sex ratio of 1.4 females/1.0 males has been estimated (58.3% females; NMFS–SEFSC, 2001). However, this estimate of juvenile sex ratio may be skewed because reproductively mature females may be smaller than 145 cm (Stewart et al., submitted A). Stranding information is also available for adults but because of the likelihood that more females strand than males due to the need to come ashore to nest, estimates of sex ratios based on adult stranding records are not used (NMFS–SEFSC, 2001).

Pritchard (1971) estimated that the worldwide female leatherback population was at least 29,000, but later adjusted that figure to 115,000 leatherbacks worldwide (Pritchard, 1982). There has been considerable recent discussion of the number of leatherbacks globally. The most recent estimates for the western Atlantic and Caribbean are 17,640 female turtles (Spotila, 2004), which includes 40 females nesting per year in Florida. This is an underestimate of the Florida population, as we see more than 40 individuals each year (Stewart and Johnson, unpubl. data). A few of these populations (Florida and St. Croix) have been increasing in recent years (Witherington and Koeppel, 2000; Dutton et al., 2005), while others are considered stable or, similar to Caribbean Central America, in slight decline (Troëng et al., 2004). For the Eastern Atlantic (mainly Gabon), Spotila (2004) estimated there were 9890 females in the population. The Eastern Pacific estimates are the most devastating figures, with only 910 females; down from 1965–2675 in 1996 (Spotila et al., 1996) and down even further from 75,000 in 1980 (Pritchard, 1982). This drastic decline is alarming and it is uncertain whether the population can recover, even with the best protection in place for the remaining nesting females (Spotila et al., 2000). Indian Ocean and Western Pacific estimates are near 7420 females (Spotila, 2004). The total current world estimate is 35,860 female leatherbacks (Spotila, 2004).

In Florida, studies are underway to determine the size of the nesting population. Across the state, nesting has been increasing (Fig. 7-5) over the past ten years (Witherington

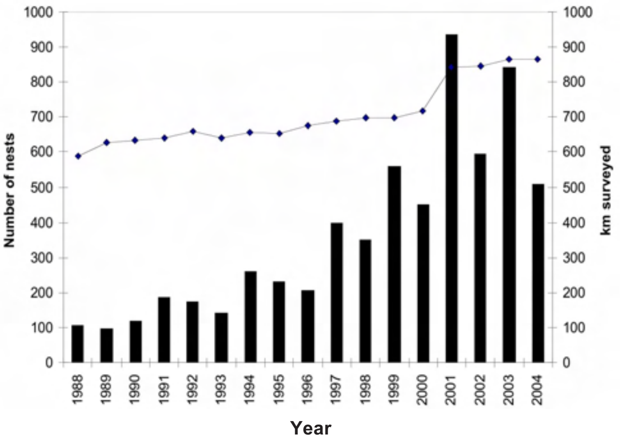

Figure 7-5. The number of leatherback nests recorded on Florida beaches from 1988–2004, as well as the number of km surveyed each year. Data derived from www.floridamarine.org (FWRI, 2006).

and Koeppel, 2000; FWRI, 2006). It is unclear whether this increase is due to new recruits to the population or if it represents migrants from other Caribbean nesting beaches, but as of 2005, there were at least 200 individual females nesting in Florida (Stewart and Johnson, unpubl. data; D. Bagley, *pers.comm.*).

Population models have been used extensively when considering the conservation of endangered species and they are useful in examining results of protecting specific life stages of the animal. However, because the time to sexual maturity, longevity and mortality estimates are poorly understood for the leatherback, there are too many unknown variables to construct a valid model for leatherback populations. Information such as fecundity, life span, and certain hatchling productivity measures, for which we do have estimates, are insufficient to produce useful population estimates (Crouse et al., 1987; NMFS-SEFSC, 2001).

INTERSPECIFIC INTERACTIONS

Community Structure. — Leatherbacks are not generally found in the company of any other sea turtle, except possibly when taking advantage of jellyfish concentrations (Leary, 1957), and when mating (Reina et al., 2005). All evidence indicates that they are solitary, pelagic animals.

Diet and Feeding. — The diet of the leatherback is mainly comprised of gelatinous organisms, such as *Aurelia*, *Cyanea*, and *Stomolophus* jellies. However, most information about the diet of leatherbacks has come from stomach content analysis of stranded dead specimens. Few reports of leatherback feeding in the wild were available until recently (James and Herman, 2001). Unlike some sea turtles, it is thought that female leatherbacks eat during the internesting period (Eckert et al., 1989b). The jaw and tongue movement involved in feeding for leatherbacks was described by Bels et al. (1998).

A study of the gut contents of six leatherback turtles from the North Sea revealed that the turtles had fed almost exclusively on jellies (Den Hartog and Van Nierop, 1984). This was determined by identifying the nematocysts microscopically, and recording the species from which they came. Included in that list of prey items were: *Cyanea capillata*, *Cyanea lamarckii*, *Chrysaora hysoscella*, *Pelagia noctiluca*, *Aurelia aurita*, and *Rhizostoma octopus*. Desjardin (2005) found nematocysts from Cnidarian Classes Hydrozoa, Scyphozoa, Anthozoa, Cubozoa and Staurozoa within stranded leatherback guts from the eastern United States. Some other organisms were also noted, including siphonophores, and *Hyperia* (an amphipod scyphozoan commensal species) (Den Hartog and Van Nierop, 1984; Desjardin, 2005). In 3 of 6 turtle guts from the North Sea specimens, plastic bags were found (Den Hartog and Van Nierop, 1984). Desjardin (2005) also documented plastic material in 7 of 12 (58%) leatherback stomachs from stranded animals. There is some discussion as to whether leatherbacks seek out gelatinous prey or if they just find it available and easy to catch – in the pelagia there is little food and leatherbacks are not fast enough to catch other prey items (Den Hartog and Van Nierop, 1984).

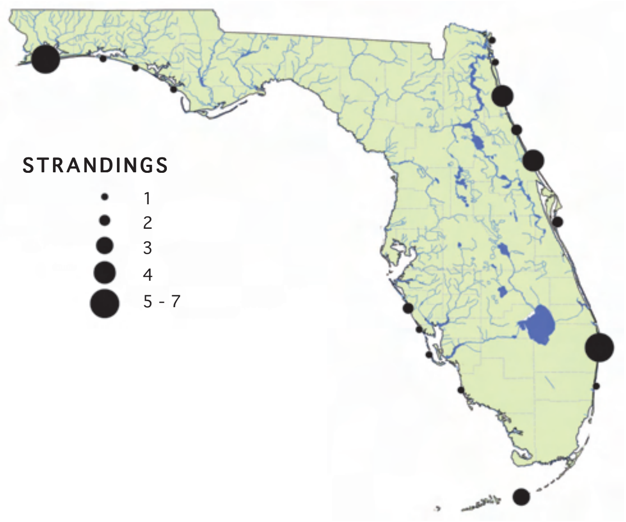

Figure 7-6. Distribution of Florida stranding records for *Dermochelys coriacea* from 2004.

Grant and Ferrell (1993) observed leatherbacks feeding on cannonball jellies (*Stomolophus meleagris)* in North Carolina during May and June. The appearance of leatherbacks seemed to coincide with high densities of these jellies. Leatherbacks have been noted in other areas of high jelly concentrations (Leary, 1957; Collard, 1990). Leatherbacks were observed feeding on *Cyanea capillata* at the surface in the northwest Atlantic (James and Herman, 2001). It has been suggested that leatherbacks may be able to locate jellies at depth by looking for bioluminescence (Davenport, 1988).

Predation. — Leatherback egg predation by mammalian, avian, reptilian, and invertebrate predators is well documented (Stancyk, 1982). In Florida, the usual suspects are raccoons; however, poaching by humans has also been a minor problem. There are a few reports of predation of adult and hatchling leatherbacks. Adult leatherback remains were found in the stomach of killer whales (*Orcinus orca*) captured near St. Vincent in the Lesser Antilles (Caldwell and Caldwell, 1969), and in Mexico (Sarti et al., 1994). Jaguars have also taken and killed nesting females in Suriname (Autar, 1994), and at Tortuguero, Costa Rica (Troëng, 2000).

Predation by fish on leatherback hatchlings has been documented by Vose and Shank (2003), who found hatchlings in the stomachs of snappers off the coast of Florida. Hatchlings leaving Sandy Point, St. Croix, were heavily preyed upon by tarpon. This was determined by snorkeling after swimming hatchlings and watching them from shore (Nellis and Henke, 2000).

THREATS

Documented Threats. — Leatherbacks face many threats to their survival, beginning with the nest environment. Most of the available information on cause of death is contained in strandings reports (NMFS-SEFSC, 2001). The most specific information is available for US waters. In Florida, since 1992, an average of 26 leatherbacks (range = 14–40) per year have stranded dead, during all months of the year (Florida Fish and Wildlife Conservation Commission – FWC, 2002; Fig. 7-6). Of 458 dead leatherbacks documented from 1992–2002, many (but not all) were evaluated for anomalies or apparent cause of death. Specific injuries noted were as follows (# of turtles in parentheses): boat related injuries (79), entanglement in monofilament fishing line (6), entanglement in net, crab trap line, or other debris (33), shark bite wounds (39), and mutilations (12) (FWC, 2002).

Entanglement in various fishing gear appears to be more of a threat to leatherbacks than to other turtle species (NMFS-SEFSC, 2001; James et al., 2005b). In the northwest Atlantic, leatherbacks have been known to become entangled in fish traps, lobster pots and crab pots (NMFS-SEFSC, 2001; Dwyer et al., 2003; James et al., 2005b). Entanglements may be responsible for most of the strandings in that region. In Cape Cod Bay, the majority (89%) of observed leatherback strandings were apparently due to death caused by entanglement in lobster pot gear (Prescott, 1988).

The Sea Turtle Stranding and Salvage Network (STSSN) data from 1980–99 indicate that significantly more leatherbacks strand due to entanglement from Virginia to Maine (62%) than North Carolina to Florida (18%), or the Gulf Coast (19%) (NMFS-SEFSC, 2001). Gill nets also capture leatherbacks (Fig. 7-7). In observer programs operated by NMFS, leatherbacks have reportedly been caught in low numbers in this fishery; however, observer coverage is low (maximum 5% of fishery; NMFS-SEFSC, 2001). In the northwest Atlantic, leatherbacks are routinely caught in gill nets (Goff and Lien, 1988; Goff et al., 1994). Documented deaths occur in this fishery in Africa (Castroviejo et al., 1994), in Nicaragua (Lagueux et al., 1998), in French Guiana (Chevalier et al., 1999), and in Trinidad (Eckert and Lien, 1999; Lee Lum, 2003).

Leatherbacks encounter trawls (mostly shrimp operations) during migrations along the eastern seaboard of the US. Even with the legislated requirement of turtle excluder devices (TEDs) in shrimp trawls, large turtles (including leatherbacks) are still captured (Henwood and Stuntz, 1987; Epperly and Teas, 1999). In response to this, leatherback conservation zones have been established, with more TED regulations in place (see next section).

Figure 7-7. A leatherback entangled in a gill net at Cape Lookout Bight, North Carolina. The turtle was released alive. Photo by Keith Rittmaster, North Carolina Maritime Museum.

Leatherbacks in the northwest Atlantic are caught incidentally in the longline fishery. However, turtles are usually hooked in the shoulder and neck region; few are hooked in the mouth (S. Epperly, *pers. comm.*; Garrison, 2003), and there is little mortality recorded at capture (Garrison, 2003). However, the pelagic longline fishery has been implicated in the worldwide decimation of leatherback populations, especially in the Eastern Pacific (Lewison et al., 2004) and this threat remains a serious concern for the conservation of the species (Lewison et al., 2004).

There are few leatherbacks taken in other fisheries operations. Incidental captures may occur with rod and reel fishing, or pound net fishing (NMFS-SEFSC, 2001). In other places, such as Indonesia, West Africa, and the Grenadines, leatherbacks are targeted and harvested for meat (Suarez and Starbird, 1996).

Boat traffic is becoming a big problem for leatherbacks. Propellers can easily mutilate or kill leatherbacks. The STSSN reported 231 strandings due to boat strikes between 1980 and 1999. Some of these boat strikes may occur postmortem when the carcasses are floating at the surface.

Eggs, juveniles, and adult turtles are targeted in several places. In Florida, the take of eggs is an uncommon occurrence, but there are usually a few cases each year, although most nests poached in Florida are loggerhead nests. Nesting turtles are extremely vulnerable and are killed and eaten in West Africa (Graff, 1995), some Caribbean islands (Eckert and Honebrink, 1992; d'Auvergne and Eckert, 1993), Guyana (Pritchard, 1988), and Indonesia (Suarez and Starbird, 1996). Eggs are collected by poachers in Costa Rica (Campbell et al., 1996) and Panama (A. and P. Meylan, *pers. comm.*). Eggs have been legally collected in Suriname (Mohadin, 1999).

Potential Threats. — It is likely that leatherbacks are at higher risk for marine debris ingestion than other turtles (NMFS-SEFSC, 2001). Leatherbacks, being pelagic in nature and in combination with their tendency to feed along convergence areas of the ocean, are more likely to encounter floating debris (such as plastic bags that look like jellies) and ingest it (Shoop and Kenney, 1992; Lutcavage et al., 1997). Among 189 turtles examined in several studies, 36 had plastic in their stomachs (Mrosovsky, 1981; Fritts, 1982; Sadove and Morreale, 1990). It has been suggested that leatherbacks may not be able to distinguish between a prey item and a prey-shaped plastic item (Mrosovsky, 1981; Balazs, 1985). Egg harvest on many nesting beaches throughout the leatherback's range remain a significant threat to its survival (Sarti Martinez, 2000). The pelagic longline fisheries of the world also represent a major potential threat to leatherbacks (Lewison et al., 2004).

STATUS

The leatherback is considered to be Endangered in Florida waters and on its beaches by the U.S. Fish and

Wildlife Service, the Florida Fish and Wildlife Conservation Commission, and the FCREPA. The World Conservation Union (IUCN) lists the leatherback as Critically Endangered throughout its range (IUCN, 2004). The leatherback is also protected by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) under Appendix I (UNEP-WCMC, 2006).

CONSERVATION OPTIONS AND SOLUTIONS

The conservation of leatherbacks globally is expected to be a challenge since it will require the participation of many nations (Crowder, 2000). In the US, there is a recovery plan for the leatherback (NMFS and USFWS, 1992). However, it is cautionary in approach as several variables are unknown. Because leatherbacks are officially listed as endangered they are already afforded protection by law. For the long-term conservation of the species, nest protection should continue, as well as reduction of in-water mortality. Continuing to enforce lighting ordinances and limiting or mitigating effects of coastal development will ensure that adequate nesting habitat is available.

Nesting Beach Habitat. — In Florida, nesting beach protection seems to be adequate. Beach surveys and nest monitoring are standardized by state protocols. The Statewide Nesting Beach Survey or SNBS (FWRI, 2006) is conducted from March 1 – October 31 yearly. Each nest or false crawl is recorded along most of Florida's coastline. The Index Nesting Beach Survey or INBS is a more detailed program which runs from May 15 to August 31 each year. This survey takes place on selected beaches and incorporates measures of productivity (such as nest hatching success) into the data collected (FWRI, 2006). These surveys allow detailed and consistent long-term records to be kept for the state and are extremely useful in reliably determining trends for nesting sea turtles.

In some areas, such as Miami Beach and Ft. Lauderdale, turtle nests (including leatherback nests) are relocated to hatcheries, where they are monitored and protected. In most cases this is because the nesting beaches are used heavily by humans during the summer months. Lighting ordinances in many coastal cities have helped to eliminate or reduce hatchling and nesting female disorientations. New methods for light reduction or redirection are constantly being tested and improvements can still be made to remove this threat entirely.

In-Water Mortality. — Reducing in-water mortality is probably the biggest challenge to conserving leatherbacks in Florida. Leatherbacks are killed in many ways (see above), with the majority being boat-struck or becoming entangled in fishing gear. Turtle excluder devices (TEDs) are also required by law in nets used for catching shrimp. When original TED regulations came into effect, they were designed to protect Kemp's ridley and juvenile loggerhead turtles (Epperly and Teas, 2002). The escape opening in the hard TED measured 35 inches in width and 12 inches in height. This was expected to be successful in excluding sea turtles 97% of the time (US Environmental Protection Agency, 2003). In recent years, however, there has been increasing concern that these TEDs were not excluding larger loggerheads, green turtles, and especially large leatherbacks which are often found in shrimping areas (Epperly and Teas, 2002). This concern led to new regulations for the industry and the opening on hard TEDs is now required to be 32 inches wide by 32 inches high. This is expected to be successful in excluding large leatherbacks. In testing, using a leatherback model, the opening was sufficient to allow the turtle to escape (Epperly and Teas, 2002).

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LITERATURE CITED

Andrews, H. and Shanker, K. 2002. A significant population of leatherback turtles in the Indian Ocean. Kachhapa 6:19.

Autar, L. 1994. Sea turtles attacked and killed by jaguars in Suriname. Marine Turtle Newsletter 67:11-12.

Baird, R.W., Ligon, A.D., Hooker, S.K., and Gorgone, A.M. 2001. Subsurface and nighttime behaviour of pantropical spotted dolphins in Hawai'i. Canadian Journal of Zoology 79(6):988-996.

Baird, R.W., Borsani, J.F., Hanson, M.B., and Tyack, P.L. 2002. Diving and night-time behavior of long-finned pilot whales in the Ligurian Sea. Marine Ecology Progress Series 237:301-305.

Balazs, G.H. 1985. Impact of ocean debris on marine turtles: entanglement and ingestion. In: Shomura, R.S., Yoshida, H.O. (Eds.). Proc. of the Workshop on the Fate and Impact of Marine Debris. NOAA Tech. Memo. NMFS-SWFC-54. pp. 387-429.

Bels, V.L., Davenport, J., and Renous, S. 1998. Food ingestion in the estuarine turtle *Malaclemys terrapin*: comparison with the marine turtle *Dermochelys coriacea*. Journal of the Marine Biological Association of the United Kingdom 78:953-972.

Bhaskar, S. 1993. The status and ecology of sea turtles in the Andaman and Nicobar Islands. Centre for Herpetology, Madras Crocodile Bank, India. Publication No. ST 1/93. 41 pp.

Billes, A. and Fretey, J. 2004. Nesting of leatherback turtles in Gabon: Importance of nesting population is confirmed. In: Proc. of the Twenty-first Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memo.NMFS-SEFSC-528. p. 6-8.

Birkenmeier, E. 1971. Juvenile leathery turtles, *Dermochelys coriacea* (Linneaus), in captivity. Brunei Museum Journal 2:160-172.

Boulenger, G. 1889. Catalogue of the chelonians, rhyncocephalians and crocodiles in the British Museum (Natural History). London, U.K. 311 pp.

Boulon, R.H., Jr., Dutton, P.H., and McDonald, D.L. 1996. Leatherback turtles (*Dermochelys coriacea*) on St. Croix, U.S. Virgin Islands: fifteen years of conservation. Chelonian Conservation and Biology 2(2):141-147.

Caldwell, D.K., Carr, A., and Hellier, T.R., Jr. 1955. A nest of the Atlantic leatherback turtle, *Dermochelys coriacea coriacea* (Linnaeus), on the Atlantic coast of Florida, with a summary of American nesting records. Quarterly Journal Florida Academy Science 18(4):279-284.

Caldwell, D.K. 1959. On the status of the Atlantic leatherback sea turtle, *Dermochelys coriacea coriacea*, as a visitant to Florida nesting beaches, with natural history notes. Quarterly Journal Florida Academy Science 21(3):285-291.

Caldwell, D.K. and Caldwell, M.C. 1969. Addition of the leatherback sea turtle to the known prey of the killer whale *Orcinus orca*. Journal of Mammology 50(3):636.

Campbell, C.L., Lagueux, C.J., and Mortimer, J.A. 1996. Leatherback turtle, *Dermochelys coriacea*, nesting at Tortuguero, Costa Rica, in 1995. Chelonian Conservation and Biology 2(2):169-172.

Carr, A. 1952. Handbook of turtles. Comstock Publishing Associates, Cornell University Press, Ithaca, NY. 542 pp.

Carr, T. and Carr, N. 1986. *Dermochelys coriacea* (Leatherback sea turtle) copulation. Herpetological Review 17(1):24-25.

Castroviejo, J., Juste, B.J., Perez Del Val, J., Castelo, R., and Gil, R. 1994. Diversity and status of sea turtle species in the Gulf of Guinea islands. Biodiversity and Conservation 3(9):828-836.

Chan, E.-H. and Liew, H.-C. 1996. Decline of the leatherback population in Terengganu, Malaysia, 1956-1995. Chelonian Conservation and Biology 2(2):196-203.

Chaverri, D.C. 1999. Anidación de la tortuga *Dermochelys coriacea* (Testudines: Dermochelyidae) en Playa Gandoca, Costa Rica (1990-1997). Revista de Biologia Tropical 47:225-236.

Chaves, A., Serrano, G., Marin, G., Arguedas, E., Jimenez, A., and Spotila, J.R. 1996. Biology and conservation of leatherback turtles, *Dermochelys coriacea*, at Playa Langosta, Costa Rica. Chelonian Conservation and Biology 2(2):184-189.

Cheong, L.C. 1990. Observations on the nesting population of leatherback turtles *Dermochelys coriacea* in Trindad. Caribbean Marine Studies 1:48-53.

Chevalier, J., Desbois, X., and Girondot, M. 1999. The reason of decline of leatherback turtles (*Dermochelys coriacea*) in French Guiana: a hypothesis. In: Guyetant, R., Miaud, C. (Eds.). 9th Extraordinary Meeting of the Societas Europaea Herpetologica. pp. 1-10.

Collard, S.B. 1990. Leatherback turtles feeding near a watermass boundary in the Eastern Gulf of Mexico. Marine Turtle Newsletter 50:12-14.

Crouse, D.T., Crowder, L.B., and Caswell, H. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412-1423.

Crowder, L.B. 2000. Leatherback's survival will depend on an international effort. Nature 405:881.

D'Auvergne, C. and Eckert, K.L. 1993. WIDECAST Sea Turtle Recovery Action Plan for St. Lucia. In: Eckert, K.L. (Ed.). CEP Technical Report 26. UNEP Caribbean Environment Program, Kingston, Jamaica. 70 pp.

Davenport, J. 1988. Do diving leatherbacks pursue glowing jelly? British Herpetological Society Bulletin 24:20-21.

Den Hartog, J.C. and Van Nierop, M.M. 1984. A study on the gut contents of six leathery turtles *Dermochelys coriacea* (Linnaeus) (Reptilia: Testudines: Dermochelyidae) from British waters and from the Netherlands. Zoologische Verhandelingen (Leiden) 209:1-36.

Deraniyagala, P.E.P. 1939. The tetrapod reptiles of Ceylon: Volume 1. Testudinates and Crocodilians. London, England: Colombo, Ceylon, and Dulau and Co., Ltd., England. 421 pp.

Desjardin, N.A. 2005. Spatial, temporal, and dietary overlap of leatherback sea turtles (*Dermochelys coriacea*) and ocean sunfishes (Family Molidae). Masters Thesis. Dept. of Biology. Florida Atlantic University, Boca Raton, FL. 87 pp.

Duque, V.M., and Paez, V.P. 2000. Nesting ecology and conservation of the leatherback turtle, *Dermochelys coriacea*, at La Playona, Chocoan Gulf of Uraba (Colombia), in 1998. Actualidades Biologicas Medellin 22(72):37-53.

Dutton, P. and McDonald, D. 1995. Hatch rates of leatherback (*Dermochelys coriacea*) clutches reburied with and without yolkless eggs. In: Richardson, J.I., and Richardson, T.H. (Compilers). Proc. of the Twelfth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-361. pp. 177-178.

Dutton, P.H., McDonald, D., and Boulon, R.H. 1992. Tagging and nesting research on leatherback sea turtles (*Dermochelys coriacea*) on Sandy Point, St. Croix, US Virgin Islands. PC-P&NR-287-91.

Dutton, P.H., Bowen, B.W., Owens, D.W., Barragan, A., and Davis, S.K. 1999. Global phylogeography of the leatherback turtle (*Dermochelys coriacea*). Journal of Zoology. 248:397-409.

Dutton, P.H., Dutton, D.L., and Frey, A.N. 2002. Familial relationships among nesting female leatherbacks examined with genetic markers In: Mosier, A., Foley, A., and Brost, B. (Compilers), Proc. of the Twentieth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-477, p. 20.

Dutton, P.H., Roden, S., Galver, L.M., and Hughes, G.R. 2003. Genetic population structure of leatherbacks in the Atlantic elucidated by microsatellite markers. In: Seminoff, J.A. (Compiler), Proc. of the Twenty-second Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-503. p. 44.

Dutton, D.L., Dutton, P.H., Chaloupka, M.Y., and Boulon, R.H. 2005. Increase of a Caribbean leatherback turtle *Dermochelys coriacea* nesting population linked to long-term nest protection. Biological Conservation 126(2):186-194.

Dwyer, K.L., Ryder, C.E, and Prescott, R. 2003. Anthropogenic mortality of leatherback turtles in Massachusetts waters. In: Seminoff, J.A. (Compiler), Proc. of the Twenty-second Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-503. p. 260.

Eckert, S.A. 1998. Perspectives on the use of satellite telemetry and other electronic technologies for the study of marine turtles, with reference to the first year long tracking of leatherback sea turtles.

In: Epperly, S.P., and Braun, J. (Compilers). Proc. of the Seventeenth Annual Sea Turtle Symposium. NOAA Tech. Memo. NMFS-SEFSC-415. pp. 44-46.

Eckert, S.A. 2002a. Distribution of juvenile leatherback sea turtle *Dermochelys coriacea* sightings. Marine Ecology Progress Series 230:289-293.

Eckert, S.A. 2002b. Swim speed and movement patterns of gravid leatherback sea turtles (*Dermochelys coriacea*) at St Croix, US Virgin Islands. Journal of Experimental Biology 205(23):3689-3697.

Eckert, K.L. and Eckert, S.A. 1988. Pre-reproductive movements of leatherback sea turtles (*Dermochelys coriacea*) nesting in the Caribbean. Copeia 1988(2):400-406.

Eckert, K.L. and Honebrink, T.D. 1992. WIDECAST Sea Turtle Recovery Action Plan for St. Kitts and Nevis. CEP Technical Report 17. UNEP Caribbean Environment Program, Kingston, Jamaica. 116 pp.

Eckert, S.A. and Lien, J. 1999. Eliminating the incidental mortality of leatherback sea turtles by commercial fisheries in Trinidad and Tobago. Draft report. 5 pp.

Eckert, K.L. and Luginbuhl, C. 1988. Death of a giant. Marine Turtle Newsletter 43:2-3.

Eckert, S.A., Nellis, D.W., Eckert, K.L., and Kooyman, G.L. 1986. Diving patterns of two leatherback sea turtles (*Dermochelys coriacea*) during internesting intervals at Sandy Point, St. Croix, U.S. Virgin Islands. Herpetologica 42(3):381-388.

Eckert, K.L., Eckert, S.A., Adams, T.W., and Tucker, A.D. 1989a. Inter-nesting migrations by leatherback sea turtles (*Dermochelys coricea*) in the West Indies. Herpetologica 45(2):190-194.

Eckert, S.A., Eckert, K.L., Ponganis, P., and Kooyman, G.L. 1989b. Diving and foraging behavior of leatherback sea turtles (*Dermochelys coriacea*). Canadian Journal of Zoology 67(11):2834-2840.

Eckert, S.A., Liew, H.C., Eckert, K.L., and Chan, E.H. 1996. Shallow water diving by leatherback turtles in the South China Sea. Chelonian Conservation and Biology 2(2):237-243.

Eckert, S., Bagley, D., Kubis, S., Ehrhart, L., Johnson, C., Stewart, K., and DeFreese, D. In press. Inter-nesting, post-nesting movements and foraging habitats of leatherback sea turtles (*Dermochelys coriacea*) nesting in Florida. Chelonian Conservation and Biology 5(2).

Epperly, S.P. and Teas, W.G. 1999. Evaluation of TED opening dimensions relative to size of turtles stranding in the western North Atlantic. NMFS - SEFSC Contribution PRD-98/99-08. 31 pp.

Epperly, S.P. and Teas, W.G. 2002. Turtle excluder devices - are the escape openings large enough? Fishery Bulletin 100(3):466-474.

Ferraroli, S., Georges, J.-Y., Gaspar, P., and Le Maho, Y. 2004. Where leatherback turtles meet fisheries. Nature 429:521-522.

Florida Fish and Wildlife Conservation Commission (FWC). 2002. Florida Sea Turtle Stranding and Salvage Network Database. Florida Marine Research Institute, St. Petersburg, FL.

Frair, W., Ackman, R.G., and Mrosovsky, N. 1972. Body temperature of *Dermochelys coriacea*: warm turtle from cold water. Science 177:791-793.

Fretey, J. 2004. Status and nesting of *Dermochelys coriacea* in West and Central Africa. In: Coyne, M.S., and Clark, R.D. (Compilers). Proc. of the Twenty-first Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-528. p. 10-11.

Fretey, J. and Bour, R. 1980. Redecouverte du type de *Dermochelys coriacea* (Vandelli) (Testudinata, Dermochelyidae). Bolletin di Zoologia 47(1-2):193-205.

Fretey, J. and Girardin, N. 1989. La nidification de la tortue luth, *Dermochelys coriacea* (Vandelli, 1761) (Chelonii, Dermochelyidae) sur les côtes du Gabon. Revue de Zoologie Africaine – Journal of African Zoology 102:125-132.

Fretey, J., Dontaine, J.F., and Neves, O. 1999. São Tomé et Príncipe: Zone de croissance pour les tortues-luths? Canopée 15:1-2.

Fritts, T.H. 1982. Plastic bags in the intestinal tracts of leatherback marine turtles. Herpetological Review 13(3):72-73.

Fritts, T.H., Hoffman, H., and McGehee, M.A. 1983. The distribution and abundance of marine turtles in the Gulf of Mexico and nearby Atlantic waters. Journal of Herpetology 17:327-344.

FWRI. 2006. Fish and Wildlife Research Institute – Florida Fish and Wildlife Conservation Commission. (Sea Turtle pages). http://research.myfwc.com/features/view_article.asp?id=2479.

Garrison, L.P. 2003. Estimated bycatch of marine mammals and turtles in the U.S. Atlantic pelagic longline fleet during 2001–2002. NOAA Tech. Memo. NMFS-SEFSC-515, 52 pp.

Girondot, M. and Fretey, J. 1996. Leatherback turtles, *Dermochelys coriacea*, nesting in French Guiana, 1978-1995. Chelonian Conservation and Biology 2(2):204-208.

Godfrey, M.H. and Barreto, R. 1998. *Dermochelys coriacea* (Leatherback sea turtle) copulation. Herpetological Review 29(1):40-41.

Godfrey, M.H. and Drif, O. 2002. *Dermochelys coriacea* (Leatherback Sea Turtle). Size. Herpetological Review 33(3):200-201.

Godley, B., Broderick, A., Blackwood, S., Collins, L., Glover, K., McAldowie, C., McCulloch, D., and McLeod, J. 1993. 1991 survey of marine turtles nesting in Trinidad and Tobago. Marine Turtle Newsletter 61:15-18.

Goff, G.P. and Lien, J. 1988. Atlantic leatherback turtles, *Dermochelys coriacea*, in cold water off Newfoundland and Labrador. Canadian Field-Naturalist 102(1):1-5.

Goff, G.P., Lien, J., Stenson, G.B., and Fretey, J. 1994. The migration of a tagged leatherback turtle, *Dermochelys coriacea*, from French Guiana, South America to Newfoundland, Canada in 128 days. Canadian Field-Naturalist 108(1):72-73.

Graff, D. 1995. Nesting and hunting survey of the marine turtles of the island of São Tomé. ECOFAC Componente de São Tomé et Príncipe. 38 pp.

Grant, G.S. and Ferrell, D. 1993. Leatherback turtle, *Dermochelys coriacea* (Reptilia: Dermochelyidae): Notes on near-shore feeding behavior and association with Cobia. Brimleyana 19: 77-81.

Grant, G.S., Malpass, H., and Beasley, J. 1996. Correlation of leatherback turtle and jellyfish occurrence. Herpetological Review. 27(3):123-125.

Greer, A.E., Lazell, J.D., and Wright, R.M. 1973. Anatomical evidence for a counter-current heat exchanger in the leatherback turtle (*Dermochelys coriacea*). Nature 244(5412):181.

Hall, K.V. 1993. Marine turtle nesting in western Puerto Rico, 1993. Final Report for the Cooperative Agreement between USFWS and the Sea Grant Program, Univ. of Puerto Rico, Mayaguez Campus. Cooperative Agreement No. 1448-0004-93-929. PRU-T-94(3). 28 pp.

Hays, G.C., Houghton, J.D.R., and Myers, A.E. 2004. Pan-Atlantic leatherback turtle movements. Nature 429:522.

Henwood, T. and Stuntz, W.E. 1987. Analysis of sea turtle captures and mortalities during commercial shrimp trawling. Fishery Bulletin 85:813-817.

Hilterman, M.L. and Goverse, E. 2005. Annual report on the 2004 leatherback turtle research and monitoring project in Suriname. World Wildlife Fund - Guianas Forests and Environmental Conservation Project (WWF-GFECP) Technical Report of the Netherlands Committee for IUCN (NC-IUCN), Amsterdam, the Netherlands, 18 pp.

Hirth, H.F. 1980. Some aspects of the nesting behavior and reproductive biology of sea turtles. American Zoology 20(3):507-523.

Hoffman, W. and Fritts, T.H. 1982. Sea turtle distribution along the boundary of the Gulf Stream Current off Eastern Florida.

Herpetologica 38:405-409.

Hughes, G.R. 1996. Nesting of the leatherback turtle (*Dermochelys coriacea*) in Tongaland, KwaZulu-Natal, South Africa, 1963-1995. Chelonian Conservation and Biology 2(2):153-158.

Hughes, G.R., Luschi, P., and Papi, F. 1998. The 7000-km oceanic journey of a leatherback turtle tracked by satellite. Journal of Experimental Marine Biology and Ecology 229:209-217.

IUCN 2004. 2004 IUCN Red List of Threatened Species. www.iucnredlist.org.

James, M.C. and Herman, T.B. 2001. Feeding of *Dermochelys coriacea* on medusae in the northwest Atlantic. Chelonian Conservation and Biology 4(1):202-205.

James, M.C., and Mrosovsky, N. 2004. Body temperatures of leatherback turtles (*Dermochelys coriacea*) in temperate waters off Nova Scotia, Canada. Canadian Journal of Zoology 82(8):1302-1306.

James, M.C., Myers, R.A., and Ottensmeyer, C.A. 2005a. Behaviour of leatherback sea turtles, *Dermochelys coriacea*, during the migratory cycle. Proceedings of the Royal Society B - Biological Sciences 272(1572):1547-1555.

James, M.C., Ottensmeyer, C.A., and Myers, R.A. 2005b. Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. Ecology Letters 8:195-201.

James, M.C., Eckert, S.A., and Myers, R.A. 2005c. Migratory and reproductive movements of male leatherback turtles (*Dermochelys coriacea*). Marine Biology 147:845-853.

King, F.W. and Burke, R.L. 1997. Crocodilian, Tuatara, and Turtle Species of the World: An Online Taxonomic and Geographic Reference Association of Systematics Collections, Washington, D.C. 294 p.; http://www.flmnh.ufl.edu/natsci/herpetology/turtcroclist/

Knowlton, A.R. and Weigle, B. 1989. A note on the distribution of leatherback turtles (*Dermochelys coriacea*) along the Florida coast in February 1988. NOAA Tech. Memo. NMFS-SEFSC-232 pp. 83-85.

Lagueux, C.J., Campbell, C., and Herbst, L.H. 1998. Demography of marine turtles harvested by Miskitu Indians of the Atlantic Nicaragua. NOAA Tech. Memo. NMFS-SEFSC-412 p. 90.

Leary, T.R. 1957. A schooling of leatherback turtles, *Dermochelys coriacea coriacea*, on the Texas coast. Copeia 1957(3):232.

Lee Lum, L. 2003. An assessment of incidental turtle catch in the gillnet fishery in Trinidad and Tobago, West Indies. Institute of Marine Affairs, Trinidad, 22 pp., Project no. 00-026-005.

Leslie, A.J., Penick, D.N., Spotila, J.R., and Paladino, F.V. 1996. Leatherback turtle, *Dermochelys coriacea*, nesting and nest success at Tortuguero, Costa Rica, in 1990-1991. Chelonian Conservation and Biology 2(2):159-168.

Lewison, R.L., Freeman, S.A., and Crowder, L. 2004. Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. Ecology Letters 7:221-231.

Lutcavage, M.E., Plotkin, P., Witherington, B., and Lutz, P.L. 1997. Human impacts on sea turtle survival. In: Lutz, P.L., and Musick, J.A. (Eds.). The Biology of Sea Turtles. Boca Raton, FL. CRC Press, pp. 387-409.

McDonald, D., Dutton, P., Brandner, R., and Basford, S. 1996. Use of pineal spot ('pink spot') photographs to identify leatherback turtles. Herpetological Review 27(1):11-12.

Meylan, A., Meylan, P., and Ruiz, A. 1985. Nesting of *Dermochelys coriacea* in Caribbean Panama. Journal of Herpetology 19(2):293-297.

Mohadin, K. 1999. Sea turtle research and conservation in Suriname: history, constraints and achievements. In: Kelle, L., Lochon, S., Thérèse, J., and Desbois, X. (Eds). Proc. of the 3rd Meeting on the Sea Turtles of the Guianas.

Morgan, P.J. 1989. Occurrence of leatherback turtles (*Dermochelys coriacea*) in the British Isles in 1988 with reference to a record specimen. In: Eckert, S.A., Eckert, K.L., and Richardson, T.H. (Compilers). Proc. of the Ninth Annual Workshop on Sea Turtle Conservation and Biology. NOAA Tech. Memo. NMFS-SEFC-232 pp. 119-120.

Morreale, S.J., Standora, E.A., Spotila, J.R., and Paladino, F.V. 1996. Migration corridor for sea turtles. Nature 384:319-320.

Mrosovsky, N. 1980. Thermal biology of sea turtles. American Zoology 20(3):531-547.

Mrosovsky, N. 1981. Plastic jellyfish. Marine Turtle Newsletter 17:5-6.

Mrosovsky, N. 1987. Leatherback turtle off scale. Nature 327:286.

Mrosovsky, N. and Pritchard, P.C.H. 1971. Body temperatures of *Dermochelys coriacea* and other sea turtles. Copeia 1971(4):624-631.

Mrosovsky, N., Dutton, P.H., and Whitmore, C.P. 1984. Sex ratios of two species of sea turtle nesting in Suriname. Canadian Journal of Zoology 62(11):2227-2239.

Nellis, D.W. and Henke, S.E. 2000. Predation of leatherback turtle hatchlings by near shore aquatic predators. In: Kalb, H.J., and Wibbels, T. (Compilers). Proc. of the Nineteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-443 p. 168.

NMFS and USFWS. 1992. Recovery plan for leatherback turtles in the U.S. Caribbean, Atlantic and Gulf of Mexico. National Marine Fisheries Service, Washington, D.C.

NMFS-SEFSC. 2001. Stock assessments of loggerhead and leatherback sea turtles and an assessment of the impact of the pelagic longline fishery on the loggerhead and leatherback sea turtles of the Western North Atlantic. NOAA Tech. Memo. NMFS-SEFSC-455, 343 pp.

Paladino, F.V., O'Connor, M.P., and Spotila, J.R. 1990. Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs. Nature 344(6269):858-860.

Prescott, R.L. 1988. Leatherbacks in Cape Cod Bay, Massachusetts, 1977-1988. In: Schroeder, B.A. (Compiler). Proc. of the Eighth Annual Workshop on Sea Turtle Conservation and Biology. NOAA Tech. Memo. NMFS-SEFSC-214 pp. 83-84.

Pritchard, P.C.H. 1971. The leatherback or leathery turtle, *Dermochelys coriacea*. International Union for the Conservation of Nature, Monograph 1:39 pp.

Pritchard, P.C.H. 1982. Nesting of the leatherback turtle, *Dermochelys coriacea* in Pacific Mexico, with a new estimate of the world population status. Copeia 1982(4):741-747.

Pritchard, P.C.H. and Trebbau, P. 1984. Family Dermochelyidae, *Dermochelys coriacea*. In the Turtles of Venezuela, Society for the Study of Amphibians and Reptiles, Contribution to Herpetology No. 2:249-267.

Pritchard, P.C.H. 1988. Sea turtles in Guyana. In: Schroeder, B.A. (Compiler). Proc. of the Eighth Annual Workshop on Sea Turtle Conservation and Biology. NOAA Tech. Memo. NMFS-SEFC-214. pp. 85-87.

Pritchard, P.C.H. 1996. Are leatherbacks really threatened with extinction? Chelonian Conservation and Biology. 2(2):303-305.

Pritchard, P.C.H. 2004. Long-term sea turtle nesting cycles in the Guianas. In: Coyne, M.S., and Clark, R.D. (Compilers). Proceedings of the Twenty-First Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-528. p. 66-68.

Rabon, D.R., Johnson, S.A., Boettcher, R., Dodd, M., Lyons M., Murphy, S., Ramsey, S., Roff, S., and Stewart, K. 2003. Confirmed leatherback turtle (*Dermochelys coriacea*) nests from North Carolina, with a summary of leatherback nesting activities north of Florida. Marine Turtle Newsletter 101:4-8.

Reina, R.D., Mayor, P.A., Spotila, J.R., Piedra, R., and Paladino, F.V. 2002a. Nesting ecology of the leatherback turtle, *Dermochelys* *coriacea*, at Parque Nacional Marino Las Baulas, Costa Rica: 1988-1989 to 1999-2000. Copeia 2002(3):653-664.

Reina, R.D., Jones, T.T., and Spotila, J.R. 2002b. Salt and water regulation by the leatherback sea turtle *Dermochelys coriacea*. Journal of Experimental Biology 205(13):1853-1860.

Reina, R.D., Abernathy, K.J., Marshall, G.J., and Spotila, J.R. 2005. Respiratory frequency, dive behaviour and social interactions of leatherback turtles, *Dermochelys coriacea* during the inter-nesting interval. Journal of Experimental Marine Biology and Ecology 316(1):1-16.

Rhodin, A.G.J. 1985. Comparative chondro-osseous development and growth of marine turtles. Copeia 1985(3):752-771.

Rhodin, J.A.G., Rhodin, A.G.J., and Spotila, J.R. 1996. Electron microscopic analysis of vascular cartilage canals in the humeral epiphysis of hatchling leatherback turtles, *Dermochelys coriacea*. Chelonian Conservation and Biology 2(2):250-260.

Sadove, S.S. and Morreale, S.J. 1990. Marine mammal and sea turtle encounters with marine debris in the New York Bright and the northeast Atlantic. In: Shomura, R.S., Godfrey, M.L. (Eds.). Proc. of the Second International Conference on Marine Debris. NOAA Tech. Memo. NMFS-SWFSC-154. pp. 562-570.

Sarti, M.L., Flores, O.L., and Aguayo, L.A. 1994. Evidence of predation of killer whale (*Orcinus orca*) on a leatherback sea turtle (*Dermochelys coriacea*) in Michoacan, Mexico. Revista de la Investigacion Cientifica 2 (No. Esp. SOMEMMA 2): 23-26.

Sarti, L.M., Eckert, S.A., Garcia, N.T., and Barragan, A.R. 1996. Decline of the world's largest nesting assemblage of leatherback turtles. Marine Turtle Newsletter 74:2-5.

Sarti, L., Eckert, S.A., Dutton, P., Barragan, A., Garcia, N. 2000. The current situation of the leatherback population on the Pacific coast of Mexico and Central America, abundance and distribution of the nestings: an update. In: Kalb, H.J. and Wibbels, T. (Compilers). Proc. of the Nineteenth Annual Symposium on Sea Turtle Biology and Conservation. U.S. Dept. Commerce. NOAA Tech. Memo. NMFS-SEFSC-443. p. 85-87.

Sarti Martinez, A.L. 2000. *Dermochelys coriacea*. In: IUCN 2004. *2004 IUCN Red List of Threatened Species.* www.iucnredlist.org.

Schroeder, B.A. and Thompson, N.B. 1987. Distribution of the loggerhead turtle *Caretta caretta*, and the leatherback turtle, *Dermochelys coriacea*, in the Cape Canaveral, Florida area: results of aerial surveys. NOAA Tech. Report NMFS-53, 80 pp.

Shoop, C.R. and Kenney, R.D. 1992. Seasonal distributions and abundances of loggerhead and leatherback sea turtles in waters of the Northeastern United States. Herpetological Monographs 6:43-67.

Smith, H.M. and Smith, R.B. 1979. Synopsis of the herpetofauna of Mexico. Volume VI. Guide to Mexican turtles. Bibliographic addendum 3. North Bennington, VT: John Johnson. 1044 pp.

Spotila, J.R. 2004. Sea Turtles: A complete guide to their biology, behavior, and conservation. Johns Hopkins University Press, Baltimore, Maryland. 228 pp.

Spotila, J.R., Dunham, A.E., Leslie, A.J., Steyermark, A.C., Plotkin, P.T., and Paladino, F.V. 1996. Worldwide population decline of *Dermochelys coriacea*: Are leatherbacks going extinct? Chelonian Conservation and Biology 2(2):209-222.

Spotila, J.R., Reina, R.D., Steyermark, A.C., Plotkin, P.T., and Paladino, F.V. 2000. Pacific leatherback turtles face extinction. Nature. 405:529-530.

Stancyk, S.E. 1982. Non-human predators of sea turtles and their control. In: Bjorndal, K. (Ed.). The biology and conservation of sea turtles. Smithsonian Institution Press, Washington, D.C. pp.19-38.

Starbird, C.H., Balbridge, A., and Harvey, J.T. 1993. Seasonal occurrence of leatherback sea turtles (*Dermochelys coriacea*) in the Monterey Bay region, with notes on other sea turtles, 1986-1991. California Fish and Game 79(2):54-62.

Stewart, K., Johnson, C., and Godfrey, M.H. Submitted A. Leatherback sea turtle size and reproductive effort, with a review of the smallest reproductive individuals worldwide. Herpetological Journal.

Stewart, K., Johnson, C., Eckert, S.A., Bagley, D.A., Ehrhart, L.M., and Desjardin, N. Submitted B. Nesting beach fidelity in leatherback sea turtles (*Dermochelys coriacea*) along the coast of Florida, USA. Journal of Animal Ecology.

Steyermark, A.C., Williams, K.L., Spotila, J.R., Paladino, F.V., Rostal, D.C., Morreale, S.J., Koberg, M.T., and Arauz, R. 1996. Nesting leatherback turtles at Las Baulas National Park, Costa Rica. Chelonian Conservation and Biology 2(2):173-183.

Suarez, A. and Starbird C.H. 1996. Subsistence hunting of leatherback turtles, *Dermochelys coriacea*, in the Kai Islands, Indonesia. Chelonian Conservation and Biology 2(2):190-195.

Suarez, A., Dutton, P.H., and Bakarbessy, J. 2000. Leatherback (*Dermochelys coriacea*) nesting on the north Vogelkop coast of Irian Jaya, Indonesia. In: In: Kalb, H.J., and Wibbels, T. (Compilers). Proc. of the Nineteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-443 p. 260.

Thompson, N.B. and Huang, H. 1993. Leatherback turtle in Southeast U.S. waters. NOAA Tech. Memo. NMFS-SEFSC-318. 11 pp.

Troëng, S. 2000. Predation of green (*Chelonia mydas*) and leatherback (*Dermochelys coriacea*) turtles by jaguars (*Panthera onca*) at Tortuguero National Park, Costa Rica. Chelonian Conservation and Biology 3(4):751-753.

Troëng, S., Chacón, D., and Dick, B. 2004. Possible decline in leatherback turtle *Dermochelys coriacea* nesting along the coast of Caribbean Central America. Oryx 38(4):395-403.

Tucker, A.D. and Frazer, N.B. 1991. Reproductive variation in leatherback turtles, *Dermochelys coriacea*, at Culebra National Wildlife Refuge, Puerto Rico. Herpetologica 47(1):115-124.

US Environmental Protection Agency. 2003. Federal register. http://www.epa.gov/fedrgstr/EPA-IMPACT/2003/February/Day-21/i4136.htm

UNEP-WCMC. 2006. *UNEP-WCMC Species Database: CITES-Listed Species.* http://sea.unep-wcmc.org/isdb/CITES/Taxonomy/index.cfm.

Van Buskirk, J. and Crowder, L.B. 1994. Life-history variation in marine turtles. Copeia 1994:66-81.

Vose, F.E. and Shank, B.V. 2003. Predation on loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) hatchlings in offshore waters by gray snapper (*Lutjanus griseus*). Marine Turtle Newsletter 99:11-13.

Wallace, B.P., Sotherland, P.R., Spotila, J.R., Reina, R.D., Franks, B.F., and Paladino, F.V. 2004. Biotic and abiotic factors affect the nest environment of embryonic leatherback turtles, *Dermochelys coriacea*. Physiological & Biochemical Zoology 77(3):423-432.

Wibbels, T. 2003. Critical approaches to sex determination in sea turtles. In: Lutz, P.L., Musick, J.A., and Wyneken, J. (Eds.). The Biology of Sea Turtles. Volume II. Boca Raton: CRC Marine Biology Series, CRC Press, Inc, pp. 103-134.

Witherington B.E. and Koeppel, C.M. 2000. Sea turtle nesting in Florida, USA, during the decade 1989-1998: an analysis of trends. In: Kalb, H.J., and Wibbels, T. (Compilers). Proc. of the Nineteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-443 pp. 94-96.

Zug, G.R. and Parham, J.F. 1996. Age and growth in leatherback turtles, *Dermochelys coriacea* (Testudines: Dermochelyidae): a skeletochronological analysis. Chelonian Conservation and Biology 2(2):244-249.

Florida Softshell Turtle, *Apalone ferox* (Trionychidae).
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Introduction to the Softshell Turtles: Family Trionychidae

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Softshell turtles comprise the family Trionychidae. These are the only turtles with a flat leathery shell that has a flexible margin, and they are the only turtles in North America with a tubular snout. Although most of the bones that make up the turtle shell are present in softshells, the suprapygal(s) and peripheral bones are absent and the plastron bones are much reduced. All softshells have a long neck and three clawed digits on the hands and feet.

Content. — Following the work of Meylan (1987) this family was considered to include two subfamilies, 14 genera, and 22 species. More recent studies suggest recognition of at least 5 additional species, all from Asia. Only one genus, *Apalone*, and three species occur in the Western Hemisphere. All three of these species occur in Florida.

Relationships. — The family Trionychidae is most closely related to the family Carettochelyidae which is represented by one living species, the Fly River turtle or pig-nosed turtle (*Carettochelys insculpta*) from New Guinea and northern Australia. These two families share a long list of unique anatomical features (Meylan, 1987).

Living softshells belong to two subfamilies, the Trionychinae and Cyclanorbinae. The North American genus, *Apalone*, belongs to the former. Morphological data suggested that the closest relatives of *Apalone* are members of the Asian genus *Rafetus*. Engstrom et al. (2004) have been able to corroborate this relationship in a combined molecular and morphological study of softshell phylogeny. There is less agreement between morphological and molecular data sets concerning the relationships among the species of *Apalone*. Meylan (1987) suggested that *A. mutica* plus *A. spinifera* formed a group. The molecular data suggest that *ferox* plus *spinifera* form a group (Weisrock and Janzen, 2000; Engstrom et al., 2004).

Geologic Distribution. — The age of the evolutionary split between the softshell turtle family Trionychidae, and their closest relatives, the carettochelyids, can be based on the Asian fossil softshell, *Aspideretes kyrgyzensis*. This fossil species is reported to be from the lower Cretaceous (early-middle Albian) of Kyrgyzstan (former Soviet Union) (Nessov, 1995). It is sufficiently well known that we can be certain that its relationships lie within the Trionychidae, and in fact, within the subfamily Trionychinae. This first appearance of the family Trionychidae indicates that the trionychid – carettochelyid split must be older than 105 million years. The North American softshell turtle genus, *Apalone*, is not much younger. A detailed study of the softshell turtles of the Cretaceous Judith River Formation in Alberta (Gardner et al., 1993), revealed species belonging to four genera of softshells, including *Apalone*. The age of the Judith River *Apalone* is about 76 million years old.

Geographic Distribution. — The family Trionychidae has previously been found on most of the world's continents, but living species are now found only in North America, Asia, and Africa, with none in Europe, Central or South America, or Australia. Fossils are common in North America, Asia, Africa, and Europe, with only isolated fossil records from South America and Australia.

Status. — Many of the species in this family are used for food. The Chinese softshell (*Pelodiscus sinensis*) in particular has a long history of being farmed for human consumption. But this and other species, including the Florida softshell, are also taken from the wild. The combination of high palatability, restricted ranges, and habitat loss appear to be responsible for making three Asian softshells critically endangered, three others endangered, and six vulnerable to extinction, according to a panel of Asian turtle experts (IUCN/SSC, 2000). It is likely that as Asian softshell species are further depleted and/or removed from trade, additional commercial pressure will be placed on softshell species in North America, a situation that has already emerged as a potential threat.

LITERATURE CITED

Engstrom, T.N., Shaffer, H.B., and McCord, W.P. 2004. Multiple data sets, high homoplasy and the phylogeny of softshell turtles (Testudines: Trionychidae). Systematic Biology 53:693-710.

Gardner, J.D., Russell, A.P., and Brinkman, D.B. 1995. Systematics and taxonomy of soft-shelled turtles (family Trionychidae) from the Judith River Group (mid-Campanian) of North America. Canadian Journal of Earth Science 32:631-643.

IUCN/SSC Tortoise and Freshwater Turtle Specialist Group and Asian Turtle Trade Working Group. 2000. Recommended changes to 1996 IUCN Red List status of Asian turtle species. In: van Dijk, P.P., Stuart, B.L., and Rhodin, A.G.J. (Eds.). Asian Turtle Trade: Proceedings of a Workshop on Conservation and Trade of Freshwater Turtles and Tortoises in Asia. Chelonian Research Monographs 2:156-164.

Meylan, P.A. 1987. The phylogeny of softshelled turtles (Family Trionychidae). Bulletin of the American Museum of Natural History 186:1-101.

Nessov, L.A. 1995. On some Mesozoic turtles of the Fergana depression (Kyrgystan) and Dzhungar Alatau ridge (Kazakhstan). Russian Journal of Herpetology 2:134-141.

Weisrock, D.W. and Janzen, F.J. 2000. Comparative molecular phylogeography of North American softshell turtles (*Apalone*): implications for regional and wide-scale historical evolutionary forces. Molecular Phylogenetics and Evolution 14:152-164.

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Apalone ferox – Florida Softshell Turtle

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Summary. – The Florida softshell turtle, *Apalone ferox*, is a large and often highly visible resident of many freshwater ecosystems in Florida. Softshells constitute a distinctive family of turtles that are easily recognized by their flat leathery shell and distinctive tubular snout. The Florida softshell is easily distinguished from the other two softshells found in Florida by its dull coloration as an adult and relatively dark coloration as a juvenile. The Florida softshell is the most heavily harvested turtle in Florida. Large numbers are taken in the central and southern peninsula every year to supply domestic and international food trade. In spite of this high level of use, the species remains remarkably abundant throughout much of its range, and it appears to flourish in highly modified habitats. It can be one of the most common turtles in the canal systems of south Florida and remains abundant in urbanized areas. Many tons of softshell turtle are removed from freshwater ecosystems in Florida on an annual basis. However, its population densities and ecological role are not well understood. Management for this species should consider both maintenance of the ecological role of this turtle as a large predatory species and the health of the fishery that depends on adequate populations for harvest. The level and impact of commercial use of this species are completely unmonitored at this time. An effort must be made to monitor the level of use of this important renewable resource.

Conservation Status. – FNAI Global - G5 (Demonstrably Secure), State - S5 (Demonstrably Secure); ESA Federal - Not Listed; State - Not Listed; CITES - Not Listed; IUCN Red List - Not Listed (LC-Least Concern).

Species Recognition. — The Florida softshell, *Apalone ferox*, is the largest of the three softshell turtle species found in Florida and has the darkest coloration. It is also the only softshell species found throughout the length of the peninsula. Adults are large to very large (up to 43.6 kg and 73.6 cm carapace length), flat, brown turtles with a cartilaginous shell that is covered by skin rather than by the hard scutes typical of most other families of turtles (Fig. 8-1). All softshells have strongly webbed feet with three claws on each foot. They also have a long neck, a distinct tubular snout, and fleshy lips that cover their jaws (Figs. 8-2, 8-3). The bones of the plastron are visible through the connective tissue of the shell and are much reduced compared to those of most other turtles (Fig. 8-4). The Florida softshell can be distinguished from the other two species found in Florida by its larger size and a distinctive patch of well-developed low tubercles on the anterior margin of the carapace that grade laterally into a marginal ring (Fig. 8-2). In the smooth softshell (*Apalone mutica*) this area is smooth (Figs. 9-1, 9-2), in the spiny softshell (*Apalone spinifera*) this area is covered by numerous fine spines with a few tubercles in larger adults (Figs. 10-1, 10-2, 10-3).

Hatchlings of the Florida softshell have a light colored carapacial rim that is lost with age. Hatchlings and juveniles have a tan to light brown carapace with chocolate brown mottling and a gray or black plastron (Figs. 8-3, 8-5). With age the mottling intensifies and covers most or all of the carapace, making it all dark brown. The head of juveniles is brown to black and streaked with yellow stripes or blotches that are usually lost in adults. Juveniles and males of the two other softshells found in Florida (*A. mutica* and *A. spinifera*) have a beige to gray carapace with distinct dark flecks or rings (Fig. 9-3). In Florida, these two species tend to retain their juvenile coloration throughout life although large adult females of both species lose the juvenile coloration. Furthermore, in these two species, the head is colored as the carapace, and any yellow lines are set off from the background color by black borders, which is usually not the case in adult *A. ferox*.

Taxonomic History. — This species was originally described as *Testudo ferox* by Schneider (1873) on the basis of material that probably came from the Savannah River, which forms the Georgia–South Carolina border. The type specimen is an entire, stuffed adult in the British Museum of Natural History, BMNH 1947.3.6.17 (Webb, 1973; King and Burke, 1989). This species and *A. spinifera* were considered to be a single species by certain authors (Neill, 1951; Carr, 1952; Crenshaw and Hopkins, 1955) until the work of Schwartz (1956) and Webb (1962). Thus, some earlier work referring to *A. ferox* may actually describe *A. spinifera* (e.g., Breckenridge, 1955).

The generic names *Trionyx, Platypeltis,* and *Amyda* have previously been used for this species. It is currently referred to the genus *Apalone* Rafinesque based on the work of Meylan (1987). No subspecies are recognized; however, distinctive genetic variation exists among populations within

Figure 8-1. Adult female Florida softshell turtle, *Apalone ferox,* from Leon Co., Florida. Photo by Matt Aresco.

Florida (Weisrock and Jansen, 2000). A phylogenetic analysis of more than 800 base pairs of the cytochrome b gene suggests that *A. ferox* in peninsular Florida and southeastern South Carolina may be more closely related to each other than they are to a sample from the Apalachicola River in the Florida panhandle.

DISTRIBUTION

Geographic Distribution. — The Florida softshell is found from the vicinity of Charleston, South Carolina, south and west across the southern third of Georgia to Mobile Bay in southernmost Alabama, and throughout the panhandle and peninsula of Florida (Webb, 1973; Mount, 1975; Iverson and Etchberger, 1989; Iverson, 1992).

This species is found throughout Florida (Fig. 8-6). Although apparently less abundant in the panhandle, it occurs in suitable habitat throughout the panhandle and the peninsula. It is generally not considered native to the Florida Keys (Pritchard, 1979; Iverson, 1992) but appears to have been introduced on Big Pine Key (Lazell, 1989; Meylan, *pers. obs*.).

Ecological Distribution. — This species utilizes all but the most temporary freshwater habitats (Carr, 1940; Duellman and Schwartz, 1958; Webb, 1962) as well as some brackish waters (Neill, 1958). It has been recorded from swamps, marshes, wet prairies, floodplain lakes, oxbow lakes, lagoons, mangrove swamps, alluvial and blackwater rivers, creeks, calcareous spring runs, upland and sinkhole ponds, and man-made ditches, lakes, retention ponds, and even phosphate pits. This species appears to be much less common in large rivers with strong currents that are the preferred habitat of *A. spinifera* and *A. mutica*. Bancroft et al. (1983) observed that *A. ferox* in a central Florida lake system near Orlando occurred in most of the available microhabitats within the lake system but was most often seen in water less than 1 m deep. But they also suggested that “adults apparently spend most of their time offshore in deeper water.” Stewart Williams (*pers. comm*.) found them to be more abundant in lakes that have sandy banks rather than those bordered by emergent vegetation or bald cypress. The senior author has noted this species in recently built stormwater retention ponds of less than 1 ha surface area, and in a cement-sided drainage ditch in a heavily populated area of

Figure 8-2. Head of adult male Florida softshell turtle, *Apalone ferox*, from Lee Co., Florida. Photo by Dick Bartlett.

Figure 8-3. Juvenile Florida softshell turtle, *Apalone ferox,* from Leon Co., Florida. Photo by Matt Aresco.

Figure 8-4. Plastron of adult male Florida softshell turtle, *Apalone ferox,* from Leon Co., Florida. Photo by Matt Aresco.

Figure 8-5. Hatchling Florida softshell turtle, *Apalone ferox,* southern peninsular Florida. Photo by Pete Carmichael.

St. Petersburg. Commercial fishermen who set trot lines for this species make large catches in the shallow, slow-moving drainage canals that abound in southern Florida, even those in highly developed areas. Carr (1952) felt that "the larger canals in the Everglades must represent something like an optimal habitat." The ability of this species to withstand moderate salinity is well documented. Carr (1940, 1952) reported that it is found in brackish water, and Neill (1958) supplied some specific records.

HABITAT RELATIONS

Activity. — This is a large and often highly visible resident of many freshwater ecosystems in Florida. When not swimming, the Florida softshell can often be found buried in sand or mud on the bottom in shallow or deep water (Marchand, 1942). It will bask on banks, floating vegetation, rocks or logs, or by floating at the surface (Duellman and Schwartz, 1958; Meylan, *pers. obs.*, D.R. Jackson, *pers. comm.*) It can be counted on to defend itself viciously with jaws and claws, hence the specific name *ferox,* which means ferocious. In addition, this species emits a foul smelling musk.

In a central Florida lake system, *A. ferox* was active day and night and more frequently encountered in summer than in winter (Bancroft et al., 1983). All but the smallest post-hatchlings move overland and can be seen crossing roads, but they are typically encountered within sight of water.

GROWTH AND REPRODUCTION

Size, Sexual Dimorphism, and Sexual Maturity. — The Florida softshell turtle shows marked sexual size dimorphism, with females reaching masses three to five times those of the largest males. Moler and Berish (1995) reported dimorphism in relative tail length of this species. Their examination of a large sample from Palm Beach Co., Florida, revealed that relative tail length (plastron length/total tail length) was greater for males than for females. A subset of their data, shown in Fig. 8-7, indicates that males have tails that average 3 cm longer than females of the same size.

The minimum size at sexual maturity for *A. ferox* has been reported in terms of carapace length (CL), plastron length (PL), and basicranial length. We have used the relationships shown in Fig. 8-8 to convert all of these reports to measures of plastron length. The smallest mature male observed by Webb (1962) was 12.0 cm PL (15 cm CL). This size for sexual maturity is smaller than that reported in several more recent studies. Dalrymple (1977) considered males from south Florida with basicranial length of 5.4 cm. (about 16.2 cm PL; 21 cm CL) to be mature. Bancroft et al. (1983) listed 17 cm (CL) (about 13.8 cm PL) as the minimum size for sexual maturity of males in a central Florida lake. All males from Palm Beach Co., Florida, examined by Meylan et al. (2002) were sexually mature; the smallest was 0.7 kg, and 15.1 cm PL. Thus, the minimal measurement of 12 cm PL from Webb (1962) seems plausible.

Bancroft et al. (1983) gave a size equivalent to 17 cm PL (21.6 cm CL) as the minimum size for sexual maturity of female *A. ferox* in a central Florida lake system. However, the smallest mature female examined by Dalrymple (1977) had a size equivalent to 19.6 cm PL (25.3 cm CL). Iverson (1985) suggested that most females mature at sizes of 21.4–22.8 cm PL (28–30 cm CL), but this was based on specimens mostly from the vicinity of Gainesville. Females from a Palm Beach Co. population, studied by Iverson and Moler (1997), appeared to mature at sizes as small as 24 cm PL (31.5 cm CL), but it seems that other females may reach 30 cm PL (40 cm CL) before attaining sexual maturity. Thus, the minimum size for maturity in *A. ferox* females is about 20 cm PL (26 cm CL). The Bancroft et al. (1983) figure of 17 cm PL has not been confirmed by recent work and is probably too low. George Heinrich and Scott Boykin (unpubl. data) provide the following statistics for nesting females from Boyd Hill Nature Park, Pinellas Co, Florida: mean PL, 36.1 cm ($n = 20$); mean mass 10.3 kg ($n = 15$). The age at first reproduction for females remains unknown.

The largest *A. ferox* are females and can reach total CL of over 70 cm. Records of large females include individuals that weighed 14.2 (Goff and Goff, 1935), 13.7, 14.1, 21.8, 29.5 kg (Allen, 1982), and 33.2 kg (62.8 cm CL) (Pritchard, 1980). The largest specimen of which we are aware weighed 43.6 kg (73.6 cm CL). It was caught by Henry Courson and

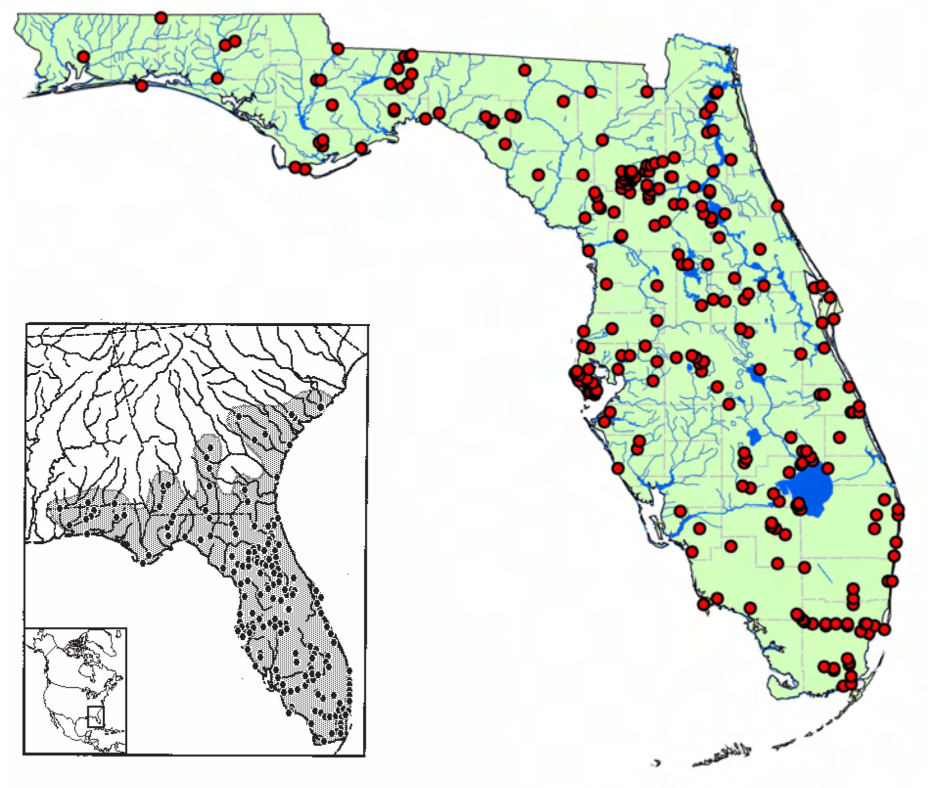

Figure 8-6. Available distribution records for the Florida softshell turtle, *Apalone ferox*, from Florida. Inset: distribution records from entire range of *A. ferox* (adapted from Iverson, 1992; distribution in inset map not current for Florida as presented here).

James Maxie where the Kissimmee River enters Lake Okeechobee in August 2000 (Pritchard, 2001).

Female Reproductive Cycle. — Iverson and Moler (1997) described the female reproductive cycle based on 220 female reproductive tracts salvaged from a commercial fishery in Palm Beach Co. between 1992 and 1995. They reported that females have oviductal eggs from 3 March to 13 July. But some of the latest samples contained a sufficient number of enlarged follicles in the ovaries to suggest that these females would have produced another clutch during August. The percentage of gravid females varied from 22% in March to 86% in May and June. However, the authors expressed misgivings about how randomly their sample was selected from the total harvest sample. Their data do suggest that a small percentage of mature females (9% in their sample) do not reproduce in a given year.

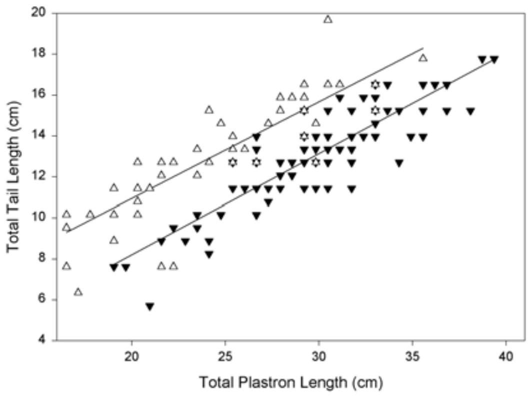

Figure 8-7. Sexual dimorphism in tail length for the Florida softshell turtle, *Apalone ferox*, from Palm Beach Co., Florida. Plastron vs. tail length is shown for 144 females (solid triangles) and 55 males (open triangles). Least squares regression line for each sex is shown.

Male Reproductive Cycle. — Meylan et al. (2002) reported on the male reproductive cycle based on 127 male reproductive tracts from the same population as the Iverson and Moler (1997) study. Data from testicular mass, seminiferous tubule diameter, and histology indicated fall (September–October) sperm production. Epididymis mass and histology suggested spring mating (March–May). These data are consistent with a postnuptial spermatogenic cycle shown in other temperate softshell turtles (Lofts, 1977; Lofts and Tsui, 1977).

Nesting. — Females in north-central peninsular Florida lay eggs from March through July (Goff and Goff, 1935; Carr, 1940; Iverson, 1985). Nesting has been observed in the panhandle (Leon and Franklin counties) during May (M. Ewert, *pers. comm.*). Females in south Florida may have shelled oviductal eggs as early as February (Meylan, *pers. obs.*) and are not generally observed to nest after August (S. Williams, *pers. comm.*). Females at Boyd Hill Nature Park, Pinellas Co., have been observed to nest between 27 March and 2 July (George Heinrich and Scott Boykin, unpubl. data), with 9 of 23 occurring in May.

George Heinrich and Scott Boykin (unpubl. data) observed the deposition of 8 nests in the vicinity of Boyd Hill Nature Park, Pinellas Co. between 1992 and 1998. All were laid in the daytime between 1055 and 1600 hrs; mean

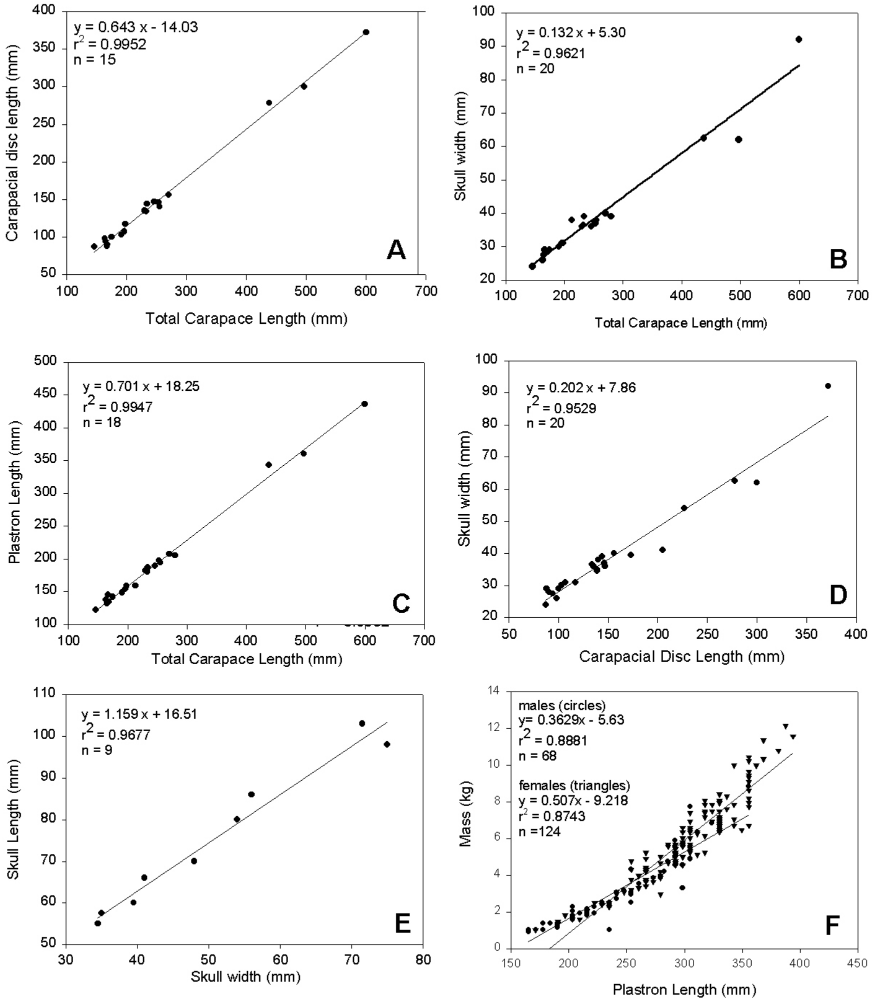

Figure 8-8. Morphometric relationships of the shell and skull of the Florida softshell turtle, *Apalone ferox*. The relationships shown here were used to facilitate size comparisons among studies in the literature. For each relationship, an equation for the regression line in the form y = m(x) + b, an r^2 value, and sample size are given. Relationships are: (A) Carapacial bony disc vs. total carapace length, (B) skull width vs. total carapace length, (C) plastron length vs. total carapace length, (D) skull width vs. carapacial bony disc length, (E) skull length vs. skull width, (F) mass vs. plastron length for males (circles) and females (triangles).

deposition time was at about 1300 hrs, and 5 of 8 nests were deposited between 1100 and 1300 hrs. The most obvious predator at this site is the raccoon; mid-day nesting may be a response to these abundant predators.

This species typically nests in sandy soils (Ehrenfeld, 1979). Hamilton (1947) reported seeing 5 nesting females along a 5 km stretch of sand road near Ft. Myers on 30 March 1940. Seventeen of 19 nests for which nesting habitat was recorded were encountered along sand roads in Boyd Hill Nature Park, Pinellas Co. by Heinrich and Boykin (unpubl. data). Another nest at this site was discovered in the apron of a gopher tortoise burrow (Heinrich and Richardson, 1993). The nest, which is dug with the hind feet, has a very narrow neck, barely wider than the egg diameter. Hamilton (1947) reported the egg chamber to be 13 cm deep and 10 cm in diameter, which agrees with the respective measurements from Heinrich and Richardson (1993) of 14 cm and 9 cm. The female may expel cloacal water over the nest site before excavation (Hamilton, 1947; Ehrenfeld, 1979). After egg-laying, an extensive effort is made to backfill and disguise the site of the nest (Hamilton, 1947; Meylan, *pers. obs.*). A female that nested in open sand along the lower Apalachicola River left an area of churned sand about 1.5 m long (M. Ewert, *pers. comm.*).

Eggs. — The eggs are white and approximately spherical with a brittle shell. Iverson (1985) reported an average maximum diameter of 28.9 mm; Heinrich and Richardson found diameters of 27.0 to 33.5 mm (average 29.4) for a sample of 16 eggs from a single clutch of 32. The eggs of 15 clutches from near Lake Iamonia (Leon Co.), ranged in mass from 10.6 to 28 g and averaged about 14 gm (Ewert, 1979; *pers. comm.*).

Clutch Size. — Webb (1962) gave complete clutch counts of 17, 20, 21, and 22, and Iverson (1985) reported clutch size in northern Florida (vicinity of Gainesville) to vary from 9 to 24 eggs with an average of 17.6. It is clear, however, that larger clutches may not be unusual. Stewart Williams (*pers. comm.*) has recorded clutches of 35 and 40 eggs laid by captive Florida softshells in an enclosure near Lake Placid, Florida. Heinrich and Richardson (1993) reported a clutch of 32 eggs from Boyd Hill Nature Park, Pinellas Co., and Heinrich and Boykin (unpubl. data) observed a mean clutch size of 26.4 for 12 nests from the same vicinity. Iverson and Moler (1997) reported that clutches from a population in Palm Beach Co. varied in size from 9–38 eggs (mean = 20.6). They gave the specific example of a large female that provided evidence in the form of corpora lutea, oviductal eggs, and ovarian eggs, of six or possibly seven large clutches (mean = 38.6 eggs per clutch), or over 225 eggs per year. Although clutch sizes can be relatively large in this species, clutch mass relative to body mass may be among the lowest for turtles (Iverson, 1985). A clear positive relationship exists between clutch size and body size in this species in Palm Beach Co. (Iverson and Moler, 1997), and in Pinellas Co. (Fig. 8-9; G. Heinrich and S. Boykin, unpubl. data).

Clutch Frequency. — This species lays more than one clutch of eggs per year. Iverson (1985) suggested that they lay 5 to 6 clutches per year. Jackson (1991) reported a female from Alachua Co., Florida, that had 5 sets of corpora lutea and contained an additional set of preovulatory follicles. He estimated the annual reproductive output for this individual as 145 eggs. Iverson and Moler (1997) reported that in Palm Beach Co., 5, 6, and occasionally 7 clutches may be laid in a single nesting season, that clutches were relatively large, and that annual output could reach more than 225 eggs. They concluded that *A. ferox* produces more eggs per year than any other known reptile other than the marine turtles or possibly the giant South American river turtle, *Podocnemis expansa*. Large Asian softshells are likely to have similar annual output.

Incubation and Hatching. — Eggs hatch in 56 (Lardie, 1973) to 80 days (Heinrich and Richardson, 1993), the length of time being inversely correlated with ambient temperature (Iverson, 1985). Goff and Goff (1935) reported a clutch hatching in 64 days; S. Williams (*pers. comm.*) reported an average of 65 days. Ewert (1979; *pers. comm.*) reported an incubation period of 82.7 days for 14 eggs from Leon Co. incubated at 26–30ºC, and 77–82 days for 26 eggs from Franklin Co. incubated mostly at 28ºC. This latter group yielded 13 males and 13 females, which is compatible with genetic sex determination, as expected for softshell turtles.

Goff and Goff (1935) reported hatchlings of 8.5–9.25 g (mean = 8.82 g). Ewert (1979) gave a slightly larger average of 10.0 g or 71.3% of egg weight. Heinrich and Richardson (1993) reported on 13 hatchlings from a single clutch that varied in CL from 36.2 to 44.3 mm (mean = 41.2) and in weight from 8.4 to 11.0 g (mean = 9.7).

POPULATION BIOLOGY

Population Structure. — This species is difficult to capture using methods that work well for mark and recapture studies of other freshwater turtles (i.e., baited traps) (Moler and Berish, 1985). Studies that have produced data on population structure (Fig. 8-10) have sampled by dipnetting from a boat (Bancroft et al., 1983) or by capturing animals at a drift fence as they departed a large drying lake (Aresco, 2003). In the former study most individuals were captured in shallow water (< 1 m), but it was noted that adult *A. ferox* are fast and agile and reside in deeper water, making their capture more difficult. Thus, adults are likely to be underrepresented in the histogram of *A. ferox* from Lake Conway, Orange Co., Florida, (Fig. 8-10A). It is less clear how the sample from Lake Jackson, Leon Co., might be biased (Fig. 8-10B). It seems likely that smaller individuals would be less able to reach the drift fence before being eaten or overcome by heat stress. Given this possible limitation, this sample

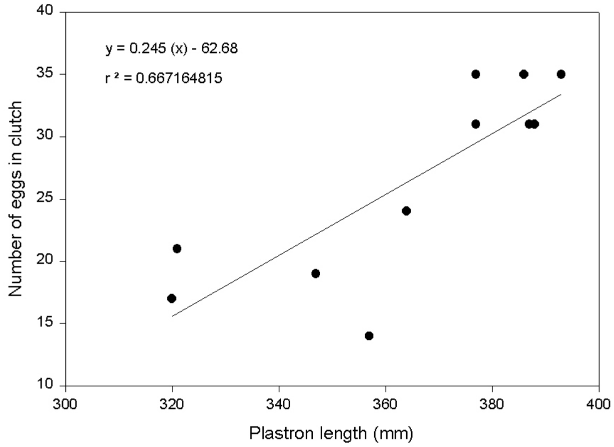

Figure 8-9. Clutch size relative to plastron length for 11 Florida softshell turtles, *Apalone ferox*, from Boyd Hill Nature Park, Pinellas Co., Florida. Data are from an unpublished study by G. Heinrich and C.S. Boykin.

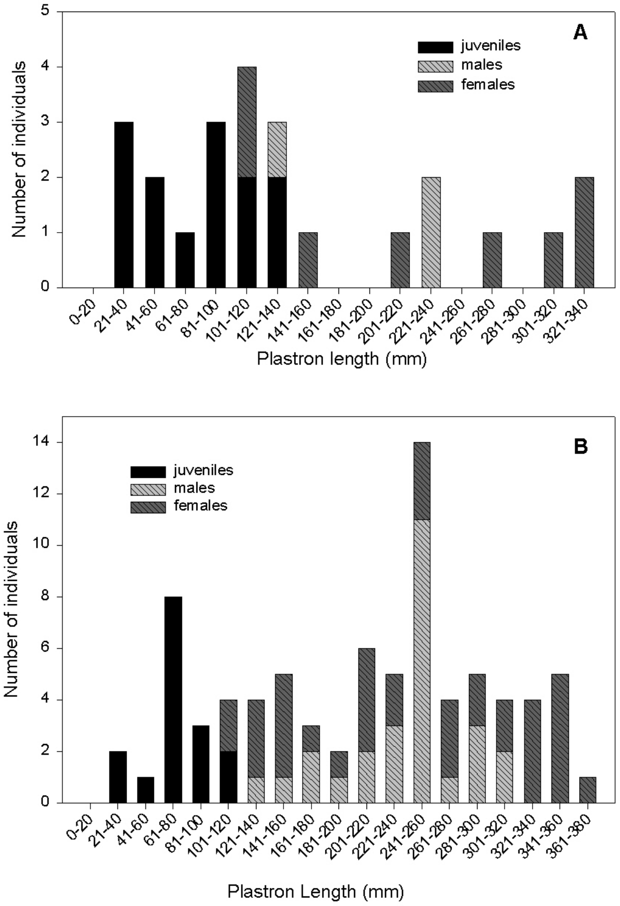

Figure 8-10. Population structure for the Florida softshell turtle, *Apalone ferox*, collected from: (A) Lake Jackson, Leon Co., Florida (M.J. Aresco, unpubl. data), and (B) Lake Conway, Orange Co., Florida (Bancroft et al., 1983).

(Fig. 8-10B) is the best estimate of population structure for this species available at present. There are no estimates of population density for this species.

INTERSPECIFIC INTERACTIONS

Feeding Biology. — Dalrymple (1977) reported on the contents of 96 digestive tracts collected in the vicinity of Lake Okeechobee and nearby St. Lucie Co., Florida, during July 1972. Fourteen tracts were empty; the most common food items in 82 others were snails (*Viviparus* and *Pomacea*) (47.2% of all food items), insects (41%), fish (7.4%), and crayfish (2.7%). Clams, snakes, turtles, and birds each constituted 1% or less of the total number of food items. Plant material was present in 29 (35%) of the tracts examined but was considered to be incidentally ingested. Some dietary changes appeared to occur with increase in size. There was an increase in the importance of snails with size, apparently due to an increase in the size of snails consumed and not an increase in number. There was also an increase in the importance of fish and a decrease in the importance of insects in relatively larger size classes. Dalrymple suggested that since females attain larger size than males, they show more extreme variation in cranial form and diet than males.

Another study of feeding in this species done in Palm Beach Co., Florida, (Moler and Berish, 1995) reported similar food items. The percentage of 233 stomachs in which the following items occurred were: fish (62.7% of all stomachs with food), snails (53.2%), crayfish (29.6%), and insects (24.5%). This study reported the occurrence of palm seeds in 12.9% of stomachs. It also suggested that sex significantly influenced the consumption of certain food items such as palm seeds, clams (primarily *Anodonta*), snails, and possibly other turtle species. All of these items were more frequently encountered in males than in females. It also showed that size influenced the probability that insects or large snails would be consumed. As in the Dalrymple (1977) study, large snails increased in importance, and insects decreased in importance with size. Moler and Berish (1995) revealed the importance of small snails in the diets of some individuals. Very large numbers of small snails (up to 2000) were found in some stomachs. Five individuals had each eaten 1200 or more snails of the genus *Melanoides.*

Predation. — Nests of this species are heavily depredated by foxes, skunks, raccoons (Hamilton, 1947; Heinrich and Boykin, *pers. comm.*), and fish crows (Meylan *pers. obs*., A. Carr, *pers. comm*.). Small individuals are taken by raptors, including the snail kite (Woodin and Woodin, 1981) and red-tailed hawk (Meylan, *pers. obs*.). Two studies of alligator predation (involving examination of a total of 463 alligator stomachs) turned up 241 turtles but no *A. ferox* (Delany and Abercrombie, 1986; Delany et al., 1988).

THREATS

The Florida softshell appears to be common to very common throughout much, if not all, of peninsular Florida and at least in parts of the panhandle. It does not appear to be in any danger at this time. It must be noted, however, that this species is the most intensively harvested freshwater turtle in Florida, and locally severe declines or extirpations from over-fishing might be possible. Pritchard (1979) suggested that "populations in northern Florida have declined markedly in the last few years" but offered no support for this statement.

Moler and Berish (1995) characterized the trade in this species as comprising four distinct components: 1) hatchlings that enter the pet trade, 2) turtles larger than 3.5 to 4.5 kg (27–29 cm PL) that are butchered and cleaned and sold as frozen meat, 3) turtles smaller than 3.5 to 4.5 kg (27–29 cm PL) that are killed, eviscerated, and frozen whole, and 4) turtles of less than about 3 kg that are marketed live.

Turtles entering the food component of this trade come from a directed fishery or are taken in conjunction with cat fishing or the haul seine fishery in Lake Okeechobee. Most are taken on trot lines that may consist of up to 500 hooks baited with fat back or fish. A typical trot line is about 200 m in length and usually consists of #22 braided nylon with 20 cm long, hook-bearing "drops" of #18 braided nylon, attached to #5 swivels at about 3 m intervals (S. Williams, *pers. comm*.) The line is set with enough slack to allow hooked turtles to carry it to the surface to breath. Using this type of equipment, Norman Padgett (*pers. comm.*) marketed 70 *A. ferox* between 15 January and 28 February 1988. The marketed turtles ranged in size from 1 to 10 kg (mean = 4.0 ± 2.5 kg).

A decade-old effort by the Florida Fish and Wildlife Conservation Commission to monitor the commercial use of native reptiles resulted in some information on the rate of use of *A. ferox* (Enge, 1993). Data on the take of *A. ferox* for human consumption were not considered to be complete, because only those persons buying turtles for resale were required to report their transactions. During the first two years of the program (July 1990 to June 1992), 5488 live individuals, 5817 kg of dressed meat, and 14,104 kg of whole frozen Florida softshell were reported sold. If an average marketed softshell weighs 4 kg (see above), and provides one-third its live weight in clean meat, or loses 25% of its weight when gutted (whole frozen turtles), these figures represent 14,982 softshells taken over two years, or about 7500 per year.

However, the largest buyer of turtle meat during this two-year period suggested that 65–85% of the turtle harvest went unreported (Enge, 1993). Thus, it appears that a far greater number of *A. ferox* may have been entering the market each year.

Nearly all of this trade occurs in the southern part of Florida, especially in and around Lake Okeechobee. But substantial harvest of softshells has been reported as far north as Lake Panasoffkee (Sumter Co.) and, in the past, has occurred as far north as Orange Lake (Moler, *pers. obs*.) and Palatka (Sandra Williams, *pers. comm*.).

The removal of large numbers of individuals within a limited area could be detrimental to the population and thus to the health of the fishery. This type of impact may already have occurred: C. Veser of The Softshell Turtle Company suggested that during 1976–82 the biomass of *A. ferox* in Lake Okeechobee was too low to support a lucrative commercial turtle fishery but that the population has subsequently recovered (Enge, 1993).

In addition to being fished for meat, this species is also taken from the wild for the pet trade. For the two-year study period July 1990 to June 1992, 373 wild-caught *A. ferox* were reported as entering the pet trade (Enge, 1993). However, at least one ranching operation in Florida was able to produce captive hatchlings at a very high rate; in one year it produced more than 13,000 hatchlings from eggs laid by females taken from the wild as adults. This type of ranching operation could easily reduce the take from the wild for the pet trade, and the take of adult females from the wild for this purpose seems insignificant relative to the number taken for food markets. Large numbers of eggs were collected from the wild in south Florida during the 1990s to produce hatchlings for the commercial trade. This kind of collection of turtle eggs is no longer permitted under state wildlife regulations.

STATUS

Although there are regulations for the take of this species in Florida, it is not listed on any State or Federal list of endangered or threatened species. In South Carolina, at the limit of its range, it is considered a Species of Concern.

CONSERVATION OPTIONS AND SOLUTIONS

It is clear that this species is the most commercially important turtle in Florida. Many tons of softshell turtle are removed from freshwater ecosystems in Florida on an annual basis. However, its ecological role is not well understood. Since *A. ferox* apparently escapes predation from alligators, it may be near the top of the food chain in some of the many ecosystems in which it occurs. Thus, management for this species should consider both maintenance of the ecological role of this turtle as a large predatory species and the health of the fishery that depends on adequate populations for harvest.

Fortunately, there are features of the biology of this species and of the nature of the fishery that appear to reduce the potential impact of the harvest (Moler and Berish, 1995). First, the species is remarkably fecund (see reproductive biology section above). Iverson and Moler (1997) suggested that the females of this species lay more eggs per year than any other freshwater turtle in Florida, and Meylan et al. (2002) indicated that males mature at a very small size (0.7 kg), perhaps in their second year of life, and are reproductive every year.

Secondly, this species uses a wide variety of habitats, including those in the vicinity of large human populations. Many of the habitats in which it occurs do not lend themselves to fishing with trot lines, which must be used in open water. Extensive areas of marsh, like those along the west side of Lake Okeechobee, in the water conservation areas of south Florida, along the St. Johns River, and elsewhere, provide significant refugia from commercial fishing. Much of the fishing appears to occur in artificial habitats, e.g., drainage canals. Furthermore, although it is highly aquatic, this species moves overland regularly, so that repopulation of even isolated habitats is likely.

Thirdly, turtle fishermen typically set trot lines only in areas where turtles are abundant (Moler and Berish, 1995). If few turtles are being captured, the trot lines are moved. Thus, following harvest, some softshells are likely to remain and can repopulate the site.

Some regulations that limit the take of Florida softshells are in place. The use of trot lines to capture softshells is apparently most effective in daylight hours during warmer months. Trot lines are prohibited in some areas and limited to night time use in others. Furthermore, effective August 1999, softshells may not be taken in Florida at the height of the nesting season, during May–July (Florida Wildlife code 68A-25.002[7]).

The Florida rule that required persons trading in this species in the state during the early 1990s to file a record of all transactions with the Florida Fish and Wildlife Conservation Commission is no longer in force. Thus, the current extent of the use of this resource is unknown. This is unfortunate given the potentially very large volume of this trade. Monitoring of the volume of the trade in this species should be resumed.

The perceived threat posed by the volume of trade in softshell turtles in the early 1990s was considered to be serious enough that a proposal was made in 1996 to list all North American softshell turtle species, including *A. ferox*, on Appendix II of CITES (Telecky and Salzberg, 1996). The proposal cited the fact that tens of thousands of individuals enter international trade each year (34,467 in 1994 alone). Although the majority of these were probably ranched hatchlings, the degree of under-reporting indicated for Florida suggests that numbers in this range may be entering the food trade as well (Enge, 1993).

Apalone ferox may be unusual among turtles in that it appears to be a sustainable resource under significant harvest pressure. To the degree that the harvest is in fact sustainable, this may serve to reduce the pressure on other turtle species that are less resilient to commercial harvest.

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LITERATURE CITED

Allen, E.R. 1982. *Trionyx ferox* (Florida softshell). Size. Herpetological Review 13:49.

Aresco, M.J. 2003. Highway mortality of turtles and other herpetofauna at Lake Jackson, Florida, USA, and the efficacy of a temporary fence / culvert system to reduce roadkills. In: Irwin, C.L., Garrett, P., and McDermott, K.P. (Eds.). Proceedings of the International Conference on Ecology and Transportation, Raleigh, NC: Center for Transportation and the Environment, North Carolina State University, pp. 433-449.

Bancroft, G.T., Godley, J.S., Gross, D.T., Rojas, N.N., Sutphen, D.A., and McDiarmid, R.W. 1983. Large-scale operations management tests of use of the white amur for control of problem aquatic plants. The herpetofauna of Lake Conway: Species accounts. Misc. Paper A-83-5. Army Engineer Waterways Exp. Stat., Vicksburg, Mississippi, 354 pp.

Breckenridge, W.J. 1955. Observations on the life history of the soft-shelled turtle *Trionyx ferox*, with especial reference to growth. Copeia 1955:5-9.

Carr, A.F. 1940. A contribution to the herpetology of Florida. University of Florida, Biological Sciences Series 3:1-118.

Carr, A.F. 1952. Handbook of turtles. The turtles of the United States, Canada, and Baja California. Comstock Publ. Assoc., Cornell University Press, Ithaca, New York, 542 pp.

Crenshaw, J.W., and Hopkins, M.N. 1955. The relationships of the soft-shelled turtles *Trionyx ferox ferox* and *Trionyx ferox aspera*. Copeia, 1955:13-23.

Dalrymple, G.H. 1977. Intraspecific variation in the cranial feeding mechanism of turtles of the genus *Trionyx* (Reptilia, Testudines, Trionychidae). Journal of Herpetology 11:255-285

Delany, M.F., and Abercrombie, C.L. 1986. American alligator food habits in north central Florida. Journal of Wildlife Management 50:348-353.

Delany, M.F., Woodward, A.R., and Kochel, I.H. 1988. Nuisance alligator food habits in Florida. Florida Field Naturalist 16:90-96.

Duellman W.E., and Schwartz, A. 1958. Amphibians and reptiles of southern Florida. Bulletin of the Florida State Museum, Biological Sciences 3:181-324.

Ehrenfeld, D.W. 1979. Behavior associated with nesting. In: Harless, M., and Morlock, H. (Eds.). Turtles: Perspectives and Research, John Wiley & Sons, New York, pp. 305-332.

Enge, K.M. 1993. Herptile use and trade in Florida, Florida Game and Fresh Water Fish Comm. Nongame Wildlife Program Final Performance Report. 102 pp, Tallahassee, FL.

Ewert, M.A. 1979. The embryo and its egg: development and natural history. In: Harless, M., and Morlock, H. (Eds.). Turtles: Perspectives and Research. John Wiley & Sons, New York, pp. 333-413.

Goff, C.C., and Goff, D.S. 1935. On the incubation of a clutch of eggs of *Amyda ferox* (Schneider). Copeia 1935:156.

Hamilton, W. J. 1947. Egg laying of *Trionyx ferox*. Copeia 1947:209.

Heinrich, G., and Richardson, D.E. 1993. *Apalone ferox* (Florida softshell) Reproduction. Herpetological Review 24:31.

Iverson, J.B. 1985. Reproduction in the Florida softshell turtle, *Trionyx ferox*. Florida Scientist 48:41-44.

Iverson, J.B. 1992. A revised checklist with distribution maps of the turtles of the world. Privately printed Richmond, Indiana. 363 pp.

Iverson, J.B., and Etchberger, C.R. 1989. The distribution of the turtles of Florida. Florida Scientist 52:119-144.

Iverson, J.B., and Moler, P.E. 1997. The female reproductive cycle of the Florida softshell turtle (*Apalone ferox*). Journal of Herpetology 31:399-409.

Jackson, D.R. 1991. *Trionyx ferox* (Florida softshell) Reproduction. Herpetological Review 22:56.

King, F.W., and Burke, R.L. 1989. Crocodilians, tuatara, and turtle species of the world: a taxonomic and geographic reference. Association of Systematics Collections, Washington, DC.

Lardie, R.L. 1973. Notes on the eggs and young of *Trionyx ferox* (Schneider). Journal of Herpetology 7:377-378.

Lazell, J.D. 1989. Wildlife of the Florida Keys. Island Press.

Lofts, B. 1977. Patterns of spermiogenesis and steroidogenesis in male reptiles. In: Tyndale-Discoe, C.H. (Ed.). Reproduction and Evolution. Proceedings of the 4th Symposium on Comparative Biology of Reproduction, Canberra, pp. 127-136.

Lofts, B., and Tsui, H.W. 1977. Histological and histochemical changes in the gonads and epididymides of the male soft-shelled turtle, *Trionyx sinensis*. Journal of Zoology 181:57-68.

Marchand, L.J. 1942. A contribution to a knowledge of the natural history of certain freshwater turtles. Master's thesis, University of Florida, Gainesville. 83 pp.

Meylan, P.A. 1987. The phylogenetic relationships of soft shelled turtles (Family Trionychidae). Bulletin of the American Museum of Natural History 186:1-101.

Meylan, P.A., Schuler, R., and Moler, P.E. 2002. The spermatogenic cycle of the Florida softshell turtle, *Apalone ferox*. Copeia 2002:779-786.

Moler, P.E, and Berish, J.E. 1995. Impact of commercial exploitation on softshell turtle populations. Florida Game and Fresh Water Fish Comm. Bureau of Wildlife Research, Final Report. 18 pp, Tallahassee, FL.

Mount, R.H. 1975. The reptiles and amphibians of Alabama. Auburn University Agricultural Experiment Station, Auburn, Alabama. 347pp.

Neill, W.T. 1951. The taxonomy of North American soft-shelled turtles, genus *Amyda*. Publications of the Research Division of Ross Allen's Reptile Institute 1:7-24.

Neill, W.T. 1958. The occurrence of amphibians and reptiles in saltwater areas, and a bibliography. Bulletin of Marine Science, Gulf and Caribbean 8:1-97.

Pritchard, P.C.H. 1979. Encyclopedia of turtles. T. F. H. Publications, Inc., Neptune, NJ.

Pritchard, P.C.H. 1980. Record size turtles from Florida and South America. Cheloniologica 1:113-123.

Pritchard, P.C.H. 2001. Observations on body size, sympatry, and niche divergence in softshell turtles. Chelonian Conservation and Biology 4:5-27.

Schneider, J.G. 1783. Allgemeine Naturgeshichte der Schildkröten, nebst einem system. Verzeichnisse der einzelnen Arten. Leipzig, 364 pp.

Schwartz, A. 1956. The relationships and nomenclature of the soft-shelled turtles (genus *Trionyx*) of the southeastern United States. Charleston Museum Leaflet 26:1-21.

Telecky, T., and Salzberg, A. 1996. Petition to CITES to list North American softshell turtle species (*Apalone*) on Appendix II of CITES.

Webb, R.G. 1962. North American Recent soft-shelled turtles (Family Trionychidae). University of Kansas Publications of the Museum of Natural History13:429-611.

Webb, R.G. 1973. *Trionyx ferox*. Catalogue of American Amphibians and Reptiles 138:1-3.

Weisrock, D.W., and Janzen, F.A. 2000. Comparative molecular phylogeography of North American softshell turtles (*Apalone*): implications for regional and wide-scale historical evolutionary forces. Molecular Phylogenetics and Evolution 14:152-162.

Woodin, M.C., and Woodin, C.D. 1981. Everglades Kite predation on a soft-shelled turtle. Florida Field Naturalist 9:64.

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Apalone mutica calvata – Gulf Coast Smooth Softshell Turtle

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Summary. – The Gulf Coast smooth softshell, *Apalone mutica calvata*, is one of two species of turtles found in Florida only in the Pensacola Bay drainage in the western panhandle. It is restricted to riverine habitats throughout its range, especially those areas with extensive sand bars. This is the smallest of three softshell turtles in Florida and the least commonly encountered. Females grow much larger than males. Nesting occurs from May to July, and females likely produce at least 2–3 clutches of 6–8 eggs annually. Eggs are deposited on open sand bars. Survival of this species in Florida depends on the continued health of the Escambia River system.

Conservation Status. – FNAI Global - G5 (Demonstrably Secure), State - S1 (Critically Imperiled/ Rare); ESA Federal - Not Listed; State - Not Listed; CITES - Not Listed; IUCN Red List - Not Listed (LC-Least Concern).

Species Recognition. — *Apalone mutica calvata* is the smallest North American softshell turtle, with females reaching a maximum carapace length (CL) of 28.7 cm (Mount, 1975). The species has the flattened leathery shell, long neck, and tubular snout typical of all softshell turtles (Figs. 9-1, 9-2). The anterior edge of the carapace is smooth, lacking the spines and tubercles characteristic of other softshell species in Florida. Hatchlings, juveniles, and most adult males have a tan carapace with numerous (27–37) large circular spots (Webb, 1959), which are not ocellate in Florida specimens (Fig. 9-3). Florida specimens have fewer and larger carapacial spots than do Louisiana specimens (Webb, 1962). Rearward from the axillae, the carapace is bordered by a single, unmarked, pale band. The carapace darkens in adult females and the spots become obscure, although the marginal pale band may still be visible. Ventral surfaces are white. The dorsal surface of the snout is unstriped (Fig. 9-2). The nostrils are round and lack the medial septal ridges found in spiny and Florida softshells.

Unlike other North American softshells, the Gulf Coast smooth softshell has a relatively mild disposition. It will occasionally attempt to bite when captured, but captives rarely attempt to do so, instead withdrawing the head into the shell if threatened.

Taxonomic History. — The smooth softshell was described as *Trionyx muticus* Lesueur on the basis of material from the Wabash River, Indiana, and most literature refers to the species under that name. The species has been referred to the genus *Apalone* Rafinesque (Meylan, 1987), but not all have followed this arrangement (e.g., Webb, 1990; Ernst et al., 1994). Two subspecies are recognized, the midland smooth softshell, *A. m. mutica*, and the Gulf Coast smooth softshell, *A. m. calvata* Webb (1959), but only *A. m. calvata* occurs in Florida. The holotype of *A. m. calvata* is from the Pearl River, Rankin County, Mississippi. However, included among the 20 paratypes are 4 specimens from the Escambia River, Florida (Webb, 1959). The relationship of *A. m. calvata* to *A. m. mutica* is unclear, although they are clearly sister taxa (Weisrock and Janzen, 2000). The two forms are generally allopatric, but S. Doody (*pers. comm.*) reported two intergrades from Louisiana.

DISTRIBUTION

Geographic Distribution. — *Apalone m. calvata* occurs in Gulf coastal drainages, primarily below the Fall Line, from the Florida Parishes of Louisiana east to the Escambia River in Florida.

In Florida this species is known to occur only in the upper reaches of the Escambia River (Fig. 9-4). It has been collected from the Alabama state line south to McDavid, Escambia County (P. Moler, unpubl. data).

Ecological Distribution. — *Apalone m. calvata* appears to be restricted to riverine habitats throughout its range. The species has also been reported in lakes and impoundments, although typically only those connected to rivers during floods (Williams and Christiansen, 1981).

This species is restricted to rivers characterized by extensive development of sandbars. It is found in the upper reaches of the Escambia River, where sandbars are numerous. Lower reaches of the Escambia flow through a drowned valley, with few if any exposed sandbars, and smooth softshells have not been recorded from those sections of the river.

HABITAT RELATIONS

Activity. — Males and juveniles are often found buried in the sand along the shallow edges of sandbars. Adult females typically frequent deeper habitats and usually retreat to deeper water when encountered in the

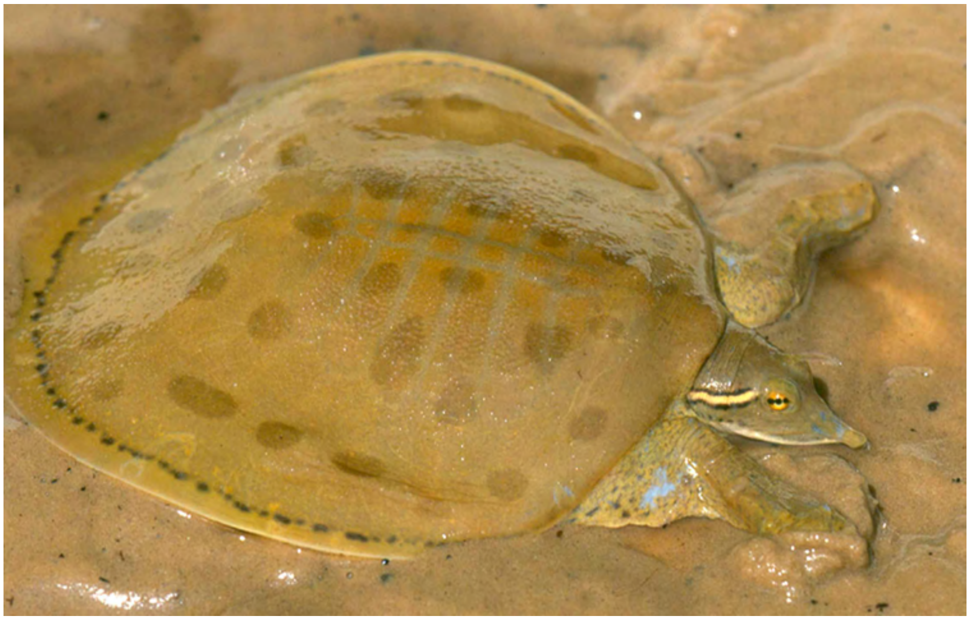

Figure 9-1. Adult Gulf Coast smooth softshell turtle, *Apalone mutica calvata*, from Escambia County, Florida. Photo by Barry Mansell.

shallows. Individuals may also leave the water to bask along the edges of sandbars, but they seldom go more than a meter from the water's edge except to nest.

GROWTH AND REPRODUCTION

Most available biological information on *A. mutica* is derived from studies of *A. m. mutica*. The taxonomic relationship between *A. m. mutica* and *A. m. calvata* is unclear, and data derived from studies of *A. m. mutica* should be extrapolated to *A. m. calvata* with caution. For example, *A. m. calvata* produces smaller clutches but larger eggs than does *A. m. mutica* (Webb, 1962).

Size Dimorphism. — *Apalone m. calvata* is sexually dimorphic, with males much smaller than females. A typical adult female from Florida measured 26.2 cm CL and weighed 1600 g, whereas a typical adult male measured 14.5 cm CL and weighed only 210 g (P. Moler, unpubl. data).

Nesting Season. — The nesting season in Florida begins in May and likely extends into July. Eggs are deposited in open portions of sandbars, where the nest is exposed to full sun. Florida nests have been recorded on 20 May (P. Moler, unpubl. data) and 1 June (Webb, 1962; banding of eggs in one clutch figured indicates that they had been deposited several days before the collection date). Reported clutch size ranges 6–8 eggs for the few Florida nests recorded (Webb, 1962; P. Moler, unpubl. data). Doody (1996) reported that clutch size averaged 7 eggs on the Comite River,

Figure 9-2. Head of adult Gulf Coast smooth softshell turtle, *Apalone mutica calvata*, from Escambia Co., Florida. Photo by Dick Bartlett.

Figure 9-3. Hatchlings of the three *Apalone* species found in Florida. Gulf Coast smooth softshell turtle, *Apalone mutica calvata* (at left), from Escambia County, Florida; spiny softshell turtle, *Apalone spinifera* (top right), from Escambia County, Florida; and Florida softshell turtle, *Apalone ferox* (bottom right), from Alachua County, Florida. Photo by Barry Mansell.

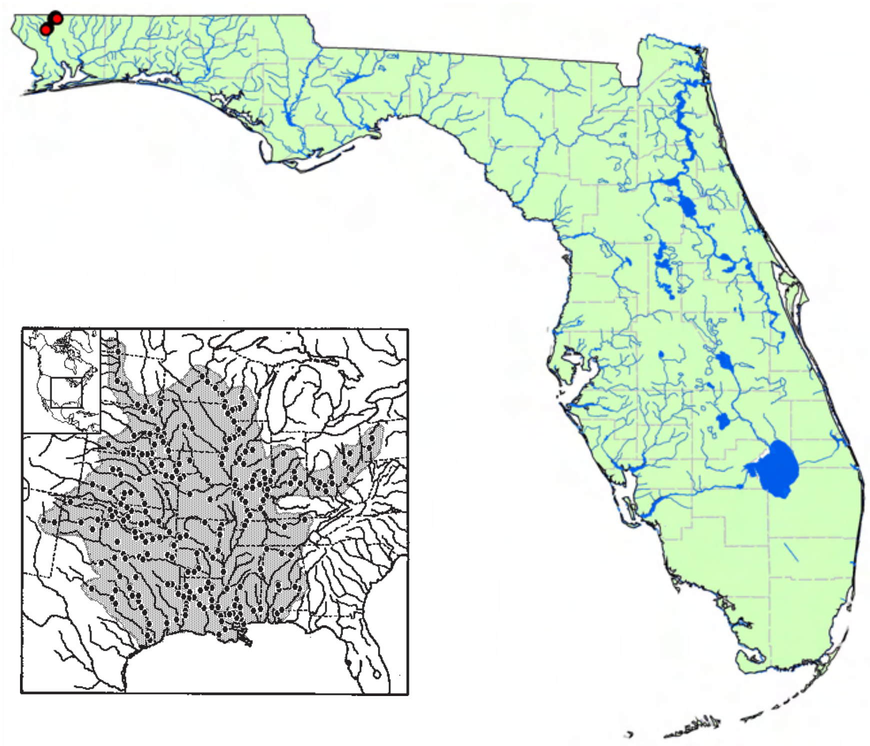

Figure 9-4. Distribution records for the Gulf Coast smooth softshell, *Apalone mutica calvata,* from Florida. Inset: distribution records from entire range of *A. mutica* (adapted from Iverson, 1992).

Louisiana. Eight eggs from a single Florida nest averaged 26 x 27 mm (Webb, 1962). The eggs are white and spherical with a brittle shell. Webb (1962) suggested that *A. mutica* (subspecies not specified) is capable of laying three clutches annually. It is likely that females in Florida populations produce at least 2–3 clutches annually, but no data are available.

Incubation. — Length of incubation is inversely proportional to temperature. Webb (1962) reported incubation periods of 65–77 days, and Doody (1996) reported that incubation averaged 64 days. Webb (1962) reported that 3 hatchlings measured 50–52 mm CL.

Approximately 34% of nests on the Comite River, Louisiana, were lost annually to flooding (Doody, 1996). Flooding was also the major cause of egg mortality in *A. m. mutica* in Kansas (Plummer, 1976).

INTERSPECIFIC INTERACTIONS

Diet and Feeding. — Data are unavailable for *A. m. calvata*. Williams and Christiansen (1981) reported that insects comprised 57.4% (by volume) of the diet of *A. m. mutica* in Iowa but only 15.1% of the diet of sympatric *A. spinifera spinifera*. They reported only 16.4% fish in the diet of *A. m. mutica*. Plummer and Farrar (1981) reported significant differences between the diets of male and female *A. m. mutica* in Kansas, with females consuming approximately 71% aquatic items and males 67% terrestrial items, reflecting the different microhabitats frequented by males and females. Fish represented 20.1% of the diet of females but only 1.7% of the diet of males in the Kansas study. Insects made up 26.3% of the male diet and 49.5% of the female diet. Mulberries and cottonwood seeds made up 49.6% of the male diet.

Predation. — In a two-year study, Doody (1996) estimated that predation on *A. m. calvata* nests was surprisingly low (10%), with predators including raccoons, fire ants, moles, dogs, and foxes. Plummer (1976) also reported low nest predation in *A. m. mutica* in Kansas, with canids being the primary nest predators. Shealy (1976) found the fish crow to be the major diurnal predator and the raccoon the major nocturnal predator on nests of the Escambia map turtle (*Graptemys ernsti*) on the Conecuh River, the major tributary of the Escambia River.

THREATS

Apalone mutica calvata is common within its very restricted Florida distribution and does not appear to be in any danger at this time. Although occasional turtles may be taken opportunistically for human consumption, there is no directed fishery for this species.

The Florida Game and Fresh Water Fish Commission attempted to monitor the commercial use of native reptiles over the two-year period 1990–92. Florida dealers reported no sales of *A. mutica* during those years (Enge, 1993).

STATUS

The Florida Committee on Rare and Endangered Plants and Animals (Pritchard, 1992) considered this species to be “Rare”. The Florida Natural Areas Inventory listed the subspecies as S1 in Florida due to its rarity.

CONSERVATION OPTIONS AND SOLUTIONS

Florida prohibits the collection of all softshells between 1 May and 31 July (Rule 68A-25.002[7], Florida Administrative Code). However, *A. m. calvata* does not currently appear to be subject to significant harvest in Florida. The greatest threat to the Florida population would be significant degradation of the Escambia River. Upper sections of the Escambia River occupied by *A. mutica* are largely undeveloped, and adjacent lands are increasingly being brought into public ownership. However, tributaries in Alabama receive industrial effluent.

Acknowledgments

Steve Santhuff assisted with field investigations on the Escambia River. Robert Webb and Sean Doody read and commented on a draft of this account.

LITERATURE CITED

Doody, J.S. 1996. Summers with softshells. Bulletin of the Chicago Herpetological Society 31:132-133.

Enge, K.M. 1993. Herptile Use and Trade in Florida. Final performance Report. Florida Game and Fresh Water Fish Commission, Tallahassee.

Ernst, C.H., Barbour, R.W., and Lovich, J.E. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington, D.C.

Iverson, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately printed, 363 pp.

Meylan, P.A. 1987. The phylogenetic relationships of soft shelled turtles (Family Trionychidae). Bulletin of the American Museum of Natural History 186:1-101.

Mount, R.H. 1975. The Reptiles and Amphibians of Alabama. Agric. Exp. Sta., Auburn University, Auburn, Alabama.

Plummer, M.V. 1976. Some aspects of nesting success in the turtle, *Trionyx muticus*. Herpetologica 32:353-359.

Plummer, M.V., and Farrer, D.B. 1981. Sexual dietary differences in a population of *Trionyx muticus*. Journal of Herpetology 15:175-179.

Pritchard, P.C.H. 1992. Rare: Gulf Coast smooth softshell. In: Moler, P.E. (Ed.). Rare and Endangered Biota of Florida, Volume III. Amphibians and Reptiles. University Press of Florida, Gainesville. pp. 210-213.

Shealy, R.M. 1976. The natural history of the Alabama map turtle, *Graptemys pulchra* Baur, in Alabama. Bulletin of the Florida State Museum, Biological Sciences 21:47-111.

Webb, R.G. 1959. Description of a new softshell turtle from the southeastern United States. University Kansas, Publications of the Museum Natural History 11:517-525.

Webb, R.G. 1962. North American recent soft-shelled turtles (Family Trionychidae). University Kansas, Publications of the Museum Natural History 13:429-611.

Webb, R.G. 1973. *Trionyx muticus* Lesueur: Smooth softshell turtle. Catalogue of American Amphibians and Reptiles. 139.1-139.2.

Weisrock, D.W., and Janzen, F.J. 2000. Comparative molecular phylogeography of North American softshell turtles (*Apalone*): Implications for regional and wide-scale historical evolutionary forces. Molecular Phylogenetics and Evolution 14:152-164.

Williams, T.A., and Christiansen, J.L. 1981. The niches of two sympatric softshell turtles, *Trionyx muticus* and *Trionyx spiniferus*, in Iowa. Journal of Herpetology 15:303-308.

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Apalone spinifera aspera – Gulf Coast Spiny Softshell Turtle

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Summary. – The Gulf Coast spiny softshell, *Apalone spinifera aspera*, is one of three species of softshell turtles found in Florida. It is intermediate in size between the smaller Gulf Coast smooth softshell and the larger Florida softshell. It is distinguished by the presence of small, pointed, soft spines along the anterior margin of the carapace. It is strongly sexually dimorphic, with females growing much larger than males. Maximum reported carapace length is 45.4 cm for females and 20.3 cm for males. It has a limited distribution in north Florida, occurring in the St. Marys River and from the Ochlockonee River westward across the Florida Panhandle to Alabama. It has not been recorded from the Suwannee drainage in Florida, but it is known from two Georgia tributaries of the Suwannee, the Withlacoochee (N) and Alapaha rivers. In Florida, it is usually found in rivers and larger creeks, but outside Florida (outside the range of the Florida softshell) it utilizes a wider variety of aquatic habitats. Nesting occurs from May to July, typically in sandy soils near the water. Clutch size averages 10–12 eggs but may number up to 25. *Apalone s. aspera* may bask on logs and along the shore, but they seldom travel far from the water except to nest. This species is not uncommon in the rivers in which it occurs, and its status in Florida appears secure as long as these rivers remain healthy.

Conservation Status. – FNAI Global - G5 (Demonstrably Secure), State - S3 (Rare, Local, or Vulnerable); ESA Federal - Not Listed; State - Not Listed; CITES - Not Listed; IUCN Red List - Not Listed (LC-Least Concern).

Species Recognition. — *Apalone spinifera aspera* is intermediate in size between the two other softshells found in Florida. The Gulf Coast smooth softshell (*Apalone mutica calvata*) is smaller and the Florida softshell (*Apalone ferox*) is larger. The species has the flattened leathery shell, long neck, and tubular snout typical of all softshell turtles (Figs. 10-1 through 10-4). The anterior margin of the carapace bears small, pointed, soft spines (Fig. 10-2), which in large adults can be quite distinct (Fig. 10-3). Hatchlings, juveniles, and most adult males have a tan carapace with numerous small, dark dots (Figs. 10-1, 10-4, and 9-3). Two to four dark lines parallel the posterior margin of the carapace, but these decrease in number anteriorly with at least the innermost line interrupted. In females, borders of the carapacial dots begin to smudge within a few months after hatching, and adult females become a mottled brown (Fig. 10-5). Members of this species have a pair of pale, dark-bordered stripes on the snout that typically join together in front of the eyes, and a similar pair of uninterrupted stripes behind each eye (Figs. 10-2, 10-3). Ventral surfaces are white. Medial septal ridges extend into each nostril. Doody (1991) reported that all *A. spinifera* at his Comite River study site in Louisiana had softshell bite marks on the edge of the carapace. Like the Florida softshell, but unlike the Gulf Coast smooth softshell, the Gulf Coast spiny softshell readily attempts to bite when handled.

Taxonomic History. — The generic names *Aspidonectes*, *Platypeltis*, *Trionyx*, *Pelodiscus*, and *Amyda* have been used for this taxon. It is currently referred to the genus *Apalone* Rafinesque based on the work of Meylan (1987).

The subspecies of *A. spinifera* found in Florida was originally described as *Aspidonectes asper* Agassiz (1857). Webb (1960) designated as a lectotype a specimen from the Pearl River at Columbus, Marion County, Mississippi. The Gulf Coast spiny softshell has, at various times, been treated as a separate species or as a subspecies of either *A. spinifera* or *A. ferox*. *Apalone spinifera* and *A. ferox* were considered conspecific by some authors (e.g., Neill, 1951; Carr, 1952) until the work of Schwartz (1956) and Webb (1962). Populations in Atlantic drainages of Georgia and the Carolinas were once regarded as the separate species *Trionyx agassizii* Baur (1888).

The Gulf Coast spiny softshell is now regarded as a subspecies of *Apalone spinifera*. However, significant genetic variation exists both among the subspecies of *A. spinifera* and within *A. spinifera aspera* (Weisrock and Janzen, 2000). Populations of *A. s. aspera* from the Ochlockonee River and from southern Georgia differed from west Florida and Louisiana populations to a greater extent than either differed from populations of *A. s. spinifera* in Illinois and Ontario. The molecular genetics of *A. spinifera aspera* from the St. Marys River (Baker and Nassau counties, Florida) have not yet been studied.

DISTRIBUTION

Geographic Distribution. — *Apalone spinifera* is found throughout most of the eastern and central United States south and west of the Appalachian Mountains. *Apalone s. aspera* is found from southeastern North Carolina, south and

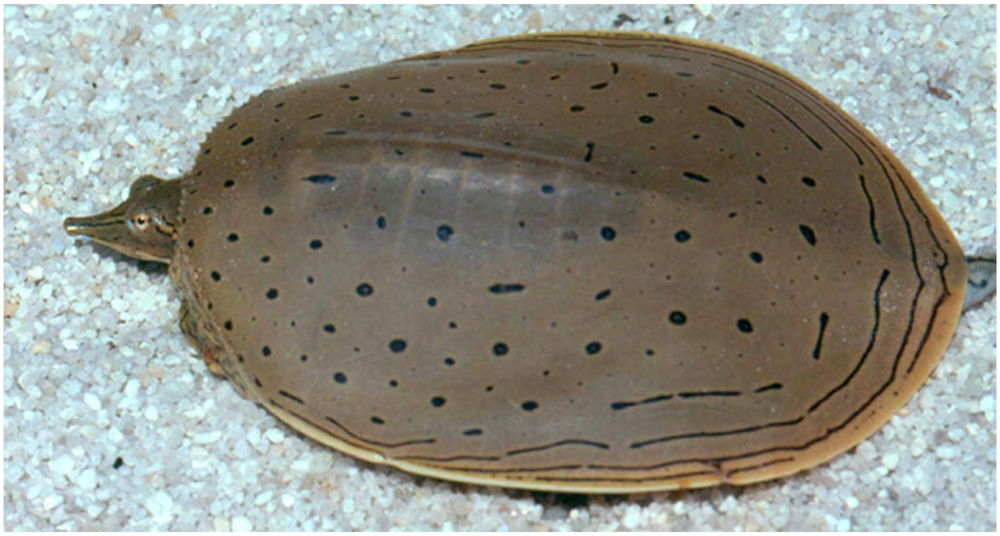

Figure 10-1. Adult male Gulf Coast spiny softshell turtle, *Apalone spinifera aspera,* from Santa Rosa County, Florida. Photo by Barry Mansell.

westward through most of South Carolina, Georgia, the Florida Panhandle, Alabama, eastern Mississippi, and the Florida parishes of Louisiana (Webb, 1973; Conant and Collins, 1991; Iverson, 1992).

In Florida, *A. s. aspera* is found from the Ochlockonee River westward throughout the Panhandle. It also occurs in the St. Marys River in Nassau and Baker counties (Campbell and Christman 1980) (Fig. 10-6). It has not been reported from the intervening Suwannee River basin in Florida, but in Georgia it is known from two tributaries of the Suwannee, the Withlacoochee River (Iverson 1992) and the Alapaha River (J. Jensen, *pers. comm*.; Weisrock and Janzen, 2000).

Ecological Distribution. — Where sympatric with *Apalone ferox*, *A. s. aspera* is primarily associated with lotic (flowing water) habitats, whereas *A. ferox* is typically associated with lentic (still water) habitats (Crenshaw and Hopkins, 1955). In the absence of *A. ferox*, *A. spinifera* will utilize almost any permanent body of water (Mount, 1975; Dundee and Rossman, 1989).

Apalone s. aspera is primarily associated with rivers and creeks in Florida, although Webb (1962) reported taking them from an isolated borrow pit near the Escambia River. They may also occupy oxbows and floodplain pools associated with rivers, but in Florida, these lentic habitats often support populations of *A. ferox*.

In the Escambia River, where *A. s. aspera* is sympatric with the Gulf Coast smooth softshell (*A. mutica calvata*), *A. mutica* is more closely associated with large sandbars, whereas *A. spinifera* may be encountered throughout the river. Hatchling *A. mutica* are rarely encountered away from sandbars, whereas hatchling *A. spinifera* are commonly found along any shallow sandy or muddy shoreline.

HABITAT RELATIONS

Activity. — The species may be found buried in sand or mud on the bottom of shallow or deep water. It will bask on banks or logs.

Figure 10-2. Head of subadult female Gulf Coast spiny softshell turtle, *Apalone spinifera aspera,* from Gulf Co., Florida. Photo by Robert T. Zappalorti.

Figure 10-3. Head of adult female Gulf Coast spiny softshell turtle, *Apalone spinifera aspera,* from Santa Rosa Co., Florida. Photo by Barry Mansell.

GROWTH AND REPRODUCTION

Size Dimorphism. — The species is strongly sexually dimorphic. Females reach much larger sizes than do males. The maximum carapace length for *A. s. aspera* is 45.4 cm in females and 20.3 cm in males (Conant and Collins, 1991). Also, males retain the juvenile pattern of sharply defined spots on a tan carapace, whereas females develop a mottled, brown carapace (Fig. 10-5). Graham (1991) reported that the smudging of the carapacial spots in *A. s. spinifera* begins within a few months after hatching, and I have observed similar early pattern changes in hatchling female *A. s. aspera* from Florida.

Maturity. — Females mature at a plastral length of approximately 20.0 cm, corresponding to a carapacial length of 28.0 cm (Webb, 1962). Based on data from other subspecies of *A. spinifera* (Webb, 1962), males of *A. s. aspera* probably mature at a plastral length of 9–10 cm.

Nesting Behavior. — Females of this subspecies have been reported to nest from May to July or August (Mount, 1975; Dundee and Rossman, 1989; Doody, 1996). Ewert (Ewert, 1979; unpubl. data) found 3 *A. s. aspera* clutches along the lower Apalachicola River on 4 July 1972. One clutch was about a week old when found, another was several weeks old.

Nesting typically occurs in sandy areas. The nests observed by Ewert on the Apalachicola had been dug in open areas of dredged spoil “sandbars.” Webb (1962) suggested that *A. spinifera* might not nest on open sand bars in areas where *A. mutica* occurs, but Doody reported no such avoidance of sympatric *A. mutica* nest sites. Doody (1996) did note that *A. mutica* tended to nest on more steeply sloped areas than did *A. s. aspera*.

Clutch Size. — Three *A. s. aspera* clutches found along the lower Apalachicola River contained 20–24 eggs (Ewert, 1979; unpubl. data). Mount (1975) reported that *A. s. aspera* in Alabama lays 3–25 eggs per clutch. Doody (1996) reported an average clutch size of about 12 eggs in Louisiana, and Webb reported an overall average of 9.6 eggs per clutch in southern *A. spinifera*. Females probably produce at least two to three clutches per year (Webb, 1962; Mount, 1975).

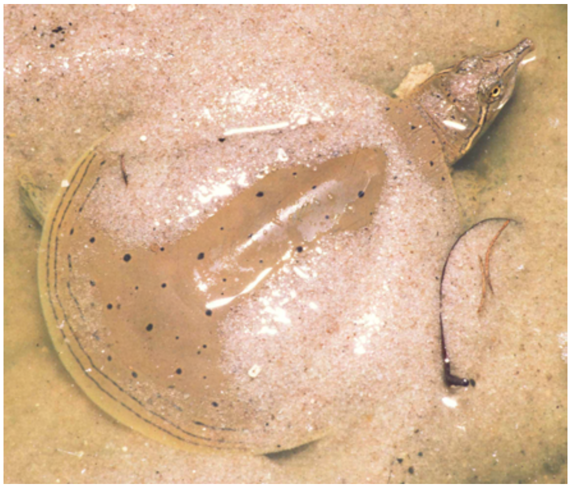

Figure 10-4. Hatchling Gulf Coast spiny softshell turtle, *Apalone spinifera aspera,* from Liberty Co., Florida. Photo by Dick Bartlett.

Figure 10-5. Adult female Gulf Coast spiny softshell turtle, *Apalone spinifera aspera,* from Bay Co., Florida. Photo by Barry Mansell.

Eggs and Juveniles. — The eggs are white and spherical with a brittle shell. Ewert (1979) reported egg weight of 11.4–14.5 g and hatchling weight of about 9.6 g, or 74.1% of egg weight for hatchlings from three Florida clutches. Average incubation time is about 64 days (Doody, 1996).

Six juveniles captured in the Escambia River, Florida, on 19–20 May 1993 measured 33.4–47.5(mean = 38.8) mm PL and 48.2-68.2 (mean = 56.3) mm CL. They weighed 14–32 (mean = 19.8) g. Presumably all had hatched the previous summer.

POPULATION BIOLOGY

In contrast to many turtles, sex is not determined by incubation temperature in *Apalone*, and sex ratios of three populations of *A. spinifera* in Mississippi and Alabama did not differ significantly from 1:1 (Vogt and Bull, 1982). No formal population surveys have been conducted in Florida, but *A. s. aspera* is commonly encountered in the Saint Marys River and in many of the rivers of the Panhandle.

INTERSPECIFIC INTERACTIONS

Community Structure. — *Apalone s. aspera* is sympatric with the Gulf Coast smooth softshell (*A. mutica calvata*) in the Escambia River. Elsewhere in Florida, it occurs also with common snapping turtles (*Chelydra serpentina*), alligator snapping turtles (*Macrochelys temminckii*), loggerhead musk turtles (*Sternotherus minor*), river cooters (*Pseudemys concinna*), Florida cooters (*Pseudemys

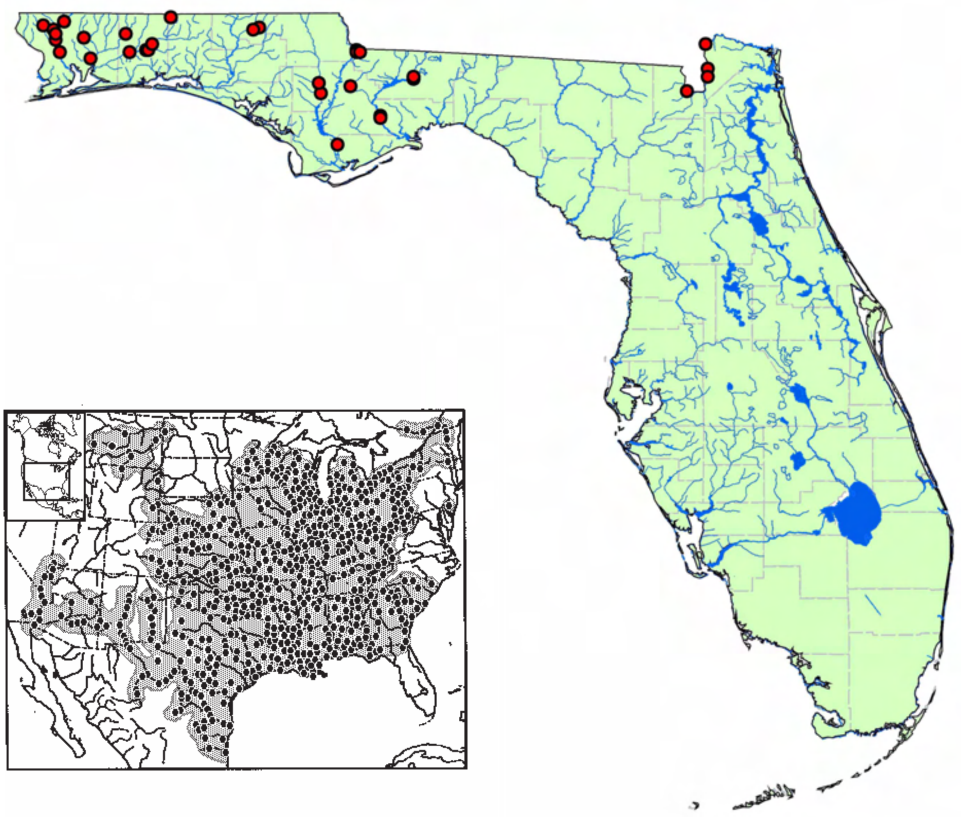

Figure 10-6. Distribution records for Gulf Coast spiny softshell turtle, *Apalone spinifera aspera,* from Florida. Inset: distribution records from entire range of *A. spinifera* (adapted from Iverson, 1992; distribution in inset map not current for Florida as presented here).

floridana), yellowbelly turtles (*Trachemys scripta*), Escambia map turtles (*Graptemys ernsti*),and Barbour's map turtles (*G. barbouri*).

Diet and Feeding. — Few data are available regarding the diet of *A. s. aspera*, although information is available from other subspecies of *A. spinifera*. Williams and Christiansen (1981) compared the diets of the eastern spiny softshell, *A. s. spinifera*, and *A. mutica* in Iowa and concluded that spiny softshells are primarily benthic feeders and scavengers. In a sample of 52 *A. s. spinifera*, frequency of occurrence was approximately 55% for crayfish and 40% for fish. They estimated that, by volume, the diet consisted of crayfish (24.2%), insects (21.6%), fish (19.4%), unidentifiable and miscellaneous animal material (19.5%), and plant material (12.8%). They also suggested that most of the fish had been consumed as carrion. Crayfish are also the major prey of the western spiny softshell, *A. s. hartwegi*, in Arkansas (M. Plummer, *pers. comm.*).

Predation. — Doody (1996) identified raccoons, fire ants, moles, dogs, and fox as predators on softshell nests (*A. s. aspera* and *A. m. calvata*) along the Comite River in Louisiana. However, he found that loss of nests to predators was surprisingly low (less than 10%), whereas estimated annual flooding mortality was 34%.

THREATS

Apalone s. aspera appears to be common in many of the rivers of the Florida Panhandle and in the Saint Marys River along the border of Georgia north and west of Jacksonville. In the Ochlockonee River downstream from the Lake Talquin dam, it is now less common than formerly (J.C. Kyle, *pers. comm.*), perhaps because of reduction in the number of sand bars due to the trapping of sand in Lake Talquin. It does not appear to be in any danger at this time.

Gulf Coast spiny softshells are taken by humans for food, but there appears to be no directed, commercial fishery for the species in Florida as there is for the Florida softshell (see *A. ferox* account). Collection for the pet trade is minimal. Enge (1993) reported a total of 59 specimens collected from the wild for the pet trade during the two year period July 1990 – June 1992. These were probably hatchlings and juveniles, in which case they would represent the reproductive potential of only 1–2 adult females.

STATUS

This species is not listed by the Florida Committee on Rare and Endangered Plants and Animals nor is it on any Federal or State list of endangered species.

CONSERVATION OPTIONS AND SOLUTIONS

The regulatory status of all softshells in Florida changed in 1999. Florida Administrative Code 68A:39-25.002 now prohibits the take of softshell turtles from 1 May to 31 July. Aside from continued protection of Florida rivers and streams, there is no apparent need for additional conservation measures for this species in Florida at present.

Acknowledgments

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LITERATURE CITED

Agassiz, L. 1857. Contribution to the natural history of the United States. Little, Brown, and Co. Boston, Massachusetts. Vols. 1-4.

Baur, G. 1888. Notes on the American Trionychidae. American Naturalist 22:1121-1222.

Campbell, H.W., and Christman, S.P. 1980. Geographic distribution: *Trionyx spiniferus asperus* (Gulf Coast spiny softshell). Herpetological Review 11:14.

Carr, A. 1952. Handbook of Turtles: The turtles of the United States, Canada, and Baja California. Comstock Publ. Assoc., Cornell University Press, Ithaca, New York.

Conant, R., and Collins, J.T. 1991. A Field Guide to Reptiles and Amphibians: Eastern and central North America. Houghton Mifflin Co., Boston, Massachusetts. 450 pp.

Crenshaw, J.W., Jr., and Hopkins, M.N., Jr. 1955. The relationships of the soft-shelled turtles *Trionyx ferox ferox* and *Trionyx ferox aspera*. Copeia 1955:13-23.

Doody, J.S. 1991. Ecology of softshell turtles (*Apalone spinifera* and *A. mutica*) in southern Louisiana: Preliminary results. (Abstract) Program 34th Annual Meeting Society for the Study of Amphibians and Reptiles and 39th Annual Meeting The Herpetologists' League. Penn State University, University Park, Pennsylvania. p. 56.

Doody, J.S. 1996. Summers with softshells. Bulletin Chicago Herpetological Society 31:132-133.

Dundee, H.A., and Rossman, D.A. 1989. The amphibians and reptiles of Louisiana. Louisiana State University Press, Baton Rouge. 300 pp.

Enge, K.M. 1993. Herptile use and trade in Florida. Final Performance Report, Bureau of Nongame Wildlife. Florida Game and Fresh Water Fish Commission, Tallahassee. 102 pp.

Ewert, M.A. 1979. The embryo and its egg: Development and natural history. In: Harless, M., and Morlock, H. (Eds.). Turtles: Perspectives and research. John Wiley and Sons, New York, pp. 333-413.

Graham, T.E. 1991. *Apalone spinifera spinifera* (Eastern spiny softshell). Pattern dimorphism. Herpetological Review 22:97.

Iverson, J.B. 1992. A revised checklist with distribution maps of the turtles of the World. Privately printed, Richmond, Indiana. 363 pp.

Meylan, P.A. 1987. The phylogenetic relationships of soft-shelled turtles (family Trionychidae). Bulletin of the American Museum of Natural History 186:1-101.

Mount, R.H. 1975. The reptiles and amphibians of Alabama. Auburn University Agricultural Experiment Station, Auburn, Alabama. 347 pp.

Neill, W.T. 1951. The taxonomy of North American soft-shelled turtles, genus *Amyda*. Publ. Research Div. Ross Allen's Reptile Inst. 1:7-24.

Schwartz, A. 1956. The relationships and nomenclature of the soft shelled turtles (genus *Trionyx*) of the southeastern United States. Charleston Museum Leaflet 26:1-21.

Vogt, R.C., and Bull, J.J. 1982. Genetic sex determination in the spiny softshell *Trionyx spiniferus* (Testudines: Trionychidae)(?). Copeia 1982:699-700.

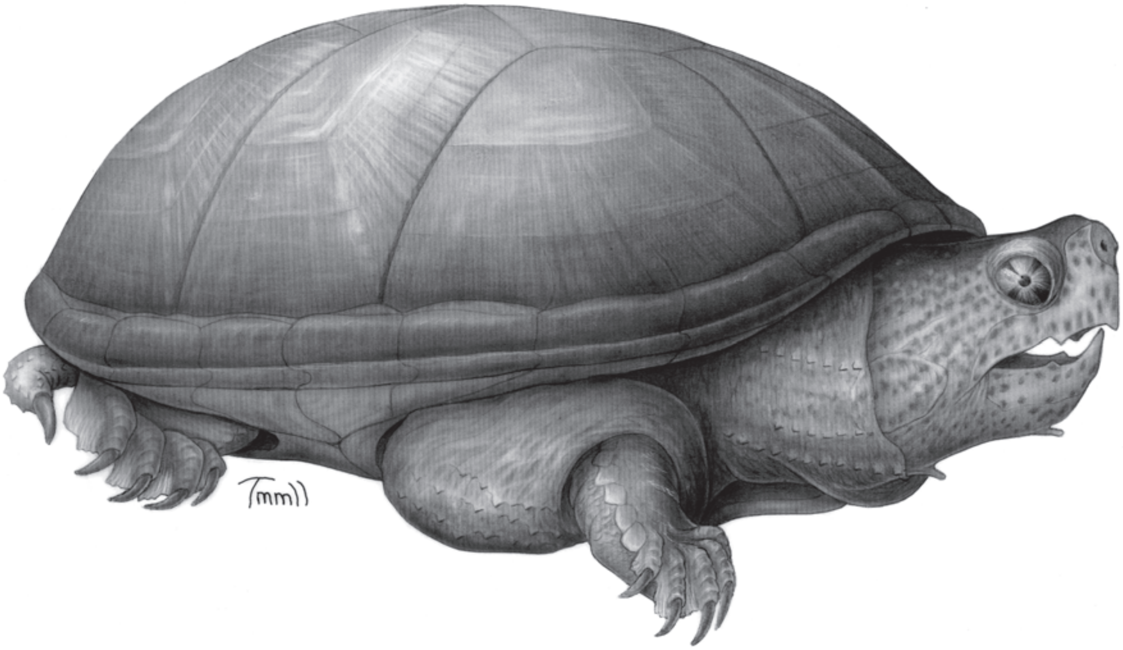
Webb, R.G. 1960. Type and type locality of the Gulf Coast spiny softshell turtle, *Trionyx spinifer asper* (Agassiz). Breviora 129:1-8.

Webb, R.G. 1962. North American recent soft-shelled turtles (family Trionychidae). University Kansas, Publications of the Museum of Natural History 13:429-611.

Webb, R.G. 1973. *Trionyx spiniferus* Lesueur: Spiny softshell turtle. Catalogue of American Amphibians and Reptiles 140.1-140.4.

Weisrock, D.W., and Janzen, F.J. 2000. Comparative molecular phylogeography of North American softshell turtles (*Apalone*): Implications for regional and wide-scale historical evolutionary forces. Molecular Phylogenetics and Evolution 14:152-164.

Williams, T.A., and Christiansen, J.L. 1981. The niches of two sympatric softshell turtles, *Trionyx muticus* and *Trionyx spiniferus*, in Iowa. Journal of Herpetology 15:303-308.



Florida Mud Turtle, *Kinosternon subrubrum steindachneri* (Kinosternidae).
Drawing by Susan Trammell.

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Introduction to the Mud and Musk Turtles: Family Kinosternidae

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Two of the four genera that comprise this family occur in Florida. They are the musk turtles (*Sternotherus*) and the mud turtles (*Kinosternon*). Two species of each genus are found within the state.

Content. — The family Kinosternidae includes four living genera, *Claudius*, *Kinosternon*, *Staurotypus*, and *Sternotherus*, and about 25 species. *Kinosternon* is the largest genus with 18 species.

Relationships. — Although it is clear that mud and musk turtles are each other's closest relatives, and that they are closely related to the two Central American kinosternid genera (*Claudius* and *Staurotypus*), the relationships of kinosternids to other turtles is in debate. Both morphological and molecular data agree that the single living member of the family Dermatemydidae (*Dermatemys mawii*) is the closest living relative to the Kinosternidae, but there is lack of agreement about where these two families fit among the Cryptodira. One line of thought, based on morphological data, is that these families are related to softshell turtles (Trionychidae) and they have been placed together in the superfamily Trionychoidea (Gaffney, 1984; Meylan and Gaffney, 1989). However, molecular data have failed to corroborate this relationship (Shaffer et al., 1997; Near et al., 2005).

Geological Distribution. — The time of divergence between the family Dermatemydidae and the family Kinosternidae can be dated by the Paleocene kinosternid, *Hoplochelys*. This genus is well known from descriptions in Hay (1908) and Gilmore (1919), and it is clearly more closely related to *Staurotypus*, *Baltemys*, and *Kinosternon* than it is to dermatemydids (Hutchison, 1991). *Hoplochelys* is known from Puercan and Torrejonian horizons in the San Juan Basin in New Mexico and suggests that the divergence of the kinosternids from dermatemydids must have occurred before 65 million years ago, near the end of the age of dinosaurs.

Fossils of this family have recently been reported from the Paleocene of South Carolina (Hutchison and Weems, 1999), but the material consists of isolated elements, which makes it difficult to determine if this fossil material can be used to date the age of the living Kinosternidae.

Within the Kinosternidae, the divergence between the two subfamilies, the Kinosterninae and Staurotypinae, can be dated by the extinct kinosternine, *Baltemys*. This genus has been described in detail (Hutchison, 1991), and is clearly more closely related to *Kinosternon* and *Sternotherus* than it is to *Staurotypus* and *Claudius*. *Baltemys* dates the split between the two subfamilies of the Kinosternidae at about 50 million years ago.

Geographic Distribution. — The family Kinosternidae is limited to the New World (Iverson, 1992). *Sternotherus* is only found in the eastern United States and Canada. *Kinosternon* has a very wide distribution, from the northeastern U.S. across the eastern two-thirds of the country, across all of Mexico and Central America, and also occurring in South America. *Staurotypus* and *Claudius*, the other two genera of the family, have a restricted distribution from southern Mexico to western Honduras.

Status. — The major threat to members of this family in Florida is the loss of suitable habitat, especially for *Kinosternon*. Members of this genus require wetlands surrounded by uplands into which they can move as wetlands dry out, as well as for egg laying. The two species of *Kinosternon* are excellent examples of the case for conserving uplands adjacent to wetlands (Burke and Gibbons, 1995); conserving the wetlands alone will not protect these species.

LITERATURE CITED

Burke, V.J. and Gibbons, J.W. 1995. Terrestrial buffer zones and wetland conservation: a case study of freshwater turtles in a Carolina Bay. Conservation Biology 9:1365-1369.

Gaffney, E.S. 1984. Historical analysis of theories of chelonian relationship. Systematic Zoology 33:283-301.

Gilmore, C.W. 1919. Reptilian faunas of the Torrejon, Puerco, and underlying Upper Cretaceous formations of San Juan County, New Mexico. U.S. Geological Survey, Professional Papers 119:1-68.

Hay, O.P. 1908. The fossil turtles of North America. Publications of the Carnegie Institute, Washington 75:1-553.

Hutchison, J.H. 1991. Early Kinosterninae (Reptilia: Testudines) and their phylogenetic significance. Journal of Vertebrate Paleontology 11:145-167.

Hutchison, J.H. and Weems, R.E. 1999. Paleocene turtle remains from South Carolina. Transactions of the American Philosophical Society 88:165-195.

Iverson, J.B. 1992. A revised checklist with distribution maps of the turtles of the world. Privately printed. Richmond, IN, 363 pp.

Meylan, P.A. and Gaffney, E.S. 1989. The skeletal morphology of the Cretaceous turtle, *Adocus*, and the relationships among the Trionychoidea. American Museum of Natural History Novitates 2941:1-60.

Near, T.J., Meylan, P.A., and Shaffer, H.B. 2005. Assessing concordance of fossil calibration points in molecular clock studies: an example using turtles. American Naturalist 165:137-146.

Shaffer, H.B., Meylan, P.A., and McKnight, M. 1997. Tests of turtle phylogeny: molecular, morphological and combined approaches. Systematic Biology 46(2):235-268.

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Kinosternon baurii – Striped Mud Turtle

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Summary. – The striped mud turtle, *Kinosternon baurii*, is a common small aquatic turtle easily recognized by three light longitudinal stripes on a darker shell. It ranges from the lower Florida Keys to southern Virginia. Although this species is known to occupy a wide range of aquatic habitats, few data exist on its precise habitat requirements in Florida. Both males and females tend to spend a considerable amount of time on land and these movements are positively correlated with precipitation. Adult females nest in the spring and fall months with the majority of nesting events recorded in September through November. This species is known to have a remarkable developmental pattern that in some cases includes two separate periods of diapause (when development temporarily shuts down). Because eggs are deposited in a relatively shallow nest, vegetative cover around the nest has been shown to be important to protect developing offspring from thermal extremes. Much of the basic population biology of this species remains poorly known. No single population has been followed for a period long enough to monitor patterns of survivorship, fecundity, or growth rates. In addition, most research on this species has focused on adult females with a paucity of data on males or juveniles. Although striped mud turtles appear relatively abundant north of the Florida Keys, populations in the lower Keys are listed as endangered by the Florida Fish and Wildlife Conservation Commission. The main threat in the lower Florida Keys appears to be intensive development of their habitat, most of which is privately owned.

Conservation Status. – FNAI Global - G5 (Demonstrably Secure), State - Species: S5 (Demonstrably Secure), Florida Keys population only: S2 (Imperiled or Rare); ESA Federal - Not Listed; State - E (Endangered); CITES - Not Listed; IUCN Red List - Not Listed (LC-Least Concern).

Species Recognition. — Striped mud turtles, *Kinosternon baurii*, are usually characterized by three light, longitudinal stripes on a tan to black carapace (Fig. 11-1). However, individuals without carapace stripes have been reported from Gulf Hammock and the lower Keys in Florida (Iverson, 1978), and from the northernmost limits of the species' range (Lamb, 1983; Lamb and Lovich, 1990) (Fig. 11-2). Adult striped mud turtles are small, with carapace length (CL) reaching about 118 mm in females and 104 mm in males. The vertebrals of the carapace may be flat or depressed, forming a shallow middorsal groove (Carr, 1952; Ernst et al., 1994). The light yellow plastron has two functional, transverse hinges bordering the abdominal scutes, and a slightly notched posterior hind lobe (Fig. 11-3). The skin is dark, but the small, conical head is mottled, with two parallel and pronounced, cream-to-yellow stripes on the sides (Iverson, 1978) (Fig. 11-4). The lower jaw ranges from completely dark to dark with anteroposterior cream to yellow streaks (Uzzell and Schwartz, 1955). A keratinized spine is present on the tip of the tail in both males and females, though it is greatly enlarged in males.

Hatchlings have a dark carapace with three light longitudinal stripes found on three distinct keels and a light to dark yellow spot on each marginal scute (Einem, 1956) (Fig. 11-5). The plastron of hatchlings is yellow except for a dark central blotch and dark bordered seams (Ernst et al., 1994) (Fig. 11-6). Head striping of hatchlings is similar to that of adults. Hatchlings usually acquire functional plastral hinges by their third month (Einem, 1956).

Taxonomic History. — The striped mud turtle was first described by Garman (1891) as *Cinosternum baurii* from 11 specimens collected in brackish water ponds in Key West, Florida. Loennberg (1894) later assigned *baurii* to the genus *Kinosternon* Spix (1824). Stejneger (1925) described a new subspecies (*Kinosternon baurii palmarum*) from 4 specimens collected from Royal Palm State Park, Dade County, Florida. These individuals differed from the "typical dark *K. baurii*" based on head and carapace coloration and head size and shape (Stejneger, 1925). Subsequently, pigmentation patterns were found to be distinguishable between individuals collected from the upper Florida Keys – Florida mainland and the lower Florida Keys (Uzzell and Schwartz, 1955). This division of the species into subspecies, however, has not been supported by studies of morphological characteristics (Iverson, 1978; Lamb and Lovich, 1990) or mitochondrial control region DNA sequences (Karl and Wilson, 2001). These authors found that levels of sequence divergence from specimens collected from ten geographic locations through the state of Florida were low. In addition, the isolated population of striped mud turtles from the lower Florida Keys did not significantly differ genetically from the upper Keys or mainland populations.

Figure 11-1. Adult female striped mud turtle, *Kinosternon baurii,* from Hillsborough Co., Florida. Photo by Dawn Wilson.

The most closely related species to the striped mud turtle is the sympatric common mud turtle, *K. subrubrum* (Frair, 1972; Sites et al., 1979; Seidel et al., 1986; Iverson, 1991, 1998; Serb et al., 2001). Recent phylogenetic analysis of combined mtDNA, morphological, and protein electromorph data supports the placement of *K. baurii* and *K. subrubrum* as sister taxa in a monophyletic *K. flavescens* group (Iverson, 1998; Serb et al., 2001). The karyotype of *K. baurii* is reported as 2n = 54 (Killebrew, 1975).

DISTRIBUTION

Geographic Distribution. — Until 1972, the range of the striped mud turtle was thought to be limited to the lower Florida Keys northward along the Atlantic Coastal Plain to Georgia. In 1972, new collection localities extended the species' range northward 200 km into southern South Carolina (Wharton and Howard, 1971; Duever, 1972). Most specimens collected in Georgia and South Carolina lack the characteristic, longitudinal carapace stripes but tend to retain some of the head stripes typical of striped mud turtles occurring throughout most of peninsular Florida (Duever, 1972; Lamb, 1983). Because of these differences in shell pigmentation patterns, some investigators considered Georgia and South Carolina specimens to be *K. subrubrum subrubrum*, a common subspecies in the area (Gibbons et al., 1979). Morphometric (Lamb, 1983; Lamb and Lovich, 1990; Lovich and Lamb, 1995) and mtDNA (Walker et al., 1998) data sets, however, have been successful in distinguishing the *baurii*-like specimens collected from Georgia, South Carolina, North Carolina, and Virginia from *K. s. subrubrum* and prompted the conclusion that striped mud turtles occur continuously from Florida north to southeastern Virginia.

Figure 11-2. Adult striped mud turtle, *Kinosternon baurii,* from Stock Island, Monroe Co., Florida. Photo by Dick Bartlett.

Figure 11-3. Plastron of adult male striped mud turtle, *Kinosternon baurii,* from Pinellas Co., Florida. Photo by Marius Moore.

Figure 11-4. Head of adult striped mud turtle, *Kinosternon baurii,* from Hillsborough Co., Florida. Photo by Dawn Wilson.

Striped mud turtles occur throughout Florida from the panhandle to the Florida Keys (Fig. 11-7). Distribution records occur in 50 of Florida's 67 counties. Based on museum locality data, striped mud turtles appear most abundant in the southern-most part of the state and are rare in the panhandle; 11 counties in Florida's panhandle have no records of occurrence. Recently, five new distribution records have extended the range of the striped mud turtle westward into the Florida panhandle from the St. Marks River drainage into the Apalachicola River drainage, including the Chipola River (Ewert et al., 2004).

Ecological Distribution. — Adult striped mud turtles can be found in a wide range of habitat types from still, shallow, often temporary bodies of water (Carr, 1952; Wygoda, 1979; Bancroft et al., 1983) to deep, flowing waters (Ernst et al., 1972). In North Carolina, striped mud turtles have been found in blackwater ponds located in areas dominated by cypress, and in various streams and swamps (Palmer and Braswell, 1995). In Virginia, striped mud turtles seem to prefer dark water with an organic substrate (Mitchell, 1994).

Few data exist concerning the precise habitat requirements of striped mud turtles in Florida. Wygoda (1979) reported that adult striped mud turtles in a central Florida population preferred shallow, still, bodies of water and were often found aestivating on land when water levels were low (see also Carr, 1952). In contrast, Ernst et al. (1972) reported that adults in southern Florida seemed to prefer relatively deep, slowly flowing water habitats and did not aestivate on land. Striped mud turtles can be found in clear, fast-flowing springs (Huestis and Meylan, 2004) and darkly-stained, slow-flowing backwaters (Wygoda, 1979). The increased aquatic specialization seen in more southern striped mud turtles may, in part, reflect the north-south clinal trend of decreasing plastral size relative to body size described by Iverson (1978). In the lower Florida Keys, Dunson (1979, 1981) found that adult striped mud turtles commonly inhabit small, ephemeral freshwater ponds and brackish water ponds that have salinities below 15 ppt, and also found dense concentrations of adults in man-made mosquito control ditches, which tend to retain water longer than natural temporary ponds. Striped mud turtles also were recorded inhabiting brackish water areas on Merritt Island, Florida (Neill, 1958).

No data are available on the habitat requirements of hatchling or juvenile striped mud turtles either within or outside Florida. Immature striped mud turtles have been observed among floating water plants (Barbour, 1920; J. Iverson, *pers. comm.*).

HABITAT RELATIONS

Activity / Movements / Seasonality. — Movements of striped mud turtles on land tend to be positively correlated with precipitation (Wygoda, 1979; Meshaka and Blind, 2001). In Everglades National Park, Meshaka and Blind (2001) found that females moved most in October when water levels were highest, and that most female movements were associated with nesting activities. In central Florida, movements by females to and from nest sites were shown to coincide with rainfall (Wilson et al., 1999). Males have been shown to make long range excursions (up to 3.4 km) across land to new aquatic habitats (Tuberville et al., 1996). Few individuals are seen moving in late summer, when temperatures are maximal, or in mid-winter, when temperatures are minimal (Iverson, 1979; Wygoda, 1979; Wilson, 1996). In a west-central Florida population, Wygoda (1979) noted seasonal shifts in migration by striped mud turtles to and from a pond that was surrounded by a drift fence. During spring through early June, 83% of movements were out of the pond, from 4 June to 21 June, 88% of movements were

Figure 11-5. Hatchling striped mud turtle, *Kinosternon baurii,* from Monroe Co., Florida. Photo by John Iverson.

Figure 11-6. Plastral view of hatchling striped mud turtles, *Kinosternon baurii,* from Alachua Co., Florida. Photo by John Iverson.

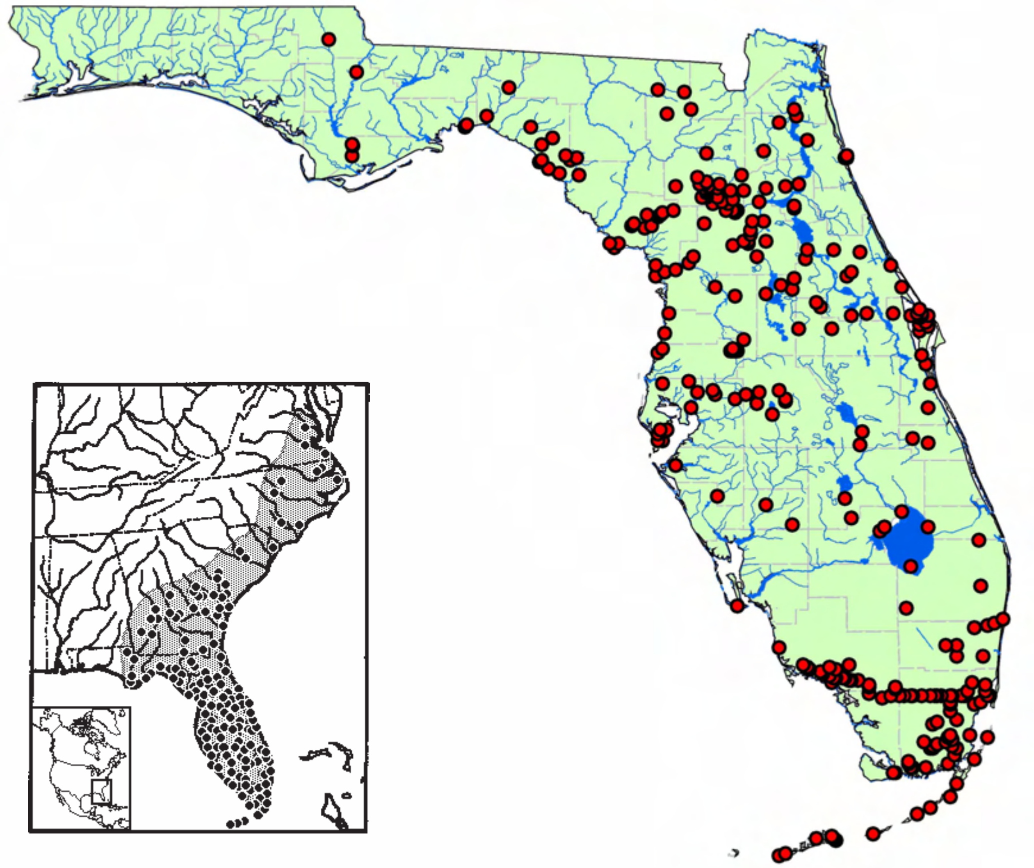

Figure 11-7. Distribution records for the striped mud turtle, *Kinosternon baurii*, from Florida. Inset: distribution records from entire range of *K. baurii* (adapted from Iverson, 1992; distribution in inset map not current for Florida as presented here).

into the pond, and from 22 June to 13 July, 76% of movements were out of the pond. Movements out of the pond by turtles in the spring to aestivation sites were correlated with decreasing water depths. Wygoda (1979) noted that during this period of pond drying, predators were attracted to the remaining water hole, and suggested that striped mud turtles may leave the pond to avoid predators and/or extreme temperatures associated with shallow water. As the pond filled during the fall rainy season, striped mud turtles returned to the pond.

Recorded terrestrial movements of males and juveniles in the Everglades National Park were restricted to the fall wet season (Meshaka and Blind, 2001). In the lower Florida Keys, Dunson (1992) found that adult striped mud turtles moved to terrestrial retreats on land as brackish ponds dry and became too saline. Most hatchlings can be found on land, moving from upland to wetland, from January to March, but a few hatchlings also can be found traveling on land from early to late fall (Meshaka and Blind, 2001; Wilson, unpubl. data). Hatchling movements typically follow heavy rain.

GROWTH AND REPRODUCTION

Growth and Longevity. — Few data are available on growth of striped mud turtles. Because striped mud turtles appear to have a bimodal annual activity pattern (spring and fall), two annuli are often produced in any given year, which makes aging this species difficult (Iverson, 1979). Growth rates have been reported for six hatchlings fed in a laboratory (Einem, 1956) and for four captive adults (Praschag, 1983). A recaptured adult female at Lake Conway grew from 89 to 96 mm in 14.2 months (Bancroft et al., 1983). No published data are available on growth rates of hatchlings or adults in the wild. Longevity in the field is unknown, but two individuals lived in captivity for approximately 20 (Desola, 1935) and 50 yrs (Johnson, 1984; estimated to be about 10 yrs old when captured).

Size Dimorphism and Sexual Maturity. — The sexes are size dimorphic with females attaining a larger maximum CL than males. Female striped mud turtles typically grow to a maximum size of 118 mm CL (Einem, 1956; Iverson, 1979; Wygoda, 1979; Wilson, 1996); however, females in southern Florida (Miami) sometimes attain 125 mm CL (Meshaka, 1988, 1990). Males reach a maximum size of 104 mm CL (Duellman and Schwartz, 1958; Iverson, 1978). Males have a longer, thicker tail than females, a slightly concave plastron, and a patch of rough scales on each inner thigh and lower leg that may aid in grasping the female during copulation (Carr, 1952; Palmer and Braswell, 1995). Females mature at 75 to 80 mm CL, and based on counts of winter annuli (which tend to be more distinct than summer annuli), age at maturity was estimated to be between 5 and 6 yrs of age (Iverson, 1979). Males probably mature earlier and at smaller sizes (Carr, 1952).

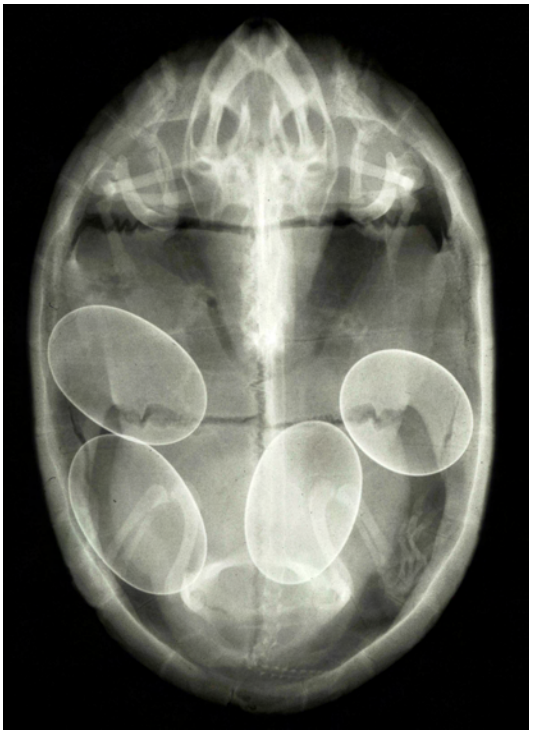

Figure 11-8. X-ray of gravid adult female striped mud turtle, *Kinosternon baurii*, from Hillsborough Co., Florida. Photo by Dawn Wilson.

Female Reproductive Cycle. — Based on dissections of museum specimens and specimens collected on roads and in water, Iverson (1979) concluded that the annual ovarian cycle of female striped mud turtles was nearly continuous. Follicular enlargement was only curtailed during a short summer quiescent period (late May through June). During the rest of the year, Iverson (1979) typically found enlarged follicles (> 7 mm) in the female reproductive tract along with oviductal eggs and/or corpora lutea. Of 50 dissected females with oviductal eggs and corpora lutea, 32% showed evidence of transuterine migration of ova which appeared to balance the number/volume of eggs in each oviduct.

Courtship. — The only record of courtship and mating behavior in striped mud turtles is from captive individuals (Sachsse, 1977). It was noted in this study that the male courted a female by sticking out his neck as far as possible and swinging his head up and down at a rate of about one swing per second. Occasionally the male would bump the snout of the female with his snout; time of copulation ranged in length from 10 to 40 minutes.

Figure 11-9. Eggs of the striped mud turtle, *Kinosternon baurii,* from Hillsborough Co., Florida, showing longitudinal cracks that occur prior to hatching, as is typical of this species. Photo by Dawn Wilson.

Nesting Season / Nest Sites / Nesting Behavior. — Nesting occurs in all months of the year, exclusive of the hottest summer months (Iverson, 1979; Meshaka and Blind, 2001). The major peak of nesting in a central Florida population is September through November, and a secondary peak occurs in June (Wilson et al., 1999). Similar peaks in nesting activity were observed in an Everglades population with most gravid females moving in October and a secondary peak of movement recorded in May (Meshaka and Blind, 2001).

In central Florida, gravid females may travel as many as several hundred meters to oviposit in upland habitats and exhibit strong nest site selection (Mushinsky and Wilson, 1992; Wilson, 1998; Wilson et al., 1999). The selection of a nesting site may take several days and females may dig in several sites before selecting a site. Females of this relatively small-bodied turtle (79–118 mm CL) tend to place nests close to vegetation and avoid open sunny sites, in contrast to relatively larger-bodied turtle species, which tend to nest in open areas of little vegetative cover (Wilson, 1998). Survivorship of embryos at nest sites selected by females has been shown to be significantly higher than survivorship of embryos placed at random sites in the habitat (Wilson, 1998). After oviposition, females often move a few meters from the nest and bury themselves under soil and/or leaf litter for as long as 35 days before moving back to their wetland habitat (Wilson et al., 1999).

Clutch Size / Reproductive Potential / Egg Size. — Female striped mud turtles usually produce several clutches of 1 to 6 (usually 2 or 3) elliptical, brittle-shelled eggs per year (Iverson, 1977; Wilson et al., 1999; Meshaka and Blind, 2001) (Fig. 11-8). Based on x-rays and dissections of females, annual clutch frequency has been estimated as 3–4 clutches in a south Florida (Everglades) population (Meshaka and Blind, 2001) and 3–6 clutches in a north Florida population (Iverson, 1979). However, based on recorded nesting events of females in a central Florida population, annual clutch frequency was recorded as 1–3 clutches (Wilson et al., 1999). Eggs range from 22.8 to 32.8 mm in length, 13.6 to 20.2 mm in width, and 3.2 to 8.0 g mass (Iverson, 1979; Wilson, 1996; Meshaka and Blind, 2001). Delayed fertilization (storage of sperm) was recorded for a female that was held in captivity without a male for 397 days (Nijs and Navez, 1990).

Incubation / Hatching / Hatchling Size. — Because the egg stage of this species is known to exhibit embryonic diapause (early arrested development; Ewert, 1991; Ewert and Wilson, 1996) and embryonic aestivation (late embryonic dormancy; Ewert, 1985), incubation times in the field may be considerably longer than those reported in the laboratory (Einem, 1956; Lardie, 1975; Iverson, 1979). In a central Florida population, eggs oviposited in the fall and winter months remain in diapause (in a gastrula stage) until spring, when they resume development and overlap the development of eggs laid in spring. Because most eggs are laid in the fall, the majority of eggs spend more than one year in the nest cavity before hatchling emergence (Wilson et al., 1999). Eggs of striped mud turtles in artificial and natural nests have been shown to exhibit mid-incubation longitudinal cracking (Einem, 1956; Iverson, 1979; Wilson, unpubl. data) (Fig. 11-9). The cracks in the eggs do not appear to hinder normal embryonic development. Hatchling striped mud turtles range from 20–25 mm CL, 17–22 mm PL, and 2.1–3.9 g (Einem, 1956; Iverson, 1979; Wilson, unpubl. data). Striped mud turtles exhibit temperature-dependent sex determination. Females are produced at hot temperatures, nearly all males at medium temperatures, and both males and females at cool temperatures (Ewert et al., 1990).

POPULATION BIOLOGY

Population Structure. — Very few data are available on the population density, biomass, and structure of striped mud turtle populations. At a study site in west-central Florida, striped mud turtles were captured in a pond, swamp and crossing a near-by road (Wygoda, 1979). The male to female sex ratio for all captures was 1:2, for swamp captures 1:1, and for road captures 1:7.

INTERSPECIFIC INTERACTIONS

Diet and Feeding. — Striped mud turtles are omnivores. They are known to consume seeds of cabbage palm (*Sabal palmetto*), leaves of the juniper, algae, snails, small bone fragments, and insects (Carr, 1952; Einem, 1956). In the lower Florida Keys, this species appears to be more carnivorous than elsewhere (Lazell, 1989).

Predation. — Few data exist on mortality of striped mud turtles. Predation on eggs is high (Wilson et al., 1999). Nest (egg) predators include a variety of mammals and snakes (Wilson, unpubl. data). All nests located in a central Florida population were destroyed by predators within 24 days of oviposition (mean = 7.6 d; Wilson et al., 1999). Many adults in a central Florida population were found to have missing legs and eyes, and damage to the shell that may be attributable to attempted predation (Wilson, unpubl. data). Juveniles and adults are commonly eaten by alligators (Delany and Abercrombie, 1986; Delany et al., 1988; D. Jackson, *pers. comm*.) and as alternate prey by the snail kite, *Rostrhamus socialbilis* (Beissinger, 1990). Of 374 turtles found as road kills on a 3.2 km stretch of road in Alachua County, Florida, striped mud turtles made up the largest percentage (37%; Smith and Dodd, 2003).

Parasites and Disease. — Most of what is known concerning disease and parasites of striped mud turtles is anecdotal. In a central Florida population, females traveling to upland habitats to oviposit often were observed with leeches attached to the limbs, carapace, and/or plastral seams (Wilson, unpubl. data). Striped mud turtles also have been reported to carry epizoophytic algae on the carapace (Loennberg, 1894; Edgren et al., 1953; Neill and Allen, 1954) and trematodes in the gut (Hughes et al., 1941).

THREATS

Striped mud turtles in Florida are relatively abundant north of the Florida Keys. Commercial harvest of this species for human consumption does not appear to be common. Because this species can be found living in such a wide range of habitat types, threats to its survival may be less than for species that live in more restricted habitats. Populations in the lower Florida Keys, however, are vulnerable because of intensive development of their habitat (Lazell, 1989), and because most of the relatively large populations are on private lands. Because mosquito-control ditches in the lower Florida Keys harbor dense populations of striped mud turtles, the lower Florida Keys populations also are threatened by the filling of these ditches in response to management plans for the endangered Key Deer (Lazell, 1989; Dunson, 1992).

Upland habitats in Florida are continually being altered and/or destroyed. Several investigators have stressed the importance of providing suitable terrestrial buffer zones around wetlands to provide adequate protection for semi-aquatic fauna (Brown et al., 1990; Semlitsch, 1998). In particular, Burke and Gibbons (1995) found that a significant increase in the buffer zone mandated by federal regulation was necessary to protect the nesting and hibernation sites of three freshwater turtle species inhabiting Carolina bays. Because female striped mud turtles have been shown to travel considerable distances (up to 240 m) from their aquatic habitats to locate suitable nesting sites (Mushinsky and Wilson, 1992; Wilson, 1998; Wilson et al., 1999), wetlands and adjacent uplands should be protected as a unit to insure adequate nesting sites for striped mud turtles.

STATUS

Kinosternon baurii in the lower Florida Keys is listed as Endangered by the Florida Fish and Wildlife Conservation Commission (http://myfwc.com/imperiledspecies/pdf/Endangered-Threatened-Special-Concern-2004.pdf).

CONSERVATION OPTIONS AND SOLUTIONS

In contrast to most turtle species that tend to nest in open areas of little vegetative cover, female striped mud turtles need the protection of vegetative cover around their relatively shallow nests to protect the developing offspring from thermal extremes (Wilson, 1998). Open sand bars, sandy beaches, or cleared upland habitats adjacent to their aquatic habitat, therefore, do not provide a suitable microclimate for the nest sites of striped mud turtles. Undisturbed or managed upland habitats consisting of lower canopy grasses and/or herbaceous plants must be protected adjacent to wetlands to assure that appropriate nesting sites are available. Also, because embryos of this species express embryonic diapause, eggs and embryos are exposed to predation for extended periods. Furthermore, investigators must be cautious when incubating eggs under controlled laboratory conditions (see incubation recommendations of Ewert and Wilson, 1996).

A thorough survey is needed of the lower Florida Keys populations to determine the proportions of striped mud turtles residing on public and private lands (Dunson, 1992). Likewise, a thorough survey is needed to determine the proportions of striped mud turtles residing in the various habitat types of the Florida Keys, especially the man-made mosquito-control ditches (Enge, 1997).

Very little is known about the reproductive ecology of striped mud turtles in the southern extent of their range, the Florida Keys. Meshaka and Blind (2001) found that much variation exists in the clutch size and body size of adult males and females in two southern Florida populations, suggesting that habitat, not latitude, may be important in controlling these two characteristics. Striped mud turtles can be found in a wide range of habitat types ranging from man-made canals to natural ponds. Considerable variation was observed between annual fecundity estimates of adult female populations studied in the canal systems of Miami and Everglades National Park (Meshaka and Blind, 2001). More work is needed on the relationships among such variables as foraging, thermoregulation, and fecundity in both natural and man-made systems.

The majority of the published research on striped mud turtles centers around females because they are most often found on land moving to and from nesting sites. Very little work has been done on males. In addition, few studies have addressed density, biomass, and population structure of striped mud turtles. A few investigators have reported on predation on adult and hatchling striped mud turtles but no data exist on survivorship within a population. More detailed studies on the population biology of striped mud turtles are needed in order to fully understand the population dynamics of this species.

The presence of roadways adjacent to aquatic habitats is also a threat to this and other species. It is recommended that the Florida Department of Transportation consider more use of measures similar to those at Payne's Prairie, near Gainesville, Florida, where a combination of barriers and wildlife tunnels greatly reduced road mortality of wildlife, including this and other turtle species (Smith and Dodd, 2003). Such actions would prevent the unnecessary loss of a demographically critical element of freshwater turtle populations, the nesting females.

The geographic range of the striped mud turtle was recently extended further west into five additional counties in the Florida panhandle (Ewert et al., 2004). No records currently exist for the presence of striped mud turtles in 11 counties in the Florida panhandle. Because of this recent range extension, more work is needed to determine if additional populations exist in the Florida panhandle. Identification of these range-extension specimens was based on a partial mid-dorsal stripe on the carapace of two of the six specimens, plastral formula scores (Lamb and Lovich, 1990), and reproductive characteristics. Because striped mud turtles in the panhandle may be lacking the characteristic striping patterns, it is important that specimens of mud turtles collected in this region be correctly identified and not confused with the sister species, *Kinosternon subrubrum*.

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LITERATURE CITED

BANCROFT, G.T., GODLEY, J.S., GROSS, D.T., ROJAS, N.N., SUTPHEN, D.A., AND MCDIARMID, R.W. 1983. The herpetofauna of Lake Conway: Species Account. Aquatic Plant Control Research Program, US Army Corps of Engineers, Miscellaneous Paper A-83-5.

BARBOUR, T. 1920. Herpetological notes from Florida. Copeia 1920:55-57.

BEISSINGER, S.R. 1990. Alternative foods of a diet specialist, the snail kite. Auk 107:327-333.

BROWN, M.T., SCHAEFER, J., AND BRANDT, K. 1990. Buffer zones for water, wetlands, and wildlife in east central Florida. CFW publication 89-07. Florida Agricultural Experiment Stations Journal Series no. T-00061. University of Florida, Gainsville.

BURKE, V.J. AND GIBBONS, J.W. 1995. Terrestrial buffer zones and wetland conservation: a case study of freshwater turtles in a Carolina Bay. Conservation Biology 9:1365-1369.

CARR, A. F., JR. 1952. Handbook of turtles: the turtles of the United States, Canada, and Baja California. Cornell Univ. Press, Ithaca, N.Y. 542 pp.

DELANY, M.F., AND ABERCROMBIE, C.L. 1986. American alligator food habits in northcentral Florida. Journal of Wildlife Management. 50:348-353.

DELANY, M.F., WOODWARD, A.R., AND KOCHEL, I.H. 1988. Nuisance alligator food habits in Florida. Florida Field Naturalist 16:86-90.

DESOLA, C.R. 1935. Herpetological notes from south-eastern Florida. Copeia 1935:44-45.

DUELLMAN, W.E. AND SCHWARTZ, A. 1958. Amphibians and reptiles of southern Florida. Bulletin of the Florida State Museum, Biological Sciences 3:181-324.

DUEVER, M. 1972. The striped mud turtle (*Kinosternon bauri* Garman) in South Carolina. Herpetological Review 4:131.

DUNSON, W.A. 1979. Salinity tolerance and osmoregulation of the key mud turtle, *Kinosternon b. baurii*. Copeia 1979:548-552.

DUNSON, W.A. 1981. Behavioral osmoregulation in the key mud turtle, *Kinosternon b. baurii*. Journal of Herpetology 15(2):163-173.

Dunson, W. . 1992. Striped mud turtle. In: Moler, P.E. (Ed.). Rare and Endangered Biota of Florida, Vol. III. Amphibians and Reptiles. Univ. Press Florida, Gainesville, pp. 105-110.

Edgren, R.A., Edgren, M. K., and Tiffany, L.H. 1953. Some north American turtles and their epizoophytic algae. Ecology 34:733-740.

Einem, G.E. 1956. Certain aspects of the natural history of the mud turtle, *Kinosternon baurii*. Copeia 1956(3):186-188.

Enge, K. M. 1997. A standardized protocol for drift-fence surveys. Tech. Report No. 14, FL Game and Fresh Water Fish Commission.

Ernst, C. H., Barbour, R.W., and Butler, J.R. 1972. Habitat preferences of two Florida turtles, genus *Kinosternon.* Transactions of the Kentucky Academy of Sciences 33:41-42.

Ernst, C. H., Barbour, R. W., and Lovich, J.E. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington. 578 pp.

Ewert, M.A. 1985. Embryology of turtles. In: Gans, C., Billett, F., and Maderson, P. F. A. (Eds.). Biology of the Reptilia, Vol. 14. John Wiley and Sons, New York, pp. 76-267.

Ewert, M.A. 1991. Cold torpor, diapause, delayed hatching and aestivation in reptiles and birds. In: Deeming, D.C., and Ferguson, M. W. J. (Eds.). Egg Incubation: Its Effects on Embryonic Development in Birds and Reptiles. Cambridge Univ. Press, pp. 173-191.

Ewert, M.A. and Wilson, D.S. 1996. Seasonal variation of embryonic diapause in the striped mud turtle (*Kinosternon baurii*) and general considerations for conservation planning. Chelonian Conservation and Biology 2:43-54.

Ewert, M.A., Etchberger, C.R. and Nelson, C.E. 1990. An apparent co-occurrence of genetic and environmental sex determination in a turtle. American Zoologist 334:56A.

Ewert, M.A., Jackson, D.R, and Guyot, G. 2004. *Kinosternon baurii* (Striped Mud Turtle). Herpetological Review 35(1):80.

Frair, W. 1972. Taxonomic relations among chelydrid and kinosternid turtles elucidated by serological tests. Copeia 1972:97-108.

Garman, S. 1891. On a tortoise found in Florida and Cuba, *Cinosternum baurii*. Bulletin of the Essex Institute 23:141-144.

Gibbons, J.W., Nelson, D.H., Patterson, K.K., and Greene, J.L. 1979. The reptiles and amphibians of the Savannah River Plant in west-central South Carolina. In: Forsythe, D.M. and Ezell, W.B., Jr. (Eds.). Proceedings First South Carolina Endangered Species Symposium, pp. 133-142.

Huestis, D.L. and Meylan, P.A. 2004. The turtles of Rainbow Run (Marion County, Florida): observations on the genus *Pseudemys*. Southeastern Naturalist 3:595-612.

Hughes, R.C., Higginbotham, J.W., and Clary, J.W. 1941. The trematodes of reptiles, Part II, Host catalogue. Proceedings of the Oklahoma Academy of Sciences 21:35-43.

Iverson, J.B. 1977. Reproduction in freshwater and terrestrial turtles of north Florida. Herpetologica 33:205-212.

Iverson, J.B. 1978. Variation in striped mud turtles, *Kinosternon baurii* (Reptilia, Testudines, Kinosternidae). Journal of Herpetology 12(2):135-142.

Iverson, J.B. 1979. The female reproductive cycle in north Florida *Kinosternon baurii* (Testudines: Kinosternidae). Brimleyana 1:37-46.

Iverson, J.B. 1991. Phylogenetic hypotheses for the evolution of modern Kinosternine turtles. Herpetological Monographs 5:1-27.

Iverson, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately printed, 363 pp.

Iverson, J.B. 1998. Molecules, morphology and mud turtle phylogenetics (family Kinosternidae). Chelonian Conservation and Biology 3:113-117.

Johnson, E.W. 1984. A longevity record for the mud turtle (*Kinosternon bauri*). Proceedings of the Staten Island Institute of Arts and Sciences 33:47-48.

Karl, S.A. and Wilson, D.S. 2001. Phylogeography and systematics of the mud turtle, *Kinosternon baurii*. Copeia 2001:797-801.

Killebrew, F. 1975. Mitotic chromosomes of turtles. III. The Kinosternidae. Herpetologica 31:398-403.

Lamb, T. 1983. The striped mud turtle (*Kinosternon bauri*) in South Carolina, a confirmation through multivariate character analysis. Herpetologica 39(4):383-390.

Lamb, T. and Lovich, J. 1990. Morphometric validation of the striped mud turtle (*Kinosternon baurii*) in the Carolinas and Virginia. Copeia 1990(3):613-618.

Lardie, R.L. 1975. Observations on reproduction in *Kinosternon*. Journal of Herpetology 9(2):257-260.

Lazell, J. D. 1989. Key mud turtle. In: Lazell, J.D. (Ed.). Wildlife of the Florida Keys. Island Press. Washington, DC, pp. 172-176.

Loennberg, E. 1894. Notes on reptiles and batrachians collected in Florida in 1892 and 1893. Proceedings of the U.S. National Museum 17:317-339.

Lovich, J.E. and Lamb, T. 1995. Morphometric similarity between the turtles *Kinosternon subrubrum hippocrepis* and *K. baurii*. Journal of Herpetology 29:621-624.

Meshaka, W.E., Jr. 1988. Reproductive characteristics of south Florida *Sternotherus odoratus* and *Kinosternon baurii* (Testudines: Kinosternidae). Proceedings of the Arkansas Academy of Science 42:111.

Meshaka, W.E., Jr. 1990. Correction - in the article “Reproductive characteristics of south Florida *Sternotherus odoratus* and *Kinosternon baurii* (Testudines: Kinosternidae)” that appeared in Vol. 42 (1988) pp. 111. Proceedings of the Arkansas Academy of Science 44:136.

Meshaka, W.E., Jr. and Blind, E. 2001. Seasonal movements and reproduction in the striped mud turtle (*Kinosternon baurii*) from the southern everglades, Florida. Chelonian Conservation and Biology 4(1):75-80.

Mitchell, J.C. 1994. The Reptiles of Virginia. Smithsonian Institution Press, Washington, DC.

Mushinsky, H.R. and Wilson, D.S. 1992. Seasonal occurrence of *Kinosternon baurii* on a sandhill in central Florida. Journal of Herpetology 26(2):207-209.

Neill, W.T. 1958. The occurrence of amphibians and reptiles in saltwater areas, and a bibliography. Bulletin of Marine Science of the Gulf and Caribbean 8:1-97.

Neill, W.T. and Allen, E.R. 1954. Algae on turtles: some additional considerations. Ecology 35:581-584.

Nijs, J. and Navez, C. 1990. Delayed fertilization in the striped mud turtle, *Kinosternon baurii*. Bulletin Chicago Herpetological Society 25:146.

Palmer, W.M. and Braswell, A.L. 1995. Reptiles of North Carolina. University of North Carolina Press.

Praschag, R. 1983. Zur Fortpflanzungsbiologie von *Kinosternon baurii* (Garman, 1891) mit Bemerkungen über eine abnorme Gelegehäufigkeit und die Embryonalentwiklung (Testudines: Kinosternidae). Salamandra 19:141-150.

Sachsse, W. 1977. Normale und pathologische Phänomene bei Zuchtversuchen mit Schildkröten, hier anhand von *Kinosternon bauri* (Reptilia, Testudines, Kinosternidae). Salamandra 13:22-35.

Seidel, M. E., Iverson, J. B., and Adkins, M. D. 1986. Biochemical comparisons and phylogenetic relationships in the family Kinosternidae (Testudines). Copeia 1986:285-294.

Semlitsch, R.D. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conservation Biology 12:1113-1119.

Serb, J.M., Phillips, C.A., and Iverson, J.B. 2001. Molecular phylogeny and biogeography of *Kinosternon flavescens* based on complete mitochondrial control region sequences. Molecular Phylogenetics and Evolution 18:149-162.

Sites, J.W., Jr., Bickham, J.W., Haiduk, M.W., and Iverson, J.B. 1979. Banded karyotypes of six taxa of kinosternid turtles. Copeia 1979:692-698.

Smith, L.L., and Dodd, C.K., Jr. 2003. Wildlife mortality on Highway U.S. 441 across Payne's Prairie, Alachua County, Florida. Florida Scientist 66:128-140.

Spix, J.B. 1824. Animalia nova sive Species novae Testudinum et Ranarum quas in itinere per Brasiliam annis MDCCCXVII-MDCCCXX jussu et auspiciis Maximiliani Josephi I. Bavariae Regis. München: F.S. Hübschmann

Stejneger, L. 1925. New species and subspecies of American turtles. Journal of the Washington Academy of Sciences 15:462-463.

Tuberville, T.D., Gibbons, J.W., and Greene, J.L. 1996. Invasion of new aquatic habitats by male freshwater turtles. Copeia 1996:713-715.

Uzzell, T.M., Jr. and Schwartz, A. 1955. The status of the turtle *Kinosternon bauri palmarum* Stejneger with notes on variation in the species. Journal of the Elisha Mitchell Society 71:28-35.

Walker, D., Moler, P.E., Buhlmann, K.A., and Avise, J.C. 1998. Phylogeographic patterns in *Kinosternon subrubrum* and *K. baurii* based on mitochondrial DNA restriction analyses. Herpetologica 54:174-184.

Wharton, C.H. and Howard, J.D. 1971. Range extensions for Georgia amphibians and reptiles. Herpetological Review 3(4):73.

Wilson, D.S. 1996. Nesting ecology and nest site selection in the striped mud turtle, *Kinosternon baurii*, in central Florida. Ph.D. Dissertation, University of South Florida, Tampa.

Wilson, D.S. 1998. Nest-site selection: microhabitat variation and its effects on the survival of turtle embryos. Ecology 79:1884-1892.

Wilson, D.S., Mushinsky, H.R., and McCoy, E.D. 1999. Nesting behavior of the striped mud turtle, *Kinosternon baurii* (Testudines: Kinosternidae). Copeia 1999(4):958-968.

Wygoda, M.L. 1979. Terrestrial activity of the striped mud turtle, *Kinosternon baurii* (Reptilia, Testudines, Kinosternidae) in west-central Florida. Journal of Herpetology 13(4):469-480.

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Kinosternon subrubrum – Eastern Mud Turtle

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Summary. – The eastern mud turtle, *Kinosternon subrubrum*, is one of two species of mud turtle found in Florida. Unlike the striped mud turtle (*K. baurii*), the eastern mud turtle shows significant geographic variation in morphology, with three subspecies known, all occurring in Florida (*K. s. subrubrum*, *K. s. steindachneri*, and *K. s. hippocrepis*). One of these, *K. s. steindachneri*, is endemic to the Florida peninsula and differs significantly from the other subspecies in morphology, genetics, and possibly reproductive biology. This aquatic subspecies is found in lentic or slow-moving systems, with a preference for well-vegetated, sandy-bottomed littoral zones. It is active night or day, with a possible reduction in activity during the summer. Its reduced plastron may be in response to a more extensive aquatic existence. Males of this form are larger in body size than females. In northern Florida, the reproductive season of *K. subrubrum* is longer and the clutch sizes are smaller than in more northerly populations. In central Florida, *K. s. steindachneri* is sensitive to certain kinds of habitat modifications. Habitat destruction and modification, such as roads adjacent to canals and ditches, negatively impact what is otherwise an uncommon and ecologically poorly-studied Florida endemic subspecies.

Conservation Status. – FNAI Global - G5 (Demonstrably Secure), State - S5 (Demonstrably Secure); ESA Federal - Not Listed; State - Not Listed; CITES - Not Listed; IUCN Red List - Not Listed (LC-Least Concern).

Species Recognition. — *Kinsoternon subrubrum* is a small, low-domed turtle in which the carapace of adults is usually dark brown to black, sometimes olive (Figs. 12-1, 12-2). The plastron is dull yellow to dark brown (Fig. 12-3) and the head and neck are dark green or brown and may be mottled or striped with yellow (Figs. 12-1, 12-4). The average size of adults is about 85 mm carapace length (CL) with the largest individuals reaching lengths of 120 mm. Hatchlings are black above and may have a bright yellow, orange, or red plastron (hence the name *subrubrum*) with some dark central markings (Fig. 12-5). The plastron of subadult and adult *K. subrubrum* has a double hinge, permitting complete closure of the shell in some individuals. The anterior hinge is between the epiplastra and hyoplastra (the entoplastron is absent); the posterior hinge is between the hypoplastra and xiphiplastra. The feet are webbed and the legs are dark and without markings. Coloration of the head differs among the three subspecies found in Florida. Two of the subspecies, *K. s. subrubrum* (eastern mud turtle) and *K. s. steindachneri* (Florida mud turtle), have plain heads or dull yellow mottling, whereas *K. s. hippocrepis* (Mississippi mud turtle) has two yellow stripes on each side of the head.

The carapace is oval in dorsal view, smooth, and rounded on the sides. It has 11 marginal scutes on each side, and the 10th marginal extends further dorsally than the others. The first vertebral scute is longer than wide and does not contact the 2nd marginal scute. The other vertebrals (2–5) are usually wider than long. The plastral formula is anal > abdominal > humeral > femoral >< gular > pectoral (Ernst and Barbour, 1989); however, this formula is highly variable in species to which it has been applied (Lovich and Ernst, 1989; Lovich et al., 1991; Ernst et al., 1997). The snout protrudes slightly and the upper jaw is hooked. Tails of adult males are larger than those of females and have a claw-like tip. Enlarged scales are present on the inner side of the hind legs of males. *Kinosternon subrubrum* can be difficult to distinguish from *K. baurii* in the panhandle of Florida, Georgia, the Carolinas, and Virginia because of the frequent absence of carapacial stripes in *K. baurii* in these areas (Duever, 1972; Lamb, 1983; Lamb and Lovich, 1990; Ewert et al., 2004). However, *K. baurii* generally retains distinct head stripes throughout its range (Fig. 11-4), in contrast to *K. s. subrubrum* that lacks them.

Taxonomic History. — More than 20 scientific names have been used for *Kinosternon subrubrum* since its original description as *Testudo subrubra* by Lacépède in 1788 (Iverson, 1977a). All of these changes have been of a nomenclatural nature and have not been the result of phylogenetic reassignment. No serious challenges have been made in the scientific literature to suggest any uncertainty about *K. subrubrum* being a single species comprised of three subspecies: the eastern mud turtle (*K. s. subrubrum*), the Florida mud turtle (*K. s. steindachneri*), and the Mississippi mud turtle (*K. s. hippocrepis*). Notwithstanding morphological similarity between *K. s. hippocrepis* and *K. bauri* (Lamb and Lovich, 1995), an examination of mitochondrial DNA (mtDNA) of *K. subrubrum* identified sets of genotypes that generally conformed to the known distributions of these subspecies (Walker et al., 1998).

Figure 12-1. Adult Florida mud turtle, *Kinosternon subrubrum steindachneri,* from Monroe Co., Florida. Photo by John Iverson.

DISTRIBUTION

Geographic Distribution. — *Kinosternon subrubrum* ranges from southeastern New York (Craig et al., 1980; Iverson, 1986; Klemens, 1990, Klemens, 1993) southward along the Atlantic Coastal Plain and Piedmont through peninsular Florida and along the Gulf Coastal Plain to central Texas (Ernst et al., 1994). It occurs over large areas of the South, with a northward extension in the range following the Mississippi and Ohio River valleys to southwestern Indiana, southern Illinois, and southeastern Missouri. Disjunct populations occur in northwestern Indiana (Grant, 1935; Stille, 1947; Minton, 1972) and northwestern Missouri (Iverson, 1986). In the northeastern United States, the northern limit of the range of *K. subrubrum* roughly parallels the southern terminus of the Wisconsin glaciation (Craig et al., 1980).

Kinosternon s. subrubrum occupies the eastern portion of the species' range. The southern terminus of its distribution is in northern Florida, where it intergrades with *K. s. hippocrepis* in the western panhandle (Carr, 1940) and with *K. s. steindachneri* in northern peninsular Florida (Conant and Collins, 1991). The geographic range of the Florida endemic, *K. s. steindachneri,* includes only those counties in peninsular Florida south of the Suwannee River and Jacksonville (Fig. 12-6) to the southern tip of the state (but not the Florida Keys). The range of *K. s. hippocrepis* lies mostly west of the Mississippi River but has an eastward extension through southern Mississippi and southern Alabama into the panhandle of Florida where it has a wide zone of intergradation with *K. s. subrubrum* (Ernst et al., 1994).

In Florida *K. subrubrum* has been recorded from all but 11 counties (Fig. 12-6), six of which are northern localities

Figure 12-2. Juvenile Florida mud turtle, *Kinosternon subrubrum steindachneri,* from Lee Co., Florida. Photo by Dick Bartlett.

Figure 12-3. Plastron of adult *Kinosternon subrubrum steindachneri,* from Monroe Co., Florida. Photo by John Iverson.

Figure 12-4. Head of adult Florida mud turtle, *Kinosternon subrubrum steindachneri*, from Levy Co., Florida. Photo by John Iverson.

where the three subspecies meet. It presumably occurs in all counties. Unlike *K. baurii*, it does not appear to be native to the Florida Keys.

Ecological Distribution. — *Kinosternon subrubrum* inhabits shallow and generally lentic freshwater systems, but also occurs in tidal marshes (Ernst et al., 1994). In Florida, *K. s. subrubrum* occurs in small streams, drainage ditches, and ponds (Carr, 1940). Habitats of *K. s. steindachneri* are similar but also include sloughs and marshes (Carr, 1940) and canals (Duellman and Schwartz, 1958). This form generally avoids the Everglades system of marsh and prairie, where it is replaced in abundance by *K. baurii* (Duellman and Schwartz, 1958; Meshaka et al., 2000). However, individuals have been collected on the Tamiami Trail (Duellman and Schwartz, 1958), a road that parallels a canal that bisects the Everglades. In west-central Florida, it was the only kinosternid turtle found in a shallow basin marsh-sandy upland association (Enge and Wood, 2001). Systematic sampling of *K. s. steindachneri* in a central Florida lake (Bancroft et al., 1983) revealed a distinct preference by this form for vegetated littoral zones (emergent species with thin-stalks). It was almost always in shallow water (> 95% of free-ranging animals in < 1.6 m depth) with a sandy bottom and thick vegetative cover, especially *Potamogeton illinoensis*. In Alabama farm ponds, this species did not venture more than 5 m from shore and no deeper than 1 m (Scott, 1976). Ernst et al. (1972) have pointed out that *K. s. steindachneri* can occupy aquatic habitats that fluctuate widely in their pH on a daily basis. This species appears to avoid major rivers, streams, and spring runs (Gibbons, 1983, Huestis and Meylan, 2004).

Figure 12-5. Left. Plastron of hatchling *Kinosternon subrubrum subrubrum* from Okaloosa Co., Florida. Photo by John Jensen. **Right.** Plastron of hatchling *K. s. steindachneri* from Alachua Co., Florida. Photo by John Iverson.

HABITAT RELATIONS

Activity. — *Kinosternon subrubrum* is active at night and during the day. The summer diel cycle for *K. s. hippocrepis* in Oklahoma (Mahmoud, 1969) and *K. s. steindachneri* in Florida (Ernst et al., 1994) is bimodal. They are active in the morning between about 0400-0900 hrs with a peak from 0500-0800 and in the evening from 1600-2200 hrs with a peak at 1900-2000 hrs. In central Florida *K. s. steindachneri* was captured by day and night with no apparent seasonal component to its diel activity (Bancroft et al., 1983).

Seasonality. — The activity season of *K. subrubrum* is shortest in northern populations and longest in the south (Ernst et al., 1994). This species is generally active from April to November in New York (Nichols, 1947), and April to October in Oklahoma (Mahmoud, 1969) and Virginia (Ernst et al., 1994). Although it is active year-round in Florida, Bancroft et al. (1983) reported peaks in activity in early summer and fall. However, Iverson (1979) reported that only 2 of 62 *K. subrubrum* that he examined from north and central Florida had been collected between June 15 and August 15 and he suggested that this species may be inactive in warm summer months.

Movements and Home Range. — In central Florida, the average distance moved by *K. s. steindachneri* between captures was 32.8 m (Bancroft et al., 1983). Telemetric studies of home range at this site suggested that home ranges were small as they are elsewhere in the range of this species. In Oklahoma, the average home range of both sexes of *K. s. hippocrepis* was 0.05 ha (Mahmoud, 1969).

Terrestrial Activity. — Terrestriality is well developed in *K. s. subrubrum*, however, Carr (1940) considered *K. s. steindachneri* to be "very aquatic; rarely seen on land." This species will move overland in response to drought (Gibbons, 1983; Ernst et al., 1994), for hibernation (Buhlmann and Gibbons, 2001), and for nesting. *Kinosternon s. subrubrum* in South Carolina spent up to 142 consecutive days on land and moved up to 600 m (Bennett et al., 1970). In another study in the same vicinity, individuals remained on land for an average of 170 days (Buhlmann and Gibbons, 2001). Many reports document overland movements that included periods when the individuals were burrowed in soil or under leaves (Richmond, 1945; Skorepa and Ozment, 1968; Gibbons, 1970; Mount, 1975); but these reports do not pertain to *K. s. steindachneri*. There is no mention of this subspecies being found on land during a three-year study of the herpetofauna of a lake system in central Florida (Bancroft et al., 1983). The primary differences between *K. s. steindachneri* and the other Florida subspecies is the reduced

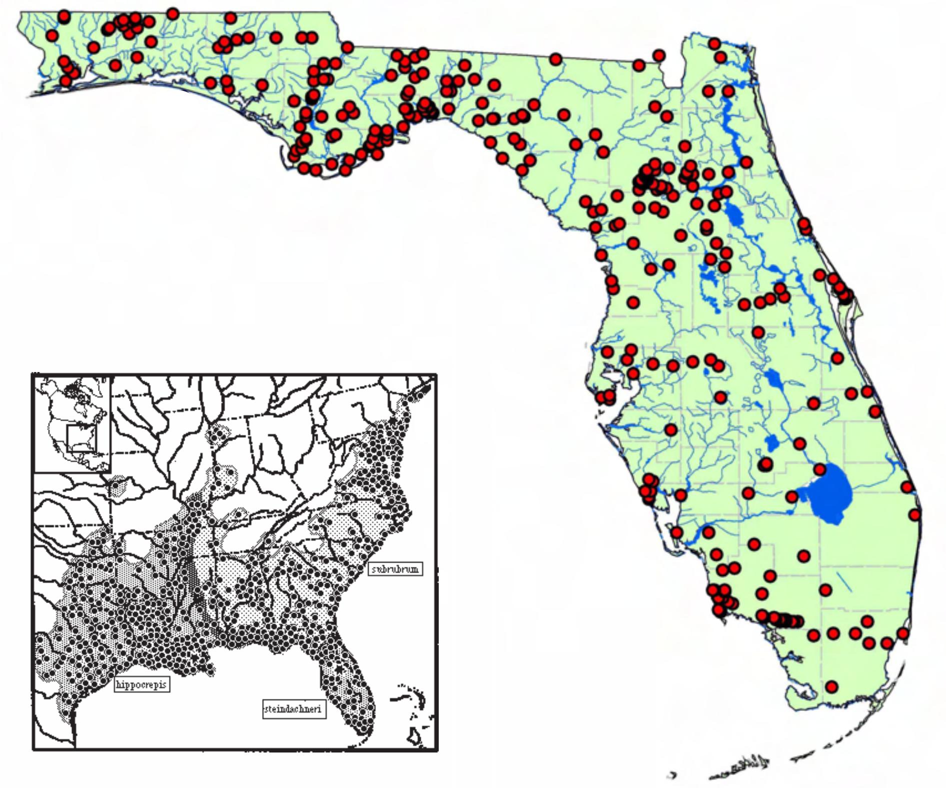

Figure 12-6. Available distribution records for *Kinosternon subrubrum* from Florida. Inset: distribution records from entire range of *K. subrubrum* (adapted from Iverson, 1992; distribution in inset map not current for Florida as presented here).

plastron and reduced bridge (Fig. 12-7), both of which might imply a more aquatic existence.

The duration of overland movements associated with nesting by this species in South Carolina was influenced by rainstorms (Burke et al., 1994). Gravid females exited the water, buried themselves until a rainstorm, and then laid their eggs. Most post-partum females then waited for another rainstorm before returning to water. The relationship between movements and rainfall in Florida populations has not been documented.

GROWTH AND REPRODUCTION

Growth and Maturation. — Ernst et al. (1973) used a mixed sample of all three subspecies to describe growth in this species in Florida. They found that growth rates were variable at all ages but in general declined from a maximum of about 11 mm/yr in posthatchlings of both sexes, to around 5 mm/yr as each sex approached maturity. Females from Florida were projected to mature at 6–8 yrs of age and 66–75 mm plastron length (PL); males in that study matured at 4–5 yrs of age at 53–60 mm PL (Ernst et al., 1973). Both sexes of *K. s. subrubrum* mature in 4–6 yrs in South Carolina (Gibbons, 1983); and females mature after 6–8 yrs in Arkansas (Iverson, 1979). Outside of Florida, adults of both sexes reach maturity at around 70–80 mm CL.

Size Dimorphism. — No sexual size dimorphism was apparent in a large sample of *K. subrubrum* in South Carolina (Gibbons and Lovich, 1990), except that at a given CL, adult males have smaller plastrons than females. Thus, Ernst et al. (1973) reported that the largest males they studied in peninsular Florida, with PL in the 90–99 mm range, had an average CL of 112.5 mm, whereas the largest females (also in the 90–99 mm PL range) had an average CL of 103.4 mm. In a central Florida population of *K. s. steindachneri*, adult females averaged 93.8 mm CL (*n* = 29), and were significantly smaller than males that averaged 101.2 mm CL (*n* = 53) (Bancroft et al., 1983). Iverson (1979) reported that in a sample of this species from throughout Florida, the largest male was 114.3 mm CL while the largest female was 106.0 mm CL. These data suggest the possibility that *Kinosternon s. steindachneri* has sexual size dimorphism, while *Kinosternon s. subrubrum* does not. In this regard, Lovich and Lamb (1995) found little body size sexual dimorphism in *K. s. subrubrum*, male-dominated dimorphism in *K. s. steindachneri*, and female-dominated dimorphism in *K. s. hippocrepis*. We suggest that this variability in body size dimorphism, unknown among other turtle subspecies, speaks to the biologically meaningful differences among these three recognized forms.

Reproductive Cycles. — In the central United States, the testis of *K. subrubrum* increased to its greatest size during June–August, and was smallest in size during September–December (Mahmoud and Klicka, 1972). Since mating in this species appears to occur in the early spring (see below), this species appears to fit a post-nuptial pattern of spermatogenesis. The female reproductive cycle of *K. subrubrum* is similar to that of most other temperate-zone turtles. Follicu-

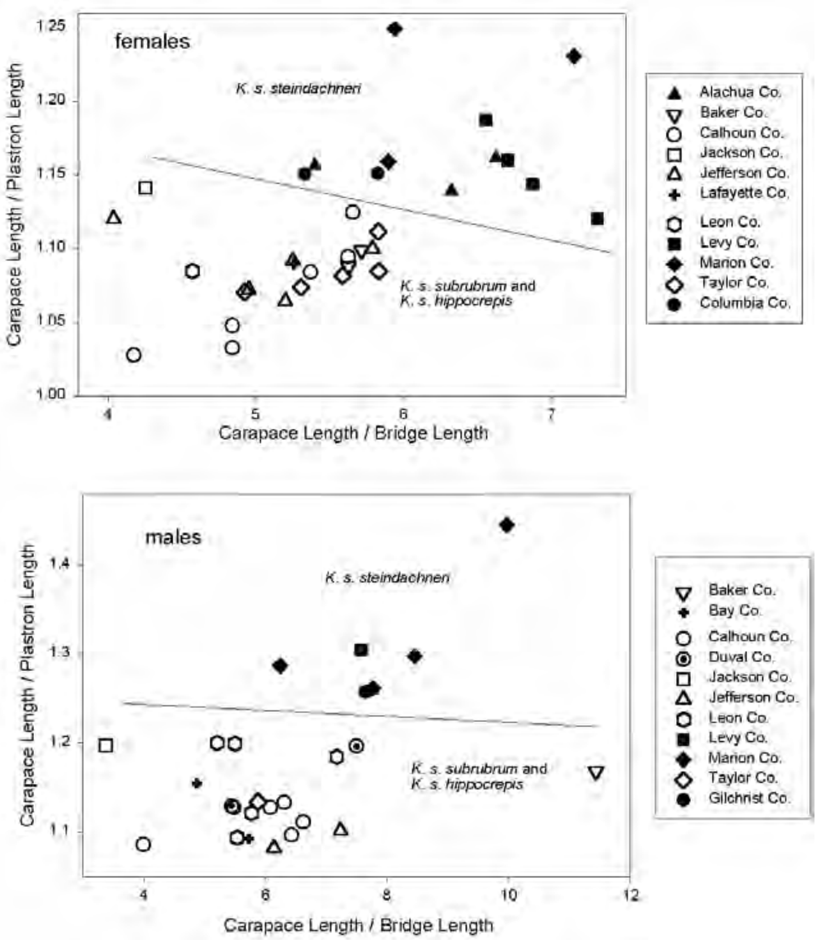

Figure 12-7. Two measures of the specialized plastron of *Kinosternon subrubrum steindachneri*. The bridge is narrow and the entire plastron smaller in both male and female *steindachneri* when compared to *subrubrum* and *hippocrepis* type turtes from elsewhere in Florida. Counties with closed figures are south of the Suwannee drainage, counties with open figures are north of the Suwannee drainage (see p. 32 for county map).

lar growth begins in late summer or early fall and increases rapidly the following spring (Iverson, 1979).

Courtship. — Copulation is preceded by an approach by the male to the tail of the female. If the female is receptive, the male moves alongside the female nudging the bridge area of the plastron, presumably to make contact with the musk glands. If the female continues to be receptive, the male then mounts her from behind and above, and while *in copula*, bites the female (Mahmoud, 1967).

Mating Season / Nesting Season. — Mating takes place during March–May, occurring earliest in the south. It typically takes place under water (Ernst et al., 1994). Although Carr (1940) reported that nesting in this species occurred from mid-March to mid-June, additional study in north Florida indicates that nesting can occur from October to June (Iverson, 1977b, 1979). Nesting seasons are progressively shorter in northern populations, with the frequency of nesting highest in the summer throughout most of the range (Gibbons 1983). Thus, *K. s. steindachneri* may have a reproductive season that is longer than northern populations.

Eggs. — The eggs of *K. s. subrubrum* are brittle-shelled with mean dimensions of 26.2 x 15.6 mm and a mean mass of 3.9 g (Congdon and Gibbons, 1985). Egg dimensions of *K. s. steindachneri* have been given as 27.5–29.2 x 16.8–18.0 mm (Carr, 1940) and 26.7 x 16.0 mm (Iverson, 1979).

Clutch Size and Reproductive Potential. — Clutch size in this species has been shown to vary geographically, seasonally, and as a function of female size (Iverson, 1979; Gibbons, 1983). Throughout the geographic range of the species it varies from 1–8 eggs (Gibbons, 1983) with larger clutches being more common in northern populations. Modal clutch size is 2 or 3 eggs (Gibbons, 1983). In north Florida, an average of 3.5 eggs is produced in each clutch (Iverson, 1977b, 1979).

In South Carolina, the species is capable of producing up to 3 clutches in a single season, although one clutch is most common (Frazer et al., 1991). In that same population, approximately half of the adult females nest each year. Across its geographic range, *K. subruburm* can lay up to 4 clutches annually (Gibbons, 1983). In Arkansas, this species appears to produce at least 3 clutches each year (Iverson, 1979). The number of clutches produced each year in Florida is not known.

Incubation and Hatching. — Incubation period is approximately 100 days, and in South Carolina hatchlings overwinter in the nest and emerge the following spring (Gibbons and Nelson, 1978). It is unknown if hatchlings of

Florida populations overwinter. Iverson (1979) reported that hatchling mud turtles in Florida are 18–23 mm CL. In a mixed sample of *K. s. subrubrum* and *K. s. steindachneri* from Florida, female hatchlings averaged 18.2 mm PL, and male hatchlings averaged 17.6 mm PL (Ernst et al., 1973).

POPULATION BIOLOGY

Density and Biomass. — Population densities of 36.5 turtles/ha in a Carolina bay, and 8.2 turtles/ha in a farm pond, are known from South Carolina (Gibbons, 1983; Congdon et al., 1986). In Oklahoma, densities of 159 and 259 turtles/ha were estimated to occur in a creek (Mahmoud, 1969). Ernst et al. (1994) suggested that permanent streams support more *K. subrubrum* than do temporary ones.

Population Structure. — In South Carolina, the sex ratio was found to be 1:1 (Gibbons, 1983), whereas in three Oklahoma populations of *K. subrubrum*, females outnumbered males (1:1.5, 1:1.5, 1:1.8) (Mahmoud, 1969). Ernst et al. (1994) questioned to what extent sampling bias is responsible for the much greater numbers of adults captured than juveniles in this species.

Population Dynamics. — Observations on this species in South Carolina suggest that annual variation in reproductive output is more strongly influenced by clutch frequency than clutch size (Gibbons, 1983). Clutch size did not vary annually but the number of clutches and the number of females laying in a given year did.

Survivorship. — Maximum survivorship in the wild is thought to exceed 30 yrs (Gibbons, 1983). A life table was constructed for *K. subrubrum* in South Carolina (Frazer et al., 1991). In their study site, annual survivorship for both sexes approached 90%, and some turtles were projected to survive to nearly 40 yrs of age. This value represented an average of two estimates that ranged from over 20 yrs to almost 50 yrs of age.

INTERSPECIFIC INTERACTIONS

Community Structure. — In central and southern Florida, *K. s. steindachneri* can be rare. For example, in a central Florida lake, *K. s. steindachneri* was the fourth most abundant species but accounted for less than 2% of the total of 4832 turtles captured (Bancroft et al., 1983). As measured by collection records and natural history observation cards in Everglades Regional Collection Center of Everglades National Park, *K. s. steindachneri*, like *Sternotherus odoratus*, is scarce as compared to *K. baurii* in the southern Everglades.

Diet and Feeding. — *Kinosternon subrubrum* is an omnivore (Mahmoud, 1968; Ernst et al., 1994), and its diet is similar in widely separated populations. Insects, crustaceans, and molluscs dominated the diet of this species in Oklahoma (Mahmoud, 1968), North Carolina (Brown, 1992), and central Florida (Bancroft et al., 1983).

Predation. — *Kinosternon subrubrum* is preyed upon by a wide range of vertebrates, such as kingsnakes (*Lampropeltis getula*), opossums (*Didelphis*), raccoons (*Procyon*), crows (*Corvus*), and gar (*Lepisosteus*), and by at least one invertebrate (blue crabs, *Callinectes*; Ernst et al., 1994). The dull brown carapace of *K. subrubrum* and its preference for vegetation cover could serve to enforce crypsis as a primary defense mechanism. Once provoked, however, this potentially large-headed turtle with a sharp beak and long neck can formidably defend itself.

THREATS

Documented Threats. — An intensive study of a central Florida lake system over a 3-yr period showed a marked reduction in the number of captures of this species in an area of shoreline where they were common at the beginning of the study (Bancroft et al., 1983). The disappearance of this species correlated with the development of the lakeshore margin for a housing complex. This study showed that this species can be quite specific in its habitat requirement and may disappear when those requirements are not met. The need to carefully evaluate the populations of *K. subrubrum* in Florida is illustrated by parallel threats to this species at the other end of its geographic range and their catastrophic results. *Kinosternon s. subrubrum* was once known from at least 20 sites in New York, primarily on Long Island, but also from Staten Island and the Hudson River estuary (Latham, 1969; Craig et al., 1980; A. Breisch, *pers. comm.*). At present only five populations are extant on Long Island and a small population may persist on Staten Island (A. Breisch, *pers. comm.*). This represents a loss of 75% of New York mud turtle populations since the 1930s. All known populations on Long Island are in wetland systems that include a combination of fresh and brackish water. Declines have been attributed to wetland destruction, mosquito ditching, habitat fragmentation, road mortality, loss of upland nesting and hibernation sites, as well as catastrophic hurricanes that have increased salinity regimes in coastal lagoons by permanently breaching barrier beaches.

Potential Threats. — With the exception of loss of hibernacula, the threats faced by *K. s. subrubrum* in New York are magnified in Florida where increased rates of poorly regulated development can have direct and cascading effects that negatively impact this species. In light of delayed maturity, low fecundity, and potential for terrestrialism from roadside canals and ditches, habitat destruction (including saltwater intrusion) and increasing numbers of highways (and the cars that use them), pose what we believe are the two greatest risks to this species in Florida.

Furthermore, a near absence of population studies of this species in Florida precludes an evaluation of its status anywhere in the state. Because *K. s. steindachneri* is a Florida endemic whose geographic range is subsumed by a rapidly developing state, and because the other two forms reside primarily elsewhere with large geographic ranges, we rank *K. s. steindachneri* highest on the list of the three forms for which population status warrants evaluation. We also recommend that evaluation of this subspecies be conducted in a way that includes its interactions with the other forms in northern Florida. Principally, we ask what is the status of *K. s. steindachneri* in Florida and what enforces the narrow band of intergradation among the three subspecies in northern Florida? The peninsular subspecies is genetically (Walker et al, 1998) and morphologically distinct (see section on subspecies), appears to be less terrestrial, shows sexual size dimorphism (not present in *K. s. subrubrum*) and may exhibit a unique reproductive pattern for the species. These differences suggest that *K. s. steindacherni* should be treated at least as a separate conservation priority, if not a separate species.

STATUS

Kinosternon subrubrum is not a listed species. We have no data to warrant changing its status. However, a careful assessment of its abundance in peninsular Florida (especially the distinct and endemic subspecies *K. s. steindachneri*) is needed at this time.

CONSERVATION OPTIONS AND SOLUTIONS

Based upon the results of a telemetry study conducted in an increasingly suburban area of Long Island, Cavanaugh and Loop (1988) recommended that terrestrial habitats be protected for a distance of 540 ft (457.2 m) from the edge of wetlands inhabited by *K. s. subrubrum*. Upland areas within this distance were to be cleared of any migration barriers including culverts, curbs, and ditches, and other structures modified to preclude capture or obstruction of migrating turtles. Cavanaugh and Loop cautioned that increased subdivision activities would result in road mortality as well as elevated predation rates by human commensal species, such as raccoons, opossums, and feral dogs and cats. Burke and Gibbons (1995) demonstrated that a 275 m buffer zone protected 100% of nest and hibernation sites for *K. subrubrum* in a South Carolina population and that a 73 m buffer zone would protect 90% of those sites. We echo their concerns in Florida, where habitat modification and destruction by humans has never been greater and whose effects are demonstrably devastating to a species that has otherwise received little attention in the state.

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LITERATURE CITED

BANCROFT, G.T., GODLEY, J.S., GROSS, D.T., ROJAS, N.N., SUTHPHEN, D.A., AND MCDIARMID, R.W. 1983. The herpetofauna of Lake Conway: species accounts. U.S. Army Corps Eng., Misc. Pap., A-83-5. Army Engineer Waterways Experiment Station, Vicksburg, Miss.

BENNETT, D.H., GIBBONS, J.W., AND FRANSON, J.C. 1970. Terrestrial activity in aquatic turtles. Ecology 51:738-740.

BROWN, E.E. 1992. Notes on amphibians and reptiles of the western piedmont of North Carolina. Journal of the Elisha Mitchell Scientific Society 108:38-54.

BUHLMANN, K.B., AND GIBBONS, J.W. 2001. Terrestrial habitat use by aquatic turtles from a seasonally fluctuating wetland: Implications for wetland conservation boundaries. Chelonian Conservation and Biology 4(1):115-127.

BURKE, V.J., GIBBONS, J.W., AND GREENE, J.L. 1994. Prolonged nesting forays by common mud turtles (*Kinosternon subrubrum*). American Midland Naturalist 131:190-195.

BURKE, V.J., AND GIBBONS, J.W. 1995. Terrestrial buffer zones and wetland conservation: a case study of freshwater turtles in a Carolina Bay. Conservation Biology 9:1365-1669.

CARR, A.F. 1940. A contribution to the herpetology of Florida. University of Florida Publications, Biological Sciences Series 3:1-118.

CAVANAUGH, J., AND LOOP, K. 1988. A radio-telemetry study of *Kinosternon subrubrum subrubrum*, Wehrmans Pond, Southampton, New York. Unpublished report, Endangered Species Unit, New York Department of Environmental Conservation, Delmar, N.Y.

CONANT, R., AND COLLINS, J.T. 1991. Reptiles and Amphibians: Eastern/Central North America. Houghton Mifflin. New York, NY.

CONGDON, J.D., AND GIBBONS, J. W. 1985. Egg components and reproductive characteristics of turtles: relationships to body size. Herpetologica 41:194-205.

CONGDON, J.D., GREENE, J.L., AND GIBBONS, J. W. 1986. Biomass of freshwater turtles: a geographic comparison. American Midland Naturalist 115:165-173.

CRAIG, R.J., KLEMENS, M.W., AND CRAIG, S.S. 1980. The northeastern range limit of the eastern mud turtle *Kinosternon s. subrubrum* (Lacépède). J. Herpetol. 14:295-297.

DUELLMAN, W.E., AND SCHWARTZ, A. 1958. Amphibians and reptiles of southern Florida. Bulletin of the Florida State Museum, Biological Sciences 3:181-324.

DUEVER, M. 1972. The striped mud turtle *(Kinosternon bauri* Garman) in South Carolina. Herpetological Review 4:131.

ENGE, K.M. AND K.N. WOOD. 2001. Herpetofauna of Chinsegut Nature Center, Hernando County, Florida. Florida Scientist 64:283-305.

ERNST, C.H. AND BARBOUR, R.W. 1989. Turtles of the World. Smithsonian Institute Press. Washington, D.C.

ERNST, C.H., BARBOUR, R.W., AND BUTLER, J.R. 1972. Habitat preference of two Florida turtles, genus *Kinosternon*. Transactions of the Kentucky Academy of Sciences 33:41-42.

ERNST, C.H., BARBOUR, R.W., ERNST, E.M., AND BUTLER, J.R. 1973. Growth of the mud turtle, *Kinosternon subrubrum*, in Florida. Herpetologica 29:247-250.

ERNST, C.H., BARBOUR, R.W., ERNST, E.M., AND BUTLER, J.R. 1977. Subspecific variation and intergradation in Florida *Kinosternon subrubrum*. Herpetologica 30:317-320.

ERNST, C.H., LOVICH, J.E., and BARBOUR, R.W. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington, U.S.A.

ERNST, C. H., J. E. LOVICH, A. F. LAEMMERZAHL, AND S. SEKSCIENSKI. 1997. A comparison of plastron scute lengths among members of the box turtle genera *Cuora* and *Terrapene*. Chelonian Conservation and Biology 2:603-607.

Ewert, M. A., Jackson, D. R., and Guyot, G. 2004. *Kinosternon baurii* (striped mud turtle). Herpetological Review 35(1):80.

Frazer, N.B., Gibbons, J.W., and Greene, J.L. 1991. Life history and demography of the common mud turtle *Kinosternon subrubrum* in South Carolina, USA. Ecology 72:2218-2231.

Gibbons, J.W. 1970. Terrestrial activity and the population dynamics of aquatic turtles. American Midland Naturalist 83:404-414.

Gibbons, J.W. 1983. Reproductive characteristics and ecology of the mud turtle, *Kinosternon subrubrum* (Lacépède). Herpetologica 39:254-271.

Gibbons, J.W., and Nelson, D.H. 1978. The evolutionary significance of delayed emergence from the nest by hatchling turtles. Evolution 32:297-303.

Gibbons, J.W., and Lovich, J.E. 1990. Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). Herpetological Monographs 4:1-29.

Grant, C. 1935. Secondary sexual differences and notes on the mud turtle, *Kinosternon subrubrum* in northern Indiana. American Midland Naturalist 16:798-800.

Huestis, D.L. and Meylan, P.A. 2004. The turtles of Rainbow Run (Marion County, Florida): observations on the genus *Pseudemys*. Southeastern Naturalist 3:595-612.

Iverson, J.B. 1977a. *Kinosternon subrubrum*. Catalogue of American Amphibians and Reptiles 193.1-193.4.

Iverson, J.B. 1977b. Reproduction in freshwater and terrestrial turtles of North Florida. Herpetologica 33:205-212.

Iverson, J.B. 1979. Reproduction and growth of the mud turtle, *Kinosternon subrubrum* (Reptilia, Testudines, Kinosternidae) in Arkansas. Journal of Herpetology 13:105-111.

Iverson, J.B. 1986. A checklist with distribution maps of the turtles of the world. Privately printed by Paust Printing. Richmond, Indiana. 283 pp.

Iverson, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately printed, 363 pp.

Klemens, M.W. 1990. The herpetofauna of southwestern New England. Ph.D. diss., Univ. Kent, Canterbury, UK.

Klemens, M.W. 1993. The amphibians and reptiles of Connecticut and adjacent regions. Bulletin of the State Geological and Natural History Survey of Connecticut 112:1-318.

Lamb, T. 1983. The striped mud turtle (*Kinosternon baurii*) from South Carolina: a confirmation through multivariate character analysis. Herpetologica 39:383-390.

Lamb, T., and Lovich, J. 1990. Morphometric validation of the striped mud turtle (*Kinosternon baurii*) in the Carolinas and Virginia. Copeia 1990(3):613-618.

Lamb, T., and Lovich, J. 1995. Morphometric similarity between the turtles *Kinosternon subrubrum hippocrepis* and *K. baurii*. Journal of Herpetology 29:621-624.

Latham, R. 1969. The eastern mud turtle and stinkpot on eastern Long Island. Engelhardtia 2:1-2.

Lovich, J. E. and C. H. Ernst. 1989. Variation in the plastral formulae of selected turtles with comments on taxonomic utility. Copeia 1989: 304-318.

Lovich, J. E., A. F. Laemmerzahl, C. H. Ernst, and J. F. McBreen. 1991. Relationships among turtles of the genus *Clemmys* (Reptilia: Testudines: Emydidae) as suggested by plastron scute morphology. Zoologica Scripta 20:425-429.

Mahmoud, I.Y. 1967. Courtship behavior and sexual maturity in four species of kinosternid turtles. Copeia 1967:314-319.

Mahmoud, I.Y. 1968. Feeding behavior in kinosternid turtles. Herpetologica 24:300-305.

Mahmoud, I.Y. 1969. Comparative ecology of the kinosternid turtles of Oklahoma. Southwestern Naturalist 14:31-66.

Mahmoud, I.Y., and Klicka, J. 1972. Seasonal gonadal changes in kinosternid turtles. Journal of Herpetology 6:183-189.

Meshaka, W.E., Jr., Loftus, W.B., and Steiner, T. 2000. The herpetofauna of Everglades National Park. Florida Scientist 63:84-103.

Minton, S.A., Jr. 1972. Amphibians and Reptiles of Indiana. Monographs of the Indiana Academy of Sciences 3:1-346.

Mount, R.H. 1975. The reptiles and amphibians of Alabama. Agricultural Experiment Station. Auburn University.

Nichols, J.T. 1947. Notes on the mud turtle. Herpetologica 3:147-148.

Pope, C.H. 1939.Turtles of the United States and Canada. Alfred A. Knopf., Inc. N.Y.

Richmond, N.D. 1945. Nesting habits of the mud turtle. Copeia 1945:217-219.

Scott, A.F. 1976. Aquatic and terrestrial movements of farm pond populations of the eastern mud turtle (*Kinosternon subrubrum subrubrum*) in east-central Alabama. PhD Dissertation, Auburn University.

Skorepa, A.C., and Ozment, J.E. 1968. Habitat, habits, and variation of *Kinosternon subrubrum* in southern Illinois. Transactions of the Illinois State Academy of Sciences 61:247-251.

Stille, W.T. 1947. *Kinosternon subrubrum subrubrum* in the Chicago area. Copeia 1947:143.

Walker, D., Moler, P. E., Buhlmann, K. A., and Avise, J. C. 1998. Phylogeographic patterns in *Kinosternon subrubrum* and *K. baurii* based on mitochondrial DNA restriction analyses. Herpetologica 54:174-184.

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Sternotherus minor – Loggerhead Musk Turtle

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Summary. – **The loggerhead musk turtle, *Sternotherus minor,* is a small, highly aquatic species that occupies a variety of habitats throughout its range in the southeastern United States. It is a conspicuous and common freshwater turtle in the spring runs, streams, and rivers of northern and western Florida. As a result, it has been subject to some pressure from commercial collectors for sale in the pet trade. Nevertheless, these turtles are prolific and populations appear to be stable in certain Florida river systems. In fact, loggerhead musk turtles reach among the highest densities known for any species of turtle. Under ideal habitat conditions at a head spring in northwest Florida, loggerhead musk turtle density was reported to be 2857 per hectare. *Sternotherus minor* can be distinguished from other musk and mud turtles by the presence of a weak single plastral hinge, dark markings against a light background on the head, two barbels on the chin, three keels on a brown carapace, and overlapping carapacial scutes. In northern Florida, mating has been observed in the field in September, November, March, and April. Female receptivity to mating peaks from April to May. Females in north central Florida may lay 2 or 3 clutches of eggs each year, with a maximum of 5 clutches. These are laid between September and July, sometimes at communal nest sites. Typical clutch size ranges from 1–5 eggs (averaging 3), with the number of eggs positively correlated with female carapace length. Incubation takes 61–119 days, with slower embryonic development resulting from cool weather. Sex is determined by mean incubation temperature; only females result from temperatures of 30ºC or higher, and mostly females are produced at temperatures 27–30ºC and 24ºC or less. Mostly males are produced at intermediate temperatures of 25–26ºC. Given their ability to thrive and reproduce in suitable freshwater habitat, loggerhead musk turtles are not likely to become seriously threatened unless the water quality in the rivers and streams deteriorates.**

Conservation Status. – **FNAI Global - G5 (Demonstrably Secure), State - S4 (Apparently Secure); ESA Federal - Not Listed; State - Not Listed; CITES - Not Listed; IUCN Red List - Not Listed (LC-Least Concern).**

Species Recognition. — The loggerhead musk turtle, *Sternotherus minor*, is a small species (up to 14.5 cm carapace length; Enge and Foster, 1986; Camp, 1986) with a highly domed brown shell with black flecks or streaks (Fig. 13-1). The brown head can be quite large, with a pointed snout and obvious, dark dots and/or blotches (Figs. 13-1, 13-2, 13-3). This species lacks prominent facial stripes. The skin is brown to gray with dark brown or black markings (Iverson, 1977b). The underside of the neck and limbs has a pink or reddish tinge, blending to brownish orange on the lower jaw and cream brown on the upper jaw (Tinkle, 1958a). Two barbels are present on the chin (Iverson, 1977b). The plastron is unmarked; pinkish to dull orange in color in juveniles, fading to a duller shade of orange, cream, or yellow in adults (Fig. 13-4), but may be stained a darker color. The carapace has overlapping scutes. The reduced plastron (Fig. 13-4) has 11 plastral scutes, including a single gular scute. There is a single, indistinct plastral hinge between the abdominal and pectoral scutes. The pectoral scutes are square in shape. The first vertebral scute does not contact the second marginal, and the tenth and eleventh marginal scutes are raised above the line formed by more anterior marginals (Iverson, 1977b).

Hatchlings have a median keel and two obvious lateral keels on a carapace that is colored as those of adults. The three keels become less apparent with increasing size and age (Tinkle, 1958a). The plastron of new hatchlings is bright pink (Fig. 13-5).

The adult head is adapted to consuming gastropods, with sizeable musculature and wide dentary surfaces for crushing shells. Adults have a pugnacious disposition and bite readily (Carr, 1952, among others). Like other musk turtles, a gland containing a malodorous yellowish secretion is located at the base of each limb near the bridge (Ehrenfeld and Ehrenfeld, 1973).

Sternotherus minor can be distinguished from other musk and mud turtles by the presence of a single plastral hinge (vs. two hinges in most mud turtles, genus *Kinosternon*), dark markings against a light background on the head (vs. prominent facial stripes), two barbels on the chin (vs. on the neck or on the neck and chin), three keels (vs. one keel), a basically brown carapace (vs. a basically black shell), and overlapping carapacial scutes (vs. carapacial scutes not

Figure 13-1. Juvenile loggerhead musk turtle, *Sternotherus minor*, from Marion Co., Florida. Photo by Alice Monroe.

overlapping those more posterior) (Iverson 1977b: Conant and Collins, 1998).

Taxonomic History. — The loggerhead musk turtle was originally described by Agassiz (1857) as *Goniochelys minor* based on a series of specimens from the neighborhood of Mobile, Alabama; Columbus, Georgia; and New Orleans, Louisiana. The type-locality was restricted to Columbus, Georgia by Schmidt (1953). Strauch (1862) assigned this turtle to the genus *Aromochelys*, but it was reassigned to the genus *Sternotherus* by Stejneger (1923). Carr (1952) referred to the loggerhead musk turtle as *Sternotherus carinatus minor*. However, Tinkle (1958a) resurrected the name *Sternotherus minor* in his review of the genus.

Turtles of the genus *Sternotherus* are members of the family Kinosternidae, subfamily Kinosterninae. "*Sternotherus*" is derived from the Greek "*sternon*" meaning "chest" and "*thairos*" meaning "hinge," in reference to the hinged plastron. The plastron opens anteriorly to permit the large head size, the consumption of large gastropods, and the defensive stance of retracting the head while keeping the jaws agape (Bramble et al., 1984). The species name *minor* refers to its smaller size when compared with *S. carinatus* (Agassiz, 1857).

There are two subspecies of *Sternotherus minor*: *Sternotherus m. minor*, the loggerhead musk turtle, and *Sternotherus m. peltifer*, the stripe-necked musk turtle (Smith and Glass, 1947). Intergradation between the subspecies occurs in Alabama and west Florida (Mount, 1975; Iverson, 1977a). Because of its similarity and complementary distribution in northern Alabama,

Figure 13-2. Head of juvenile loggerhead musk turtle, *Sternotherus minor*, from Liberty Co., Florida. Photo by Dick Bartlett.

Figure 13-3. Head of adult loggerhead musk turtle, *Sternotherus minor*, from Marion Co., Florida. Photo by Tim Walsh.

Figure 13-4. Plastral view of adult female **(left)** and adult male **(right)** loggerhead musk turtles, *Sternotherus minor*, from Marion Co., Florida. Photo by Tim Walsh.

Sternotherus depressus, the flattened musk turtle, was considered a subspecies of *S. minor* by some authors (e.g., Tinkle and Webb, 1955; Mount, 1975); however, it is now regarded as a distinct species (Seidel and Lucchino, 1981; Seidel et al., 1986; Ernst et al., 1988; Walker et al., 1995; Iverson, 1998).

Preliminary work on geographic variation in DNA sequences has been done (Walker et al., 1995). However, additional studies with more complete geographic sampling are needed in order to compare with the patterns of morphological variation on which the subspecies are based.

Sternotherus minor is known to hybridize with *S. odoratus* in captivity (Folkerts, 1967), and suspected hybrids have been found in the field in the Rainbow River in Florida (Iverson, unpubl. data). *Sternotherus minor* is suspected of hybridizing with *S. depressus* in Alabama (Estridge, 1970).

Figure 13-5. Plastral view of hatchling loggerhead musk turtle, *Sternotherus minor*, from Gilchrist Co., Florida. Photo by John Iverson.

DISTRIBUTION

Geographic Distribution. — The loggerhead musk turtle is found in the southeastern United States (Iverson, 1977b, 1992) from southwestern Virginia (Mitchell, 1994), eastern Tennessee (Scott et al., 2000), and western North Carolina (Palmer and Braswell, 1995), south through eastern Georgia (Williamson and Moulis, 1994) to central Florida (Iverson and Etchberger, 1989), and west through Alabama (Mount, 1975) to the Pearl River system of south-central Mississippi and Washington Parish, Louisiana (Dundee and Rossman, 1989).

The distribution of the loggerhead musk turtle in Florida includes at least 29 counties from as far south as the central peninsula close to Orlando (Seminole County) in the St. John's drainage system and further west in the Withlacoochee River system in Sumter County (Stevenson and Crowe, 1992). It is found across the northern one-third of the peninsula and west throughout the panhandle (Iverson and Etchberger, 1989; Fig. 13-6). The population in the Withlacoochee drainage in Marion, Citrus, and Sumter counties appears to have been introduced to that river system in the late 1950s (Meylan et al., 1992; Iverson and Paull, 2004; Huestis and Meylan, 2004). A single record for Highlands County (Meshaka and Gallo, 1990) probably represents an introduction.

Ecological Distribution. — The loggerhead musk turtle is a highly aquatic species that inhabits spring runs, creeks, rivers, oxbows, swamps, and sinkhole ponds (review in Ernst et al., 1994). It favors areas around submerged fallen trees and snags where sandy or rocky substrate is present (Jackson, 1988, among others). In northern and central Florida, it is most abundant in clear spring runs (Marchand, 1942; Carr, 1952; Berry, 1975; Iverson, 1977a; Cox and Marion, 1978, 1979; Meylan et al., 1992; Onorato, 1996; Guntermann, 1998).

HABITAT RELATIONS

Activity. — Loggerhead musk turtles are not strong swimmers and are more often seen walking along the bottom rather than swimming (Ditmars, 1936). Carr (1952) observed that their sometimes furious swimming motions only produced slow progress. In clear artesian springs and spring runs in Florida, loggerhead musk turtles are often seen walking on the river bottom or swimming in the aquatic vegetation at depths of 2 to 4 m (JBI and RTZ, *pers. obs.*). Hensley (1994) observed an adult male *S. minor* at 12.5 m depth in a spring-fed sinkhole at Manatee Springs State Park, Florida, feeding on a crayfish; after several seconds, the turtle retreated beneath a log 13 m deep. This observation suggests that *S. minor* can forage at considerable depths when those habitats are available. Based on trapping evidence (e.g.,

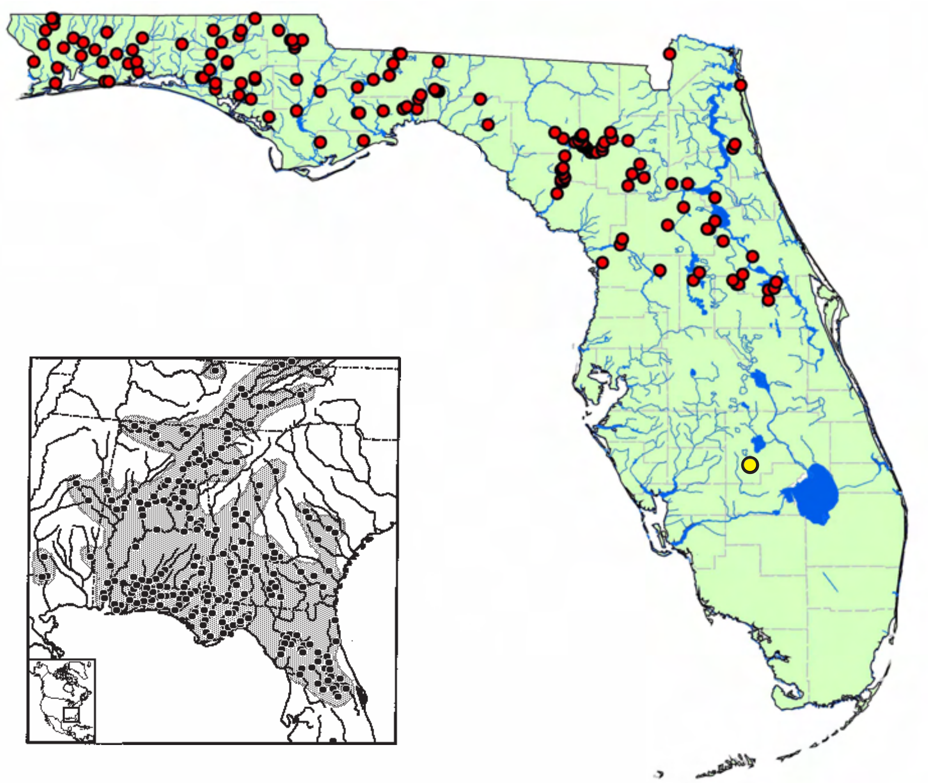

Figure 13-6. Known distribution records for the loggerhead musk turtle, *Sternotherus minor*, in Florida. Inset: distribution records from entire range of *S. minor* (adapted from Iverson, 1992; distribution in inset map not current for Florida as presented here). This species is thought to be introduced to the Withlacoochee River (south) system (Meylan et al., 1992; Huestis and Meylan, 2004). The southeastern-most record in Highlands Co. (yellow dot) probably represents an escaped individual.

Tinkle, 1958b), loggerhead musk turtles feed mostly at dawn and dusk; however, they have also been observed foraging throughout the daytime, as well as late after dark (P. Meylan and JBI, *pers. obs.*).

Hatchling, juvenile, and adult loggerhead musk turtles often seek shelter in submerged crevices or root-snags (Jackson, 1988). They also occupy crayfish burrows and submerged hollow logs as retreats (JBI and P. Meylan, *pers. obs.*). During periods of cooler weather they remain hidden in the safety of these retreats (RTZ, *pers. obs.*).

Loggerhead musk turtles spend nearly all of their time in water; terrestrial records are very rare (JBI, unpubl. data). They have the ability to remain submerged indefinitely in well-oxygenated water (Belkin, 1968). Ditmars (1936) kept several in a deep aquarium with no means of leaving the water. The turtles came to the surface occasionally, but spent most of the time crawling about the bottom of the tank. Similar to many other highly aquatic turtles, this species can obtain dissolved oxygen from water via the buccopharyngeal lining (Belkin, 1968; Gatten, 1984).

In the Florida springs which have constantly warm water temperatures, *S. minor* appears to be active year-round (Iverson, 1978; Cox and Marion, 1978; Jackson, 1988; Huestis and Meylan, 2004). Farther north, loggerhead musk turtles hibernate in cold weather, from December to February, probably in soft mud bottoms of waterways, in submerged rock crevices, and in the bank burrows of muskrats (Ernst et al., 1994).

Carr (1952) thought this species to be extremely fond of basking, and willing to undergo considerable exertion to climb to the highest branch, stump, or cypress knee available to bask. One male loggerhead musk turtle that he observed was balanced precariously for over an hour on the pointed tip of a cypress knee, almost two meters above the water, its every muscle quivering in the effort to remain in the sunlit area. Later authors (Tinkle, 1958b; Mount, 1975; Mitchell, 1994) have cited the climbing ability of *S. minor*, but suggested that the turtle's basking behavior is poorly developed. On several occasions RTZ saw loggerhead musk turtles basking in April or May on fallen tree snags or in shallow water (entire carapace exposed and dry) along the Apalachicola River. At least four captured specimens had leeches attached to the soft tissue of their leg sockets or on the fleshy portion of their plastron. Basking in *S. minor* may be a function of season or environmental temperature, but this behavior by the turtle may also be an attempt to rid itself of parasites (RTZ, *pers. obs.*).

GROWTH AND REPRODUCTION

Growth. — There is considerable variation in growth rate across the range of *S. minor*. In west Florida, males reached 55 mm CL in 5.6 yrs (Cox et al., 1991), but in the Rainbow River in north Florida they attained that size in only 2 yrs (Onorato, 1996). Similarly, in west Florida females reached 80 mm CL in 8 yrs (Cox et al., 1991), but in north

Florida they attained that size in 4.5–5 (Onorato, 1996) or 5–6 yrs (Iverson, 1978).

Dimorphism. — Females grow significantly larger than males, averaging about 4 mm longer in CL (Iverson, 1977a). Carr (1952) noted that the long thickened tail of male loggerhead musk turtles is muscular and prehensile, with a terminal spine, and is often folded in two places in order to fit beneath the posterior edge of the carapace. Adult females have much shorter, slimmer tails than males. The anal opening is posterior to the carapacial margin in males (Ernst et al., 1994), and concavity of the plastron in males is slight or absent (Carr, 1952). A patch of tuberculate scales on the posterior surface of the crus and thigh of each hind leg is present in adult males (Iverson, 1977b). Both mature males and females (especially in *S. m. minor*) have noticeably enlarged (megacephalic) heads (Tinkle, 1958b). Nolan (1991) reported that the heads of adult females are noticeably paler than the darker heads of males.

Maturation. — Some geographic variation in sexual maturity exists, but in all cases males reach sexual maturity first and at smaller sizes than females. In northwest Florida, males mature at 55 mm CL (40 mm plastron length) in an average of 5.6 yrs (Cox et al., 1991), and those in central Florida mature at ca. 60 mm CL (ca. 45 mm PL) at 3 yrs (Etchberger and Stovall, 1990).

Females mature in northwest Florida at 70 mm CL (ca. 50 mm PL) after 8 yrs (Cox and Marion, 1978; Cox et al., 1991); those in north central Florida (Iverson, 1978) and in central Florida (Etchberger and Ehrhart, 1987) mature at ca. 80 mm CL (ca. 60 mm PL), but after 4.5–5.0 and 6 yrs, respectively.

Male Sexual Cycle. — In male *S. minor* from central Florida the testes enlarge from March through June as spermatogenesis begins, and maximum testis size occurs from August to October (Etchberger and Stovall, 1990). Testicular regression occurs from October to December, and by March the testes have shrunk to the size of those of juvenile males.

Agonistic behavior has been observed between males (Jackson, 1969). Captive adult males kept together in the presence of a female had to be separated due to aggressive behavior; however, the males were not aggressive toward males of other species (Nolan, 1991). Notching on the carapace edges of this species was abandoned as a marking method at Rainbow Run because in older males the margin of the shell becomes badly eroded (P. Meylan, *pers. comm.*; see also Jackson, 1965). At least part of this erosion may be due to aggressive encounters between adults (P. Meylan, *pers. comm.*).

Female Sexual Cycle. — Follicular enlargement begins in late August or September and continues through the following June (Iverson, 1978). Ovulation and oviposition occur from September or October through June or July (Iverson, 1978; Cox and Marion, 1978; Etchberger and Ehrhart, 1987). In Florida, females have no distinct period of ovarian regression during the year; however, there is a brief period of quiescence in late July and August (Iverson, 1978).

Courtship and Mating. — Courtship and mating of loggerhead musk turtles have been observed in the laboratory and in the field (Sachsse, 1977; Cox et al., 1980; Bels and LiBois, 1983; Nolan, 1991; Bels and Crama, 1994; Kirkpatrick, 1997). All wild matings were observed in early to mid-morning, and mated pairs remained completely submerged and partly concealed, and appeared to favor shaded areas (Cox et al., 1980). If disturbed, the pairs quickly uncoupled (Cox et al., 1980). As many as six males have been observed trying to mate with a single female at the same time (Ashton and Ashton, 1985). In northern Florida, mating has been observed in the field in September, November, March, and April (Cox, 1978; Cox et al., 1980). Female receptiveness to mating in northern Florida peaked from April to May; however, in captivity mating may occur virtually year-round (Nolan, 1991; Schilde, 2001). Loggerhead musk turtles reproduce readily in captivity (Rödel, 1989; Rogner 1996; Guntermann, 1998; Schilde, 2001).

No elaborate pre-copulatory behaviors have been observed on the part of the male (Cox et al., 1980; Bels and Libois, 1983; Nolan, 1991; Bels and Crama, 1994). The male rapidly approaches the female, sniffing at her cloaca and bridge. The female sometimes attempts to escape, with the male in close pursuit with his head extended toward her shell or head but without contact. Occasionally the male will face the female's head and swing his head side to side in front of her nose. In addition, he may bite at her shell or legs during sniffing or prior to mounting. The male then mounts her shell from behind and grasps the edge of her carapace with all four feet, curling his tail under hers to bring the cloacae into contact. The male then positions himself nearly perpendicular to the female's carapace, and mutual tail grasping precedes intromission. Occasionally the female may begin moving away during copulation, dragging the male upside down behind her, but still attached. In the laboratory, the entire sequence from initiation to completion took 2.67 hours (Cox et al., 1980). Coitus lasted 30 min in captives observed by Nolan (1991).

Nesting. — The only known regular terrestrial activity in this species occurs when females emerge for egg-laying (Mount, 1975; Cox and Marion, 1978; Gunterman, 1998). In northern Florida, gravid females apparently leave the water on nesting forays only in the early morning (0300 to 0900 hrs) following rain events (Cox and Marion, 1978). As a predator avoidance strategy, females may bury themselves while nesting, perhaps for several days (Cox and Marion, 1978). Eggs are sometimes laid singly or in groups in shallow holes or scrapes in the soil, especially at the base of trees or beside logs (Carr, 1952; Mount, 1975). However, most nests examined by Cox and Marion (1978) in northern Florida were located between 1 and 3.5 m above the water, and up to 40 m from the water's edge. They found the eggs at a depth of 8–15 cm below ground surface, thus supporting their speculation that females may bury themselves to nest (Cox and Marion 1978).

Eggs. — Eggs are elliptical, 21.2–33.0 mm long and 12.7–20.0 mm wide, and weigh between 2.0 and 6.7 g

(Cox and Marion, 1978; Iverson, 1978; Packard et al., 1984; Etchberger and Ehrhart, 1987; Nolan, 1991; Mitchell, 1994; Nagle et al., 1998). Egg size is generally not correlated with female body size (Iverson, 1978; Etchberger and Ehrhart, 1987); however, egg mass estimated from egg length and width was correlated with body size in one population in northwest Florida (Cox and Marion, 1978). Eggshells are about 0.32 mm thick (Packard et al., 1984), and the brittle eggshell is translucent pink when first laid, changing to white and opaque as the embryonic membranes develop (Iverson, 1978). Eggshells may crack late in incubation and extrude a viscous liquid without negative consequences to embryonic development (Iverson, 1978).

Clutch Size and Reproductive Potential. — Females in north central Florida may lay 2 or 3 clutches each year, with a maximum of 5 clutches, between September and July (Iverson, 1977c; Cox and Marion, 1978; Iverson, 1978; Etchberger and Ehrhart, 1987). Clutch size ranges from 1–5 eggs, averaging 3, with the number of eggs positively correlated with female carapacial length (Sachsse, 1977; Cox and Marion, 1978; Iverson, 1978; Etchberger and Ehrhart, 1987). Tinkle (1958b) estimated that female *S. m. minor* could produce an average of 6.3 eggs a year, but no precise localities were provided. In northwest Florida, Cox and Marion (1978) estimated annual reproductive potential to be 9.2; whereas Iverson (1978) estimated it to be 7.5 in north-central Florida, and Etchberger and Ehrhart (1987) estimated it to be 5.9 in central Florida. These data suggest a latitudinal increase in reproductive potential in this species.

Incubation and Hatching. — Incubation lasts for 61–119 days, with slower embryonic development resulting from chilling (Iverson, 1978; Ewert, 1985; Ewert and Nelson, 1991; Nolan, 1991). Sex determination in all kinosternids is also a function of incubation temperature (Ewert and Nelson, 1991). For *S. minor* only females result from temperatures of 30ºC or higher, and mostly females are produced at temperatures 27–30ºC and 24ºC or less (Ewert and Nelson, 1991). Mostly males are produced at intermediate temperatures (25–26ºC; Ewert and Nelson, 1991).

Hatchlings. — Hatchling CL is 22–30 mm; PL is 16–21 mm (Cox and Marion, 1978; Iverson, 1978). Neill (1948) found two loggerhead musk turtle eggs that a plow had unearthed on a hillside in August in Georgia. When opened, the eggs contained fully formed hatchling turtles with some yolk still attached. The hatchlings made only feeble movements, but were both fully able to void their musk glands, a defensive reaction that may reduce predation. Lehmann (1984) reported twin turtles from the same egg in captivity.

POPULATION BIOLOGY

Density and Biomass. — Loggerhead musk turtles reach among the highest densities known for any species of turtle (Iverson, 1982). Marchand (1942) reported seeing 500 or more in a day of snorkeling in the Ichetucknee River in Columbia Co., in north Florida. Cox and Marion (1979) reported the density of loggerhead musk turtles under ideal conditions in a northwest Florida head spring to be 2857 per ha. Meylan et al. (1992) estimated 127 *S. m. minor* per ha in Rainbow Run, Marion County, Florida at a site where none were found in the 1940s (Marchand, 1942). In the Tallapoosa River in northern Alabama, Guyer and Herndon (1992) reported an estimated density for *S. m. peltifer* of 105 per ha.

Population Structure. — The sex ratio of both adults and juveniles fluctuates around 1:1 (Tinkle, 1958b; Cox, 1978; Guyer and Herndon, 1992; Meylan et al., 1992). In a population study at Rainbow Run, Onorato (1996) found that juveniles (5 yrs or less) represented more than 65% of the total population, although some turtles did live beyond 21 yrs. He postulated that this was a result of humans removing the largest individuals for pets or predation on adult turtles by alligators.

INTERSPECIFIC INTERACTIONS

Community Structure. — Meylan et al. (1992) studied the turtle community in Rainbow Run, Marion Co., Florida, determined population size/structure for *S. minor* and *S. odoratus* (common musk turtle), and compared their results to a study of the same site by Marchand (1942). They found a major shift in abundance from *Pseudemys* spp. to *Sternotherus* spp. over the 50 year interval. *Sternotherus minor*, which was not observed during Marchand's study, made up 66% of the turtle composition in 1990; *S. odoratus* increased from 11.2% of the turtle community to 25% over the period.

Diet and Feeding. — The diet of wild juvenile *S. minor* includes insects, millipedes, spiders, earthworms, snails, crayfish, clams, fish, carrion, aquatic plants, and sometimes algae (Tinkle, 1958a; Folkerts, 1968; Ashton and Ashton, 1985). Like other musk turtles, they are primarily carnivorous and will swallow all kinds of bait (Carr, 1952). There is an ontogenetic shift in food preferences for *S. m. minor* from an insectivorous to molluscivorous diet (Tinkle, 1958b). Adults primarily consume snails and clams (Carr, 1952; Tinkle, 1958b; Folkerts, 1968; Palmer and Braswell, 1995), and develop powerful jaw musculature and expanded jaw surfaces to crush the shells of their prey.

This species may show cannibalistic tendencies. A captive juvenile *S. m. minor* killed and partially consumed 2 juvenile *Trachemys scripta*, a hatchling *S. m. minor* and a juvenile *S. m. peltifer* (Ernst et al., 1994).

Competition. — Carr (1952) noted that populations of this turtle were so large in some areas as to beg the question of how they all found enough to eat. Where concentrated populations of *S. minor* occurred, Carr (1952) found few or no specimens of *S. odoratus*.

Sternotherus minor is similar morphologically to other *Sternotherus*, especially *S. odoratus*, with which it is sometimes microsympatric. Where they co-occur, there is considerable overlap in their use of available food resources, and some specimens of *S. minor* lack the usual enlarged head and jaws which is typical of adults elsewhere in Florida (Berry, 1975).

Predation. — Nest destruction can be caused by small mammals, crows, and reptiles (Ernst et al., 1994), although no direct observations have been made of egg predation. In captivity, northern scarlet snakes (*Cemophora coccinea copei*) ate the eggs of *S. minor* and other species of turtles readily and with frequency (RTZ, *pers. obs.*). The only confirmed non-human predator on adults is *Macrochelys temminckii*, the alligator snapping turtle (Pritchard, 1989). However, *S. minor* can detect and avoid alligator snapping turtles in their habitat by chemosensory means (Jackson, 1990). Ernst et al. (1994) also speculated that alligators consume these musk turtles. Britson and Gutzke (1993) theorized that the brightly colored plastron of hatchlings might be a warning coloration.

Parasites. — Endoparasites of loggerhead musk turtles include roundworms, tapeworms, nematodes, trematodes, lung flukes, and protozoans (Johnson, 1967; Gibbons and Esch, 1970; Ernst and Ernst, 1977, 1978; Cox et al., 1988; Kirkpatrick, 1997). Wild-caught specimens are sometimes covered with algae (Ernst and Barbour, 1972), and are often infested with leeches (Ernst et al., 1994; RTZ, *pers. obs.*).

THREATS

Increased boat traffic on rivers and springs disturbs the habitat of these turtles. The wakes of speedboats and/or commercial tugboats pulling barges causes increased turbidity of the water and shore-line erosion, thus adversely impacting aquatic vegetation and reducing the long-term suitability of the habitat.

Musk turtles are frequently caught on baited hooks by fishermen (Carr, 1952), which often leads to the death or serious injury of the individual when the hook is removed. Several similar observations were made on the Apalachicola River when fishermen on a sand bar were seen cutting the heads off adult *S. minor* in order to retrieve their hooks (RTZ, *pers. obs.*).

Florida Game and Freshwater Fish Commission regulations allow the taking of two *S. minor* per person per year, without permit or license required. The Florida Nongame Wildlife Regulations of 2000–2001 also state: “no person shall possess more than 50 eggs taken from the wild in the aggregate of species of freshwater turtles native to Florida. The purchase or sale of turtle eggs taken from the wild is prohibited”(Florida Fish and Wildlife Conservation Commission, 2001). The state of Tennessee also permits the taking of two loggerhead musk turtles per year without restriction, and the capture of turtles “manually throughout the year or by use of baited hooks, bows, dip nets, traps, or spearing” (Tennessee Wildlife Resources Agency, 2002). Both states prohibit the sale or capture for sale of loggerhead musk turtles. All freshwater turtles not on Georgia’s Protected Species List (including *S. minor*) may be freely hunted or trapped in that state (Georgia Department of Natural Resources, 2003). The effect of unregulated harvesting on wild populations of loggerhead musk turtles is unknown. However, since this species is readily accessible to snorklers in clear spring runs, it has been a regular target of commercial collectors who take animals for the pet trade. Large numbers were taken from Ichetucknee spring run between US Hwy 27 and the Santa Fe River for the pet trade in the late 1980s (K.M. Enge, *pers. comm.* to P.A. Meylan). It is not known if commercial collecting on this scale continues at this time. Finally, automobile traffic sometimes causes road mortality of nesting females (RTZ and JBI, *pers. obs.*).

STATUS

The status of *S. minor* has been reevaluated using the criteria set out by the Florida Committee on Rare and Endangered Species. Those definitions are available in the preface to Moler (1992). While some loggerhead musk turtle populations seem to be stable in certain river systems, there is not enough known about the overall abundance or rarity of this species in Florida to warrant placing it into a particular protective status. Until more data are available it is recommended that this species be listed as Status Undetermined (SU). The Nature Conservancy has *S. minor* on its Natural Heritage Program List as “apparently secure globally, though it might be quite rare in parts of its range, especially at the periphery” (LeGrand and Hall, 1999). The Nature Conservancy estimates that there are over a thousand extant populations of loggerhead musk turtle in the wild, but assigns it to Status Unknown (LeGrand and Hall, 1999). However, given its ability to thrive and reproduce in suitable freshwater habitat, *S. minor* is not likely to become seriously threatened in Florida (or other portions of its range) unless the water quality in the rivers and streams are degraded, or the environmental health of the ecosystem is severally damaged by development activities.

CONSERVATION OPTIONS AND SOLUTIONS

Public education is essential if turtle populations are to survive in Florida. State Parks and non-profit nature centers should post fact sheets that provide general information about the life history and the role that turtles play in the aquatic ecosystems. Turtles are a key species in the food chain and the general public should be made aware of their importance through sound educational programs. Certain mammalian predators, such as raccoons and foxes, are on the increase. Predator control measures should be considered to prevent the loss of nesting females and their eggs. Since loggerhead musk turtles are easily seen in clear spring runs, they are highly susceptible to commercial collection at these sites. State regulatory agencies responsible for wildlife protection should monitor the number of individual loggerhead musk turtles (and other herpetofauna) entering the international pet trade from the wild in Florida.

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LITERATURE CITED

Agassiz, L. 1857. Contributions to the natural history of the United States of America. Vol. 1. Boston, Massachusetts: Little, Brown and Co, 452 pp.

Ashton, R.E., Jr. and Ashton, P.S. 1985. Handbook of the reptiles and amphibians of Florida. Part 2. Lizards, turtles and crocodilians. Miami, Florida: Windward Publishers, 191 pp.

Belkin, D.A. 1968. Aquatic respiration and underwater survival of two freshwater turtle species. Respiration Physiology 4:1-14.

Bels, V.L. and Crama , Y. J. M. 1994. Quantitative analysis of the courtship and mating behavior in the loggerhead musk turtle *Sternotherus minor* (Reptilia: Kinosternidae) with comments on courtship behavior in turtles. Copeia 1994:676-684.

Bels, V.L. and Libois, R. 1983. Etude comparée des parades sexuelles de quelques espècies de cheloniens: *Pelomedusa subrufa subrufa* (Lacépède), *Sternotherus minor* (Agassiz) et *Kinixys belliana nogueyi* (Bell). Cashiers d'Ethologie Appliquée 3:39-58.

Berry, J.F. 1975. The population effects of ecological sympatry on musk turtles in northern Florida. Copeia 1975:692-700.

Bramble, D.M., Hutchison, J.H., and Legler, J.M. 1984. Kinosternid shell kinesis: structure, function, and evolution. Copeia 1984:456-475.

Britson, C.A., and Gutzke, W. H. N. 1993. Antipredator mechanisms of hatchling freshwater turtles. Copeia 1993:435-440.

Camp, C.D. 1986. *Sternotherus minor* (loggerhead musk turtle). Size. Herpetological Review 17:89, 91.

Carr, A.F. 1952. Handbook of Turtles. The Turtles of the United States, Canada, and Baja California. Ithaca, New York: Cornell University Press, 542 pp.

Conant, R. and Collins, J.T. 1998. A Field Guide to Reptiles and Amphibians: Eastern and Central North America. Third Edition-Expanded. Boston, Massachusetts: Houghton Mifflin, 492 pp.

Cox, W.A. 1978. Reproduction, growth, and life history strategies in the musk turtle (*Sternotherus minor*) in north Florida. Ph.D. Dissertation. University of Alabama, Birmingham.

Cox, W.A. and Marion, K.R. 1978. Observations on the female reproductive cycle and associated phenomena in spring-dwelling populations of *Sternotherus minor* in North Florida (Reptilia: Testudines). Herpetologica 34:20-33.

Cox, W.A. and Marion, K.R. 1979. Population structure and survivorship in the musk turtle, *Sternotherus minor*, in a North Florida spring run (Reptilia: Chelonia). Bulletin of the Association of Southeastern Biologists 28:84.

Cox, W.A., Nowak, M.C. and Marion, K. R. 1980. Observations on courtship and mating behavior in the musk turtle, *Sternotherus minor*. Journal of Herpetology 14:200-204.

Cox, W.A., Wyatt, S.T., Wilhelm, W. E., and Marion, K. R. 1988. Infection of the turtle, *Sternotherus minor*, by the lung fluke, *Heronimus mollis*: incidence of infection and correlations to host life history and ecology in a Florida spring. Journal of Herpetology 22:488-490.

Cox, W.A., Hazelrig, J. B., Turner, M.E., Angus, R.A., and Marion, K. R. 1991. A model for growth in the musk turtle, *Sternotherus minor*, in a north Florida spring. Copeia 1991:954-968.

Ditmars, R. 1936. The Reptiles of North America: a review of the crocodilians, lizards, snakes, turtles, and tortoises inhabiting the United States and northern Mexico., Garden City, New York: Doubleday and Company, 476 pp.

Dundee, H.A. and Rossman, D.A. 1989. The Amphibians and Reptiles of Louisiana. Baton Rouge, Louisiana: Louisiana State Univ. Press, 300 pp.

Ehrenfeld, J. G. and Ehrenfeld, D. W. 1973. Externally secreting glands of freshwater and sea turtles. Copeia 1973:305-314.

Enge, K. M. and Foster, D. R. 1986. Life history notes: *Sternotherus minor minor* (loggerhead musk turtle). Size. Herpetological Review 17:25.

Ernst, C.H. and Barbour, R.W. 1972. Turtles of the United States. Lexington, Kentucky: University Press, 347 pp.

Ernst, C.H. and Ernst, E.M. 1978. Synopsis of protozoans parasitic in native turtles of the United States. Bulletin of the Maryland Herpetological Society 15:1-15

Ernst, C.H., Miller, J. L., Marion, K. R., and Cox, W.A. 1988. Comparisons of shell morphology among turtles of the *Kinosternon minor* complex. American Midland Naturalist 120:282-288.

Ernst, C.H., Lovich, J. E., and Barbour, R.W. 1994. Turtles of the United States and Canada. Washington D.C.: Smithsonian Institution Press, 578 pp.

Ernst, E.M. and Ernst, C.H. 1977. Synopsis of helminths endoparasitic in native turtles in the United States. Bulletin of the Maryland Herpetological Society 13:1-75.

Estridge, R.E. 1970. The taxonomic status of *Sternotherus depressus* (Testudinata, Kinosternidae) with observations on its ecology. Master's thesis, Auburn Univ., Auburn, Alabama.

Etchberger, C.R. and Ehrhart, L. 1987. The reproductive biology of the female loggerhead musk turtle, *Sternotherus minor minor*, from the southern part of its range in Central Florida. Herpetologica 43:66-73.

Etchberger, C.R. and Stovall, R.H. 1990. Seasonal variation in the testicular cycle of the loggerhead musk turtle, *Sternotherus minor minor*, from Central Florida. Canadian Journal of Zoology 68:1071-1074.

Ewert, M.A. 1985. Embryology of turtles. In: Gans, C., Billett, F., and Maderson, P. F. A. (Eds.). Biology of the Reptilia Vol. 14. New York, New York: John Wiley & Sons, pp 76-267.

Ewert, M.A., and Nelson, C.E. 1991. Sex determination in turtles: diverse patterns and some possible adaptive values. Copeia 1991:50-69.

Florida Fish and Wildlife Conservation Commission. 2001. Hunting Regulations Summary. [http://floridaconservation.org]

Folkerts, G.W. 1967. Notes on a hybrid musk turtle. Copeia 1967:479-480.

Folkerts, G.W. 1968. Food habits of the striped-necked musk turtle, *Sternotherus minor peltifer* Smith and Glass. Journal of Herpetology 2:171-173.

Gatten, R.E., Jr. 1984. Aerobic and anaerobic metabolism of freely-diving loggerhead musk turtles (*Sternotherus minor*).

Herpetologica 40:1-7.

Georgia Department of Natural Resources, 2001. General Hunting Regulations. [http://www.georgiawildlife.dnr.state.ga.us/]

Gibbons, J. W., and Esch, G. W. 1970. Some intestinal parasites of the loggerhead musk turtle (*Sternotherus m. minor*). Journal of Herpetology 4:79-80.

Guntermann, J. 1998. Beobachtungen an *Sternotherus minor minor* in natürlichen Lebensräumen in Florida. Emys 5:4-16.

Guyer, C., and Herndon, K. A. 1992. Population analysis of *Sternotherus minor peltifer*. Journal of the Alabama Academy of Science 63:48.

Hensley, F.R. 1994. *Sternotherus minor* (loggerhead musk turtle). Foraging depth. Herpetological Review 26:99.

Huestis, D.L., and Meylan, P.A. 2004. The turtles of Rainbow Run (Marion County, Florida): observations on the genus *Pseudemys*. Southeastern Naturalist 3:595-612.

Iverson, J. B. 1977a. Geographic variation in the musk turtle *Sternotherus minor*. Copeia 1977:502-517.

Iverson, J. B. 1977b. *Sternotherus minor* (Agassiz). Loggerhead musk turtle. Catalogue of American Amphibians and Reptiles 195:1-2

Iverson, J. B. 1977c. Reproduction in freshwater and terrestrial turtles of north Florida. Herpetologica 33:205-212.

Iverson, J. B. 1978. Reproductive cycle of female loggerhead musk turtles (*Sternotherus minor minor*) in Florida. Herpetologica 34:33-39.

Iverson, J.B. 1982. Biomass in turtle populations: a neglected subject. Oecologia 55:69-76.

Iverson, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, Indiana: Privately Printed, 363 pp.

Iverson, J.B. 1998. Molecules, morphology and turtle phylogenetics (Family Kinosternidae). Chelonian Conservation and Biology 3:113-117.

Iverson, J.B. and Etchberger, C.R. 1989. The distributions of the turtles of Florida. Florida Scientist 52:119-144.

Iverson, J.B. and Paull, R. C. 2004. Musk Turtle. Sumterville, Florida: Green Nature Books, 78 pp.

Jackson, C.G. 1965. Carapace erosion in the loggerhead musk turtle, *Sternotherus minor minor* Agassiz. Herpetologica 20:279-281.

Jackson, C.G. 1969. Agonistic behavior in *Sternotherus minor minor* Agassiz. Herpetologica 25:53-54.

Jackson, J.F. 1988. Crevice occupation by musk turtles: taxonomic distribution and crevice attributes. Animal Behavior 36:793-801.

Jackson, J.F. 1990. Evidence for chemosensor-mediatiated predator avoidance in musk turtles. Copeia 1990:557-560.

Johnson, C.A. 1967. *Sternotherus minor peltifer* (Chelonia) a new host record for *Heronimus chelydrae* MacCallum, 1902 (Trematoda: Digenea). Journal of Parasitology 53:617.

Kirkpatrick, D.T. 1997. The Biology, Husbandry, and Health Care of Reptiles. Vol. II: The Husbandry of Reptiles. Neptune City, New Jersey: T.F.H. Publications.

LeGrand, H.E. and Hall, S.P. 1999. Natural Heritage Program List of the Rare Animal Species of North Carolina. Raleigh, North Carolina: The Nature Conservancy.

Lehmann, H. 1984. Ein Zwillingsschlupf bei *Sternotherus minor minor* (Agassiz, 1857). Salamandra 20:192-196.

Marchand, L. J. 1942. A contribution to a knowledge of the natural history of certain freshwater turtles. Master's Thesis, Univ. Florida, Gainesville.

Meshaka, W., and Gallo, N. 1990. Geographic distribution: *Sternotherus minor* (loggerhead musk turtle). Herpetological Review 21:95.

Meylan, P.A., Stevens, C.A., Barnwell, M.E., and Dohm, E.D. 1992. Observations on the turtle community of Rainbow Run, Marion Co., Florida. Florida Scientist 55:219-228.

Mitchell, J. C. 1994. The Reptiles of Virginia. Washington D.C.: Smithsonian Institution Press, 352 pp.

Moler, P.E. 1992. Rare and Endangered Biota of Florida. Vol. III. Amphibians and Reptiles. Gainesville, Florida: University Press Florida, 291 pp.

Mount, R.H. 1975. The Reptiles and Amphibians of Alabama. Auburn, Alabama: Auburn University Agricultural Experimental Station, 347 pp.

Nagle, R. D., Burke, V. J., and Congdon, J.D. 1998. Egg components and hatchling lipid reserves: Parental investment in kinosternid turtles from the southeastern United States. Comparative Biochemistry and Physiology 120B:145-152.

Neill, W. T. 1948. Use of scent glands by prenatal *Sternotherus minor*. Herpetologica 4:148.

Nolan, D. 1991. The maintenance and breeding of the loggerhead musk turtle *Sternotherus minor minor* (Agassiz, 1857). Testudo 3(3):1-4.

Onorato, D. 1996. The growth rate and age distribution of *Sternotherus minor* at Rainbow Run, Florida. Journal of Herpetology 30:301-306.

Packard, M. J., Hirsch, K. F., and Iverson, J. B. 1984. Structure of shells from eggs of kinosternid turtles. Journal of Morphology 181:9-20.

Palmer, W. M., and Braswell, A. L. 1995. Reptiles of North Carolina. Chapel Hill, North Carolina: University of North Carolina Press, 412 pp.

Pritchard, P. C. H. 1989. The Alligator Snapping Turtle: Biology and Conservation. Milwaukee, Wisconsin: Milwaukee Public Museum, 104 pp.

Rogner, M. 1996. Schildkröten 2. Hürtgenwald, Germany: Heidi-Rogner-Verlag. 265 pp.

Rödel, M.O. 1989. Haltung und Zucht der Kleinen Moschusschildkröte *Sternotherus minor minor* (Agassiz, 1857). Aquarama 4:46-49.

Sachsse, W. 1977. *Sternotherus m. minor*, seine Nachzucht und die damit verbundenen biologischen Beobachtungen (Reptilia: Testudines: Kinosternidae). Salamandra 13:157-165.

Schilde, M. 2001. Schlammschildkröten: *Kinosternon, Sternotherus, Claudius* und *Staurotypus*. Münster, Germany: Natur und Tier Vierlag, 133 pp.

Schmidt, K. P. 1953. A check list of North American amphibians and reptiles. Sixth Edition. Chicago, Illinois: University of Chicago Press, 280 pp.

Scott, A.F., Sutton, S., and Williamson, S. 2000. New county records of amphibians and turtles from the western highland rim of central Tennessee. Herpetological Review 31:117-118.

Seidel, M.E. and Lucchino, R.V. 1981. Allozymic and morphological variation among the musk turtles *Sternotherus carinatus, S. depressus* and *S. minor* (Kinosternidae). Copeia 1981:119-128.

Seidel, M.E., Iverson, J. V., and Adkins, M. D. 1986. Biochemical comparisons and phylogenetic relationships in the family Kinosternidae (Testudines). Copeia 1986:285-294.

Smith, H.M., and Glass, B.P. 1947. A new musk turtle from southeastern United States. Journal of the Washington Academy of Sciences 37:22-24.

Stejneger, L. 1923. Rehabilitation of a hitherto overlooked species of musk turtle of the southern states. Proceedings of the U.S. National Museum 62:1-3.

STEVENSON, D. AND CROWE, D. 1992. Geographic distribution: *Sternotherus minor minor*. Herpetological Review 23:88.

STRAUCH, A. 1862. Chelonische Studien, mit besonderer Beziehung auf die Schildkrötensammlung der kaiserlichen Akademie der Wissenschaften zu St. Petersburg. Mémoirs de l'Académie Impériale des Sciences de Saint-Pétersburg 7(5)7:1-196.

TENNESSEE WILDLIFE RESOURCES AGENCY. 2002. Tennessee Animal Biogeographic System, TABS. [http://fwie.fw.vt.edu/TN/TN07092.htm]

TINKLE, D.W. 1958a. The systematics and ecology of the *Sternothaerus carinatus* complex (Testudinata: Chelydridae). Tulane Studies in Zoology 6(1):1-56.

TINKLE, D.W. 1958b. Experiments with censusing of southern turtle populations. Herpetologica 14:172-175.

TINKLE, D.W. AND WEBB, R.G. 1955. A new species of *Sternotherus* with a discussion of the *Sternotherus carinatus* complex (Chelonia, Kinosternidae). Tulane Studies in Zoology 3(3):53-67.

WALKER, D., BURKE, V.J., BARAK, I., AND AVISE, J.C. 1995. A comparison of mtDNA restriction sites vs. control region sequences on phylogeographic assessment of the musk turtle (*Sternotherus minor*). Molecular Ecology 4:365-373.

WILLIAMSON, G.K. AND MOULIS, R.A. 1994. Distribution of Amphibians and Reptiles in Georgia. Savannah Science Museum Special Publication 3:2 volumes.

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Sternotherus odoratus – Common Musk Turtle or Stinkpot

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SUMMARY. – The common musk turtle or stinkpot, *Sternotherus odoratus*, ranges across the eastern half of the United States and Canada from Maine and Ontario to Wisconsin, Texas, and Florida. It is one of the smallest turtles in Florida, and is one of two musk turtles native to the state. It is a common though secretive inhabitant of nearly any body of still water in the state, except the Keys and the extreme southern Everglades. Males are generally smaller than females in Florida, but are more nearly equal in size at more northerly sites. The smallest adult body sizes are reached in Florida. The species is primarily diurnal or crepuscular, but may also be active at night in Florida, where it can be found active year-round. Females mature in 3 to 11 yrs and males in 2 to 7 yrs, with the shortest periods occurring in Florida. The nesting season increases in length with decreasing latitude, lasting from at least February through August in central Florida and only May through June in northern states. One to six clutches of 1–9 small calcareous eggs are laid each year, with the smallest and most clutches being produced in Florida. Across the species' range egg size decreases with latitude, with the smallest eggs being produced in south Florida. Sex of hatchlings is related to nest temperature, with females predominating from nests with high temperatures, and males in nests of intermediate temperatures. As a result of this and other factors, sex ratios in populations vary from those generally male-biased in the north to those that are generally unbiased or female-dominated in south Florida. This turtle can attain extremely high densities in productive wetlands in Florida. Although they are omnivorous, they tend to prefer animal food, especially mollusks. The species' primary interaction with humans is when it is hooked on a fishing line, damaged by boat propellers, or killed on roads during nesting forays. Destruction of wetlands also takes a heavy toll on these turtles. However, despite these losses, the species is unlikely to become threatened in Florida in the foreseeable future.

CONSERVATION STATUS. – FNAI Global - G5 (Demonstrably Secure), State - S5 (Demonstrably Secure); ESA Federal - Not Listed; State - Not Listed; CITES - Not Listed; IUCN Red List - Not Listed (LC-Least Concern).

Species Recognition. — *Sternotherus odoratus* is a small turtle, less than 140 mm carapace length (CL) (see Table 14-1), with an elongate, arched, gray, brown or black carapace (Fig. 14-1) with 11 marginal scutes per side, a relatively small yellow to brown plastron with a single anterior hinge and a shallow posterior notch (Fig. 14-2), a quadrangular pectoral scute, barbels on the neck and chin, a pointed snout, usually two conspicuous white or yellow lateral stripes on the head, and a pair of glands along each bridge that produce a distinctive, pungent musk. Although the adult carapace is usually smooth, the carapace of hatchlings (Fig. 14-3) and smaller individuals has a distinct middorsal keel and a pair of weaker ridges on each side. The plastron of hatchlings is mottled black and white (Fig. 14-4). Males have longer, thicker tails than females (Fig. 14-2), more exposed skin along the medial plastral scute seams, and two small patches of elevated scales on the inner surface of each leg (Risley, 1930).

Sternotherus odoratus can be distinguished from other members of the genus by its yellow head stripes on a basically black head (Fig. 14-1) (vs. black spots or reticulations on a basically brown head), its barbels on the neck and chin (vs. only on the neck), its having a black carapace (vs. brown), and its non-overlapping carapacial scutes (vs. scutes overlapping those more posterior).

Taxonomic History. — Latreille (1801) originally described the common musk turtle as *Testudo odorata* (see Harper 1940 for confirmation of original authorship). A type specimen was not specifically designated and any types are now presumed lost. The type locality was originally described as "les eaux dormantes de la Caroline" [still waters of Carolina], but it was later restricted to Charleston, South Carolina (Harper, 1940; Schmidt, 1953).

Testudo odorata was placed in the genus *Sternotherus* (Gray, 1825), where it has remained for most of its history (see Stejneger, 1923). More recently, synonomy of *Sternotherus* with *Kinosternon* was proposed based on the lack of any character uniquely shared by all four of the species usually included in *Sternotherus* (Seidel et al., 1986; Iverson, 1991a); however, cladistic analysis of molecular (protein and mitochondrial DNA) and morphological data has since demonstrated the monophyly of the genus *Sternotherus* (Iverson, 1998), and this name is currently in use.

Figure 14-1. Adult common musk turtle, *Sternotherus odoratus*, from Volusia Co., Florida. Photo by Peter May.

The spelling of the genus name *Sternotherus* has also been controversial, with some authors arguing that the name should actually be *Sternothaerus* (e.g., Conant, 1958). However, a review of the nomenclatural history confirmed that the oldest published name (and hence, its correct spelling) is *Sternotherus* (Zug, 1971; Smith and Larson, 1974; Smith and Smith, 1979).

The genus name *Sternotherus* is from the Greek *sternon*, meaning chest or breast, and *theiros*, meaning hinge, and refers to the hinged plastron. The species name is from the Latin *odoratus*, meaning fragrant, and refers to the pungent musk produced by this turtle. Other common names used for *Sternotherus odoratus* include stinking jim (Dunn, 1918), marsh turtle (Hay, 1902), and moon turtle (Mitchell, 1994).

Sternotherus odoratus is a monotypic species but is highly variable in its morphology and genetics. Although very little geographic variation in morphology occurs across the species' range (Reynolds and Seidel, 1983), average body size of *S. odoratus* is smallest in the southern end of its geographic range and largest in northern populations (Tinkle, 1961; Ernst et al., 1994; Edmonds and Brooks, 1996; Table 14-1). Some morphological variation is associated with habitat differences in various populations. For example, adults from the Hart Springs Run of the Suwannee River averaged larger in body size than those of northern populations (JBI, unpubl. data). Moreover, individuals with larger heads and bodies occur to the west of the Blue Ridge Mountains in Virginia than to the east (Mitchell, 1994). Likewise, *S. odoratus* in the mountains of North Carolina are larger than those to the east (Palmer and Braswell, 1995), and a few individuals are megacephalic. Megacephaly appears to be a local phenomenon (presumably environmentally induced, rather than genetic) associated with an increase in mollusks in the diet. Head sizes of an Arkansas

Figure 14-2. Plastral views of adult male (left) and female (right) common musk turtle, *Sternotherus odoratus*, from Pinellas Co., Florida. Photo by Marius Moore.

Figure 14-3. Hatchling common musk turtle, *Sternotherus odoratus*, from Volusia Co., Florida. Photo by Peter May.

Figure 14-4. Plastral view of hatchling common musk turtle, *Sternotherus odoratus*, from Alachua Co., Florida. Photo by John Iverson.

population are as large as those of the loggerhead musk turtle *Sternotherus minor* (JBI, unpubl. data). Although some geographic variation in body size exists in Florida *S. odoratus*, no megacephalic specimens have been reported from the state (e.g., see Berry, 1975).

High levels of heterozygosity exist in this species, but very little variation in allelic frequency occurs among populations (Seidel et al., 1981). Considerable geographic variation in mitochondrial DNA (RFLP fragments) occurs across the southeastern United States, including Florida (Walker et al., 1997). However, in light of the local variation in body size, head size, and color patterns, and the lack of previous evidence of broad geographic patterns in morphology or serum protein allele frequency, combined with large sampling gaps, and small samples in the mtDNA study (6 of 16 sites having only one sample), we suggest that more sampling must be done before the implications of mtDNA variation can be assessed.

DISTRIBUTION

Geographic Distribution. — Sternotherus odoratus is an eastern North American species, ranging from Florida to east Texas to southern Wisconsin and to Ontario and Maine (Iverson, 1992). A single record from the state of Chihuahua, Mexico (Moll and Williams, 1963) is probably invalid (Conant and Berry, 1978; Smith and Smith, 1979). This species occurs throughout mainland Florida (Meshaka and Ashton, 2005) (Fig. 14-5), but is absent from the Florida Keys.

Table 14-1. Average body size (mm carapace length, CL) of males and females, with male:female sex ratios, in the common musk turtle, *Sternotherus odoratus*, from selected locations.

Location	Male CL	Female CL	M:F Ratio	Source
Ontario	103.6	98.7	1.05	Edmonds & Brooks, 1996
Northern Indiana	88.7	88.5	1.00	Iverson, unpubl. data
Northern Indiana	86.5	86.1	1.00	Wade & Gifford, 1965; Wade, unpubl. data
Central Indiana	98.6	107.1	0.92	Conner et al., 2005
Southern Missouri	83.6	82.8	1.01	Ford, 1999
Virginia	82.6	85.9	0.96	Mitchell, 1985b
Virginia	79.0	79.4	0.99	Mitchell, 1988
Alabama	76.8	75.0	1.02	Dodd, 1989
Northern Florida	70.0	73.9	0.95	Iverson, unpubl. data
Northern Florida	70.1	76.6	0.92	Gibbons, 1970
Central Florida	60.0	67.0	0.90	Bancroft et al., 1983
Southern Florida	68.0	77.0	0.88	Meshaka, 1988

Ecological Distribution. — Sternotherus odoratus can occur in almost any freshwater habitat. Although it has been found in rocky and gravelly streams (Ernst et al., 1994; Palmer and Braswell, 1995; JBI, *pers. obs.*) and to depths of 9 m (Carr, 1952), it seems to prefer permanent lentic systems or those with a slow current. Within these systems *S. odoratus* is most common along shallow shorelines that have abundant submergent vegetation and a soft bottom (Kingsbury, 1993; JBI, *pers. obs.*). It does not tolerate brackish water (Dunson, 1986), as evidenced by its disappearance from a freshwater site in New Jersey when a canal was opened that allowed salt water intrusion (Conant and Bailey, 1936).

In Florida, *S. odoratus* inhabits the full range of freshwater habitats, from clear to turbid waters; from marshes, ponds, retention and sewage basins, canals and roadside ditches to streams, spring runs, and rivers; and on muddy to sandy substrates. In extreme southern Florida, *S. odoratus* is particularly abundant in canals, but is rare or perhaps absent from the rocky marsh and prairie of the southern Everglades. However, it has been recorded from the deeper, soft-bottomed Taylor Slough (Dalrymple, 1988; Meshaka et al., 2000).

HABITAT RELATIONS

Activity. — Across its geographic range, the diurnal activity pattern of *S. odoratus* is generally bimodal. This species is typically active from first light to mid-morning and again from late afternoon to last light (Mahmoud, 1969; Ernst, 1986; Jackson, 1988, Smith and Iverson, 2004; contrary to Lagler, 1943; Ernst et al., 1994). Although intensive searching and trapping in Texas (Vermersch, 1992) and Indiana (Smith and Iverson, 2004) revealed no nocturnal activity in *S. odoratus*, some evidence suggests that they may be active at night in Florida (Carr, 1952; Bancroft et al., 1983; Meshaka, 1988). The observations in Florida require confirmation, and the hypothesis that the pattern is due to the warmer water temperatures in Florida (Carr, 1952; Ernst, 1986) deserves testing. When not active, turtles use retreats that are dark and provide more contact with the carapace than mud or filamentous algae (Jackson, 1988; Gad, 1993).

In Florida, this species will dive to almost 9 m (Carr, 1940, 1952). Most dives are less than 20 min in duration (Stone et al., 1992b), but deep and prolonged dives by *S. odoratus* are possible because individuals can absorb oxygen from the water via cutaneous surfaces, particularly via the bucco-pharyngeal region (Root, 1949; Stone et al., 1992a; King, 1996). This ability could be an advantage to colonizing deep rivers (e.g., Rainbow Run), deep lakes, borrow pits, and canals in Florida.

Seasonality. — Sternotherus odoratus is active year-round in north-central to southern Florida (Carr, 1952;

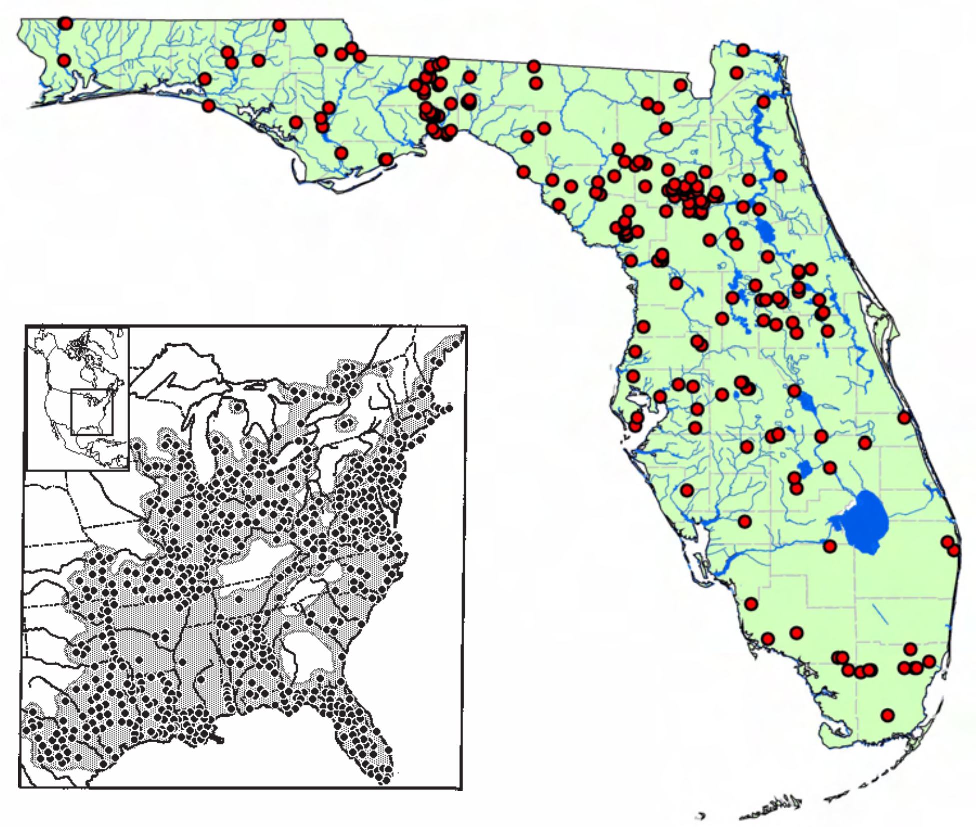

Figure 14-5. Available distribution records for the common musk turtle, *Sternotherus odoratus*, from Florida. Inset: distribution records from entire range of *S. odoratus* (adapted from Iverson, 1992; distribution in inset map not current for Florida as presented here).

Bancroft et al., 1983; Meylan et al., 1992; JBI and WEM, *pers. obs*.); however, activity is clearly seasonal in northern populations (Evermann and Clark, 1916; Risley, 1933; Conant, 1951; Mahmoud, 1969; Minton, 1972; Ernst, 1986; Mitchell, 1994). Hibernacula at northern sites range in physical structure from the soft substrate of aquatic systems (Babcock, 1919; Risley, 1933; Cagle, 1942; Vogt, 1981; Mitchell, 1994) and under substrate debris (Vogt, 1981; Mitchell, 1994; Palmer and Braswell, 1995) to muskrat burrows (Risley, 1933; Mitchell, 1994) and holes in stream banks (Carr, 1952). Occasionally this species will hibernate communally (Thomas and Trautman, 1937). While hibernating, it is sensitive to anoxic conditions, such as those associated with burrowing in mud (Jackson et al., 1984; Ultsch et al., 1984, Ultsch, 1985, 1988; Ultsch and Cochran, 1994).

Movements and Home Range. — Movements of *S. odoratus* vary greatly among populations across its range (Table 14-2), suggesting that local conditions, rather than geography, explain movement patterns. A common pattern in the movement studies was a larger home range in males than in females (Mahmoud, 1969; Bancroft et al., 1983; Ernst, 1986; Edmonds, 1998).

Homing. — Homing ability in *S. odoratus* is known from only two studies. In a Michigan lake, 15 of 50 turtles returned to the proximity of their original capture right after being displaced (Williams, 1952). Over 34 days, one individual returned to its original capture site eight different times from distances of approximately 213 m, and one turtle traveled 465 m to its capture site within 18–23 hrs (Williams, 1952). In a lake in Virginia, 34 of 118 turtles returned to their original capture site after being displaced 520 m along the shore or 100 or 550 m across open water (Smar and Chambers, 2005). Of those, 31 were males, indicating a significant gender difference in homing ability

Terrestrial Activity. — *Sternotherus odoratus* is a highly aquatic species and, with the exception of nesting activities, seldom leaves the water (Risley, 1933; Gibbons, 1970; Gibbons et al., 1983; Ernst, 1986; Ernst et al., 1994; Palmer and Braswell, 1995; Tuberville et al., 1996; Aresco, 2005a, b). This also appears to be true in Florida and is explained in part by the high rate of evaporative water loss in this species (Ernst, 1968; Costanzo et al., 2001).

Table 14-2. Average distance movements (m) between successive captures and home ranges (ha, in parentheses) of the common musk turtle, *Sternotherus odoratus*, from selected locations. * = in less than 100 days. ** = in more than 100 days.

Location	Habitat	Males	Females	Source
Ontario	bay in lake	2052 (63.4)	828 (27.8)	Edmonds, 1998
Pennsylvania	pond-marsh-stream	117 (1.75)	90 (0.94)	Ernst, 1986
Oklahoma*	stream	66	38	Mahmoud, 1969
Oklahoma**	stream	69 (0.2)	51 (0.05)	Mahmoud, 1969
Florida	lake	231	209	Bancroft et al., 1983

Temperature Relationships. — Water temperatures in the field associated with activity in *S. odoratus* ranged from 10–34°C in Oklahoma (Mahmoud, 1969) and 15–30°C in Pennsylvania (Ernst, 1986). Similarly, Graham and Hutchison (1979) found that the preferred temperature range selected by *S. odoratus* in a thermal gradient was 20.7–22.4°C. Turtles fed when cloacal and water temperatures ranged between 8–30°C, and reproductive behavior occurred at cloacal temperatures from 16–22°C (Ernst, 1986). *Sternotherus odoratus* thermoregulates by basking in shallow water (Ernst, 1986), in mats of surface vegetation (Newman, 1906; JBI, *pers. obs*.), atop partially submerged water lily pads (JBI, *pers. obs*.), and when floating at the surface of the water (Ernst and Barbour, 1972).

Basking behavior in Florida populations has not been investigated. Amenable thermal conditions throughout the year in southern Florida may reduce the need to thermoregulate actively by basking. However, basking, if it occurs in Florida, may be no less important if it accomplishes other requirements associated with drying off, such as removal of algae or ectoparasites. Outside Florida, basking is uncommon (Mahmoud, 1969; Ernst, 1986; Mitchell, 1994; Nickerson, 2000). Turtles bask most frequently during April–July (Ernst, 1986), and basking above the water occurs generally at heights of < 3 m (Vogt, 1981; Vermersch, 1992; Palmer and Braswell, 1995; Nickerson, 2000). Once disturbed, basking adults nearly always drop into the water, although younger individuals often grip the branch tightly so as not to fall off the basking site (Ernst et al., 1994).

GROWTH AND REPRODUCTION

Growth. — A mark-recapture study of *S. odoratus* in a central Florida lake revealed growth rates of 0–10 mm/yr, although most individuals grew less than 3 mm/yr (Bancroft et al., 1983). From their data on the relationship of growth rate and CL, 30 mm males were growing at a rate of 4.4 mm/yr, 40 mm males at 3.4 mm/yr, 50 mm males at 2.4 mm/yr, 60 mm males at 1.4 mm/yr, and 70 mm males at 0.4 mm per year; 30 mm females were growing at 8.7 mm/yr, 40 mm females at 7.0 mm/yr, 50 mm females at 5.2 mm/yr, 60 mm females at 3.4 mm/yr, and 70 mm females at 1.6 mm/yr. These rates are slower than those measured in more northerly populations (Risley, 1933; Ernst, 1986; Edmonds, 1998) (Table 14-3), despite the longer activity season in Florida. Specifically, mark-recapture data revealed that both sexes of *S. odoratus* from Oklahoma grow very quickly (Mahmoud, 1969): a single male between 41 and 60 mm CL grew 12.1 mm/yr, males 61-80 mm grew 1.6 mm/yr, and males > 80 mm grew 0.8 mm/yr. A single female, between 41 and 60 mm grew 26.6 mm/yr, females 61-80 mm grew 0.9 mm/yr, and those > 80 mm grew 0.2 mm/yr. Captive growth rates of hatchlings greatly exceed those in the wild (Olexa, 1969; Polder, 1979; Bancroft, 1983; Gad, 1987) and cannot be used to describe growth under natural conditions.

Table 14-3. Average size (mm CL) per year of growth for the common musk turtle, *Sternotherus odoratus*, from selected sites.

Years of age	Ontario (Edmonds, 1998)	Michigan (Risley, 1933)	Pennsylvania (Ernst, 1986)
1	30.0	32.5	32.0
2	40.0	42.5	40.0
3	47.0	52.0	48.0
4	53.0	61.0	52.0
5	60.0	67.0	60.0
6	66.0	71.0	66.0
7	70.0	74.5	70.0
8	74.0	78.0	74.0
9	77.0	88.0	77.0
10	–	–	80.0

Table 14-4. Age (yrs) and body size (mm CL) at sexual maturity in the common musk turtle, *Sternotherus odoratus*, from selected locations.

Location	Males	Females	Source
Ontario	5-6 (63)	8-9 (80)	Edmonds, 1998
Michigan	3-4 (50-60)	9-11 (80)	Risley, 1933
Indiana	–	5 (–)	Clark et al., 2001
Virginia	2 (51)	4 (66)	Mitchell, 1988
Oklahoma	4-7 (65)	5-8 (65-85)	Mahmoud, 1967
Central Florida	3 (47-50)	3-5 (57-60)	Bancroft et al., 1983
Central Florida	–	3 (64)	Powell & Phillips, 1984
Southern Florida	– (52)	– (62)	Meshaka, 1988, 1991

Dimorphism. — Males have longer and thicker tails than females, more exposed skin along the median plastral scute seams, and two small patches of elevated scales on the inner surface of each leg (Risley, 1930). Body size dimorphism is present in *S. odoratus* and is most extreme in southern populations (Table 14-1).

Maturation. — Females generally mature later and at larger body sizes than do males, and it is likely that both sexes mature earlier in southern localities than they do in more northern localities (Table 14-4). Growth rates from central Florida suggest a much longer juvenile period for males and females than that of captive counterparts (1.5 and 1.4–1.9 yrs, respectively; Bancroft et al., 1983). We are skeptical of their estimates of a protracted juvenile stage because of rapid growth of captive hatchlings, scant data available to Bancroft and colleagues (1983) for growth in small juveniles, earlier ages of maturity from other locations in central Florida (Powell and Phillips, 1984), and small body sizes at maturity in Florida. Moreover, we predict that in light of the eutrophic conditions of canals and the subtropical climate, populations of extreme southern Florida may experience growth rates that permit maturity in less than 2 yrs.

Longevity. — *Sternotherus odoratus* can live a long life in the field and in captivity. For example, individuals in Pennsylvania were estimated to be at least 28 yrs of age (Ernst, 1986). In South Carolina *S. odoratus* live to at least 15–19 yrs of age (Gibbons, 1987). The longevity record in captivity is 54 yrs, 9 mo, at the Philadelphia Zoo (Snider and Bowler, 1992), and another individual was still alive after > 28 yrs in a private collection (Slavens and Slavens, 1994). However, no studies exist on this critical life history parameter for Florida populations.

Male Sexual Cycle. — The male sexual cycle has been studied in Florida (Gross, 1982), Michigan (Risley, 1934, 1938), Virginia (Mitchell, 1985a, 1988), Oklahoma (Mahmoud and Klicka, 1972), and Alabama (McPherson and Marion, 1981a). The timing of the cycle varies somewhat latitudinally but the phases are basically the same throughout the range. The male cycle in Florida (Gross, 1982) differs substantially in timing and degree of regression of the testes from that of the more temperate sites. Relative testes mass is greatest during September–October and at its minimum during June–July. However, testicular mass does not drop to the levels observed in more northerly populations. This finding suggests that complete testicular regression may not occur in Florida populations. Unfortunately, data on seasonal variation in testicular histology are not yet available for Florida populations.

Elsewhere, spermatogenesis begins in late spring (March in Alabama, May in Virginia, and June in Michigan and Oklahoma). Common to these populations, spermiogenesis (final sperm production) begins as early as late July, peaks in late August or early September, and is completed in late September or in October in all aforementioned populations. In all populations, seminiferous tubules reach their greatest diameter in mid-August and early September, and therefore the testes reach their maximum size and mass at that time. The epididymides then begin increasing in diameter as more mature sperm are stored there. Thus, sperm are available for mating through the fall, winter, and spring. Testes size reaches its minimum during this period (sometime between September and December in Oklahoma, in May in Michigan, in May in Virginia, and in February to April in Alabama) as tissues are restored for the next cycle.

Female Sexual Cycle. — The female reproductive cycle in Florida and elsewhere begins in July or August after the last clutch of the year has been produced and ovarian follicles are of minimum size (Edgren, 1960; Mahmoud and Klicka, 1972; Iverson, 1977; Marion and McPherson, 1981; McPherson and Marion 1981b; Gross, 1982; McPherson et al., 1982; Mitchell, 1985b, 1988). At that time vitellogenesis begins, resulting in follicular enlargement. Follicles continue to enlarge through the fall, winter, and spring, although the process is slowed or stopped during hibernation. Maximum follicle diameters are reached immediately prior to ovulation in the spring. The onset of ovulation is related to latitude, beginning in late January or February in Florida (Iverson 1977; Gross, 1982), March in a pond in Alabama (McPherson and Marion, 1983), late April in a river in Alabama (McPherson and Marion, 1981a; McPherson et al., 1982), at least mid-May through June in Oklahoma (Mahmoud and Klicka, 1972), mid-April in Virginia (Mitchell, 1985b, 1988), mid-May in Michigan (Risley, 1933), and late April to early May in Wisconsin (Edgren, 1960).

Ovulated eggs are retained in the oviducts for three or four (Risley, 1933; McPherson and Marion, 1981a; Gross, 1982) to perhaps eight weeks (Edgren, 1960; although this may represent a second clutch) while albumen, shell membranes, and the egg shell are secreted around the egg. Nearly all females probably reproduce each year, although some females may skip reproduction in a given year depending on weather conditions (Gibbons, 1982; Gibbons et al., 1983). Females in most populations, including Florida (Gross, 1982; Meshaka, 1988), ovulate more than one clutch a year, so follicles continue to enlarge after early clutches and until the last clutch is ovulated (late June or early July in the north; August in central Florida) (Table 14-5).

Table 14-5. Nesting season of the common musk turtle, *Sternotherus odoratus*, from selected locations.

Location	Nesting season	Source
Ontario	Jun(?)–Jul	Lindsay, 1965
Wisconsin	May–Jun	Edgren, 1949, 1956, 1960
Michigan	Jun–Jul	Risley, 1933
Northern Indiana	Jun–Jul	Eigenmann, 1896; Newman, 1906; Iverson, unpubl. data
Western Tennessee	Jun–Jul	Cagle, 1937
Eastern Pennsylvania	Jun	Ernst, 1986
Virginia	Apr–Jul	Mitchell, 1985b, 1988
South Carolina	Apr–Jul	Gibbons et al., 1982
Central Alabama	May–Jul	McPherson & Marion, 1981b
Central Alabama	Mar–Jul	Marion & McPherson, 1981; McPherson & Marion, 1983
South-central Texas	Apr–Jul	Vermersch, 1992
North Florida	Feb–Jun	Gibbons, 1970; Iverson, 1977
Central Florida	Feb–Aug	Gross, 1982

The presence of sperm storage tubules in the oviducts of female *S. odoratus* (Gist and Jones, 1989) raises the possibility that sperm from fall matings could remain viable through the winter and fertilize eggs the following spring (Agassiz, 1857; Risley, 1933; Gist and Congdon, 1994). Low temperatures are necessary for normal follicular development, and continued exposure to high temperatures induces ovarian quiescence and regression. Short daylength is not a primary cue stimulating female sexual behavior (Mendonca and Licht, 1986; Mendonca, 1987).

Courtship and Mating. — Courtship behavior consists of three phases (Mahmoud, 1967): 1) tactile, 2) mounting and intromission, and 3) biting and rubbing. The tactile phase may last from a few seconds to three minutes, and involves the male approaching from behind, nudging the female's tail, then her bridge, and then her head. If she is receptive, he mounts the back of her shell. During this phase, the male grips the margin of the female's carapace with the claws of all four feet. The male holds the female's tail between the scale patches on the back of one of his legs, aligns his tail with the female's to oppose their cloacas, everts and inserts his penis, and extends his head to touch her head and neck. This phase typically requires only 5 to 10 seconds. During the final phase the male bites and rubs the head of the female while the female bites the head and feet of the male. Ejaculation apparently coincides with the stiffening of the male's body accompanied by spastic contractions. Actual copulation lasts for five minutes to two hours. Although this mating behavior has been called forced insemination (Berry and Shine, 1980), it remains to be demonstrated that the female is not a willing partner, particularly when the male is not typically larger than the female. The only significant deviations from this description are the observations of a plastron-to-plastron copulation (Finneran, 1948) and the absence of biting during the final phase of courtship (Gross, 1982).

Mating occurs throughout the year (Ernst and Barbour, 1972), but peaks in spring (especially April–May) and fall (September–October). The only report of mating in Florida was for 23 July, but was based on a captive female in an outdoor enclosure (Gross, 1982). No other reports of mating have been published for Florida (Carr, 1952). However, courtship was observed along Anhinga Trail in Everglades National Park during late January (JBI, *pers. obs.*). Fall matings are known from Michigan (Lagler, 1941), Indiana (Evermann and Clark, 1916), Illinois (Andrews and Andrews, 1992), and Alabama (McPherson and Marion, 1981a). April and May matings have been reported from Pennsylvania (Ernst, 1986), and a single May copulation was reported from North Carolina (Palmer and Braswell, 1995). Mating occurs in the water (Ernst and Barbour, 1972), but can occur above the water at the water's edge (Andrews and Andrews, 1992). Although most matings occur in the morning (Lagler, 1941; Gross, 1982; Ernst, 1986), *S. odoratus* may also mate at night (Ernst and Barbour, 1972).

Nesting. — The length of the nesting season decreases with increasing latitude, with southernmost populations having a nesting season up to five months longer than northernmost populations (Table 14-5). Although females are gravid during the summer (Meshaka, 1988), the full extent of the nesting season in extreme southern mainland Florida remains unknown.

Nesting activity occurs day or night. It has not been described from Florida where high mid-day summer air temperatures could restrict diurnal nesting to early morning and late afternoon. In Ontario, nesting appears to be confined to the late evening (Lindsay, 1965), and in Pennsylvania, nesting occurs in the evening between ca. 1900–2100 hrs (Ernst, 1986). One nesting record at 2030 hrs exists, presumably from Massachusetts (Agassiz, 1857). In Michigan, *S. odoratus* nests "any time of day from early morning to twilight" (Risley, 1933). In North Carolina a female was discovered having just completed her nest at 1030 hrs (Palmer and Braswell, 1995).

Most nests are laid within 11 m of the water (Risley, 1933; Ernst, 1986). However, in Tennessee most nests were found 14–18 m from the water (Cagle, 1937), and some nests, like one in Pennsylvania (Ernst, 1986) and one in northern Indiana (P. Meyer, *pers. obs.*), were found 45 and 49 m, respectively, from the water.

By nearly all accounts, nest construction by *S. odoratus* is minimal. For example, some females lay their eggs on the open ground (Cagle, 1937; Palmer and Braswell, 1995), but most nests are very shallow, having been constructed by merely scraping away the surface matter (leaves, grass, moss, mold, rotting wood, and/or soil). Eggs are deposited, and surface material is scraped back over the eggs. However, some females bury their eggs in excavated nests up to 10 cm deep (Carr, 1952; Ernst 1986), and nests have been found under logs (Cagle, 1937; Palmer and Braswell, 1995), in muskrat lodges (Hankinson, 1908; Risley, 1933), in accumulated organic matter between the buttresses of cypress and tupelo trees (Carr, 1952), and in stumps and mats of dead vegetation (Eigenmann, 1896; Cagle, 1937). One nest was even found 1.5 m above the ground on a rotting stump (Cagle, 1937). Although a wide range of sites are satisfactory for nesting, *S. odoratus* will use communal nesting sites. For example, 362 eggs were found in a mucky area at the edge of a lake in northern Indiana (Eigenmann, 1896), three separate muskrat lodges contained 179, 196, and 253 eggs in Michigan (Risley, 1933), two separate muskrat lodges contained 70 and 91 eggs in Michigan (Hankinson, 1908), 16

Table 14-6. Egg sizes of common musk turtle, *Sternotherus odoratus*, in approximate order of declining latitude. Means and range (in parentheses). * = egg mass estimated from mean egg length and width using the equation in the text.

Location	Egg length, mm	Egg width, mm	Egg mass, g	Source
Maine	26.6 (23.5-31.5)	16.0 (15.0-17.6)	4.30*	Graham and Forsberg, 1986
Wisconsin	26.7 (23.4-28.9)	15.1 (14.2-16.6)	3.80*	Edgren, 1949
Wisconsin	26.1 (24.7-27.7)	14.7 (14.3-15.2)	3.49*	Edgren, 1956
Michigan	27.1 (24-31)	15.5 (14.2-17.0)	4.12*	Risley, 1933
Indiana	26.6 (24.3-28.7)	14.9 (13.5-16.0)	3.87	Iverson, unpubl. data
Indiana	26.8 (–)	15.4 (–)	3.95	Clark et al., 2001
Indiana	27.3 (–)	15.3 (–)	4.07	Clark et al., 2001
Indiana	26.9 (–)	15.0 (–)	3.75	Clark et al., 2001
New York	25.7 (25.1-26.7)	15.1 (14.9-15.6)	3.64*	Schlauch, 1969
Pennsylvania	26.2 (23.0-28.0)	15.5 (13.6-15.3)	3.46*	Ernst, 1986
Northern Virginia	– (24-30)	– (14-16)	–	Ernst et al., 1997
Virginia	24.6 (–)	14.1 (–)	2.88*	Mitchell, 1985b
Virginia	25.9 (22.2-28.5)	14.7 (13.0-16.8)	3.3 (2.1-4.6)	Mitchell, 1994
North Carolina	25.9 (22.0-29.3)	15.3 (11.7-18.2)	3.78*	Palmer and Braswell, 1995
Oklahoma	26.3 (21.5-30.2)	15.5 (13.6-16.8)	3.97*	Mahmoud and Klicka, 1972
Arkansas	28.6 (25.9- 32.0)	16.4 (14.3-18.0)	4.87 (3.37-6.43)	Iverson, unpubl. data
South Carolina	27.06	15.47	4.04	Congdon and Gibbons, 1985
South Carolina	– (23.2-25)	– (15.1-15.4)	– (3.5-3.6)	Conant and Downs, 1940
Alabama	26.7 (23.5-30.3)	15.9 (14.2-16.7)	4.2 (3.28-5.21)	McPherson and Marion, 1981
Northwest Florida	25.3 (23.0-28.0)	14.9 (14-16)	3.45*	Sanderson, 1970
Florida	23.6 (19.8-27.0)	13.5 (11.2-15.0)	2.57 (1.96-3.28)	Gross, 1982
Southern Florida	22.6 (20.0-29.0)	13.6 (12.2-15.0)	2.24*	Meshaka, 1988

nests were found under a single 1 m log in Tennessee (Cagle, 1937), 130 eggs were found under debris in an abandoned duck blind in Wisconsin (Edgren, 1942), and 39 eggs were found in a rotted stump about 1 m above the water and about 90 m from shore in northwestern Florida (Sanderson, 1970).

Eggs. — The eggs of *S. odoratus* are more blunt-ended than an ellipsoid in shape (Iverson and Ewert, 1991), with a brittle white calcareous shell (Carr, 1952; Ewert, 1985), and typically about 26 mm long and 15 mm wide (Table 14-6). They do not increase in size during incubation (Edgren, 1956; Palmer and Braswell, 1995). Egg length (EL, mm), egg width (EW, mm), and egg mass (EM, g) across multiple populations are related by the equation: EM = 0.186EL + 0.549EW - 9.433 (n = 272; r = 0.98) (JBI, unpubl. data). Components of its eggs (e.g., shell, water, lipids, etc.) are discussed elsewhere (Ewert, 1979; Congdon et al., 1983; Congdon and Gibbons, 1985; Nagle et al., 1998).

Egg size is positively correlated with female body size in some populations (Mitchell, 1985b, 1988; Clark et al., 2001; Wilkinson and Gibbons, 2005), but not in others (Iverson, 1977; McPherson and Marion, 1981b; Congdon and Gibbons, 1985), including those in Florida (Gross, 1982; Meshaka, 1988). Eggs tend to be more elongate in smaller (younger) females, and in smaller clutches (Clark et al., 2001). No evidence of constraint by the pelvic canal on egg size has been demonstrated (Clark et al., 2001; Wilkinson and Gibbons, 2005). However, in Indiana, about 25% of females produced eggs that were larger than the caudal gap between the carapace and the plastron, but posterior plastral kinesis allows these eggs to pass unbroken (Clark et al., 2001).

Egg size is generally positively correlated with latitude (Table 14-6). Relative egg mass (REM = mean egg mass/gravid body mass) has been reported only from central Florida (mean = 4%; Gross, 1982); however, spent REM (mean egg mass/spent female mass) averaged 2.1–3.3% among three Indiana populations (Clark et al., 2001).

Clutch Size and Reproductive Potential. — *Sternotherus odoratus* is a fecund turtle. One female lays up to 9 eggs in a single clutch in northern populations and up to 6 clutches of fewer eggs (1–6) each year in southern populations (Table 14-7). However, in captivity northern females have produced as many as 6 clutches per year (Thierfeldt and Höfler-Thierfelt, 2005), suggesting that clutch frequency is more environmentally than genetically determined. Generally speaking, this species produces the fewest but largest clutches each year in the north and the highest number of small clutches in the south (Table 14-7). However, a latitudinal component to clutch size, first proposed by Tinkle (1961), is complicated by the larger body size of northern females, and so the role of body size in this geographic trend remains unclear. In most populations, including some in Florida, body size and clutch size are positively correlated (Gibbons, 1970; Iverson, 1977; Marion and McPherson, 1981; McPherson and Marion, 1981b; Gibbons et al., 1982; Gross, 1982; Mitchell, 1985b; Ernst, 1986; Clark et al., 2001; Wilkinson and Gibbons, 2005; but see Meshaka, 1988) (Fig. 14-6). Although expected on theoretical grounds, clutch size and egg size are not inversely related when the effect of body size is removed (Clark et al., 2001; Wilkinson and Gibbons, 2005). In central Florida, females may split clutches, whereby they lay the eggs from a single clutch in more than one nest (Gross, 1982).

Annual reproductive potential (RP) represents an estimate of the total number eggs that can be produced each year

Table 14-7. Geographic variation in mean clutch size (CS) and annual clutch frequency (CF) in the common musk turtle, *Sternotherus odoratus*.

Location	CS (range)	CF	Source
Maine	6.3 (3-9)	–	Graham & Forsberg, 1986
Wisconsin	– (1-8)	–	Edgren, 1956
Wisconsin	– (1-8)	1	Vogt, 1981
Michigan	– (2-9)	1	Risley, 1933
Illinois	–	3	Moll, 1979
Northern Indiana	3.7 (2-6)	–	Iverson, unpubl. data
Northern Indiana	– (4-7)	–	Eigenmann, 1896
Central Indiana	6.7 (–)	–	Clark et al., 2001
Central Indiana	3.8 (–)	–	Clark et al., 2001
Central Indiana	3.2 (–)	–	Clark et al., 2001
Pennsylvania	3.25 (2-4)	≥ 1	Ernst, 1986
Northern Virginia	3.4 (2-4)	–	Ernst et al., 1997
Northern Virginia	3.4 (2-4)	–	Ernst, in Mitchell, 1994
Eastern Virginia	3.2 (2-7)	2	Mitchell, 1985b, 1988
Eastern Virginia	2.7 (1-5)	2	Mitchell, 1988
Virginia	3.6 (1-9)	2	Mitchell, 1994
Western Tennessee	2.3 (1-3)	–	Cagle, 1937
North Carolina	3.1 (2-8)	–	Palmer & Braswell, 1995
Oklahoma	3.0 (2-5)	1	Mahmoud & Klicka, 1972
Arkansas	4.5 (2-8)	2-3	Iverson, unpubl. data
South Carolina	5.6 (2-8)	–	Gibbons et al., 1982
South Carolina	5.0 (–)	1?	Wilkinson & Gibbons, 2005
Alabama	2.6 (1-6)	2-3	Marion & McPherson, 1981
Alabama	2.75	3-4	McPherson & Marion, 1981b, 1983
Louisiana	–	3	Moll, 1979
North Florida	3.2 (2-6)	3-4	Iverson, 1977
North Florida	2.4 (1-4)	≥ 2	Gibbons, 1970
Central Florida	1.7 (1-3)	1-6	Gross, 1982
Southern Florida	2.3 (1-3)	3-4	Meshaka, 1988

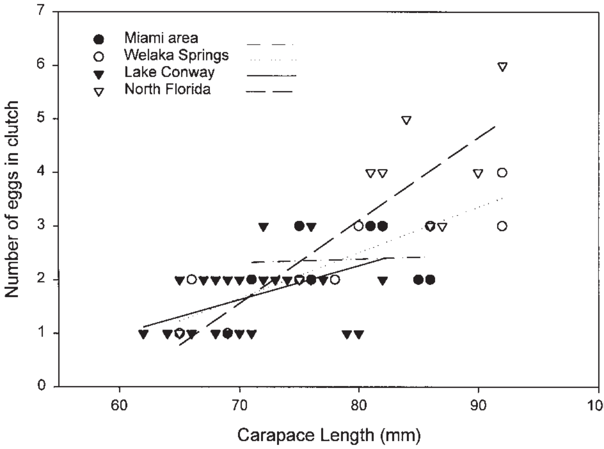

Figure 14-6. Clutch size (CS; based on oviductal egg counts) as a function of female CL in *Sternotherus odoratus* at four sites in Florida. For Miami, CS = 0.007 CL + 1.84 ($r^2 = .01$; $n = 9$), for Welaka Springs (Putnam Co.,), CS = 0.085 CL - 4.3 ($r^2 = .78$; $n = 8$), for Lake Conway (Orange Co.), CS = 0.063 CL – 2.82 ($r^2 = .25$; $n = 53$), for north Florida, CS = 0.155 CL - 9.30 ($r^2 = .69$; $n = 11$). The Miami data are from Meshaka (1988), the Welaka data are from Gibbons (1970), the Lake Conway data are from Gross (1982), and the north Florida data are from Iverson (1977). All regressions except that for Miami are significant at $p < 0.05$.

by a single female and is available for many populations. In northern, single-clutch populations, maximum RP may reach 9 eggs/yr, but probably averages closer to 5 or 6 (Risley, 1933; Edgren, 1956; Tinkle, 1961; Vogt, 1981). In Pennsylvania, estimated RP is 6.5 eggs/yr if 2 clutches are produced and 9.3 eggs/yr if 3 clutches are produced (Ernst, 1986). In Virginia, estimates of RP average about 6 eggs/yr (Mitchell, 1985b, 1988). In Alabama, RP may range from 7.8 to 8.3 eggs/yr (McPherson and Marion, 1981b, 1983). In north Florida, estimated RP is about 9.6 eggs/yr (Iverson, 1977). In central Florida, RP averages about 5.4 eggs/yr (Gross, 1982) with a maximum potential of 16 eggs/yr. In southern Florida, estimated RP is 6.3 eggs/yr with a maximum of over 9 eggs/yr (Meshaka, 1988). Although preliminary, these data suggest that contrary to Tinkle's (1961) hypothesis, southern females actually produce about the same number of eggs each year (in more but smaller clutches) than northern females, even though southern females are smaller in body size (see above).

Estimates of relative clutch mass (RCM = clutch mass/gravid body mass) for *S. odoratus* are available for populations in central Florida (Gross, 1982), South Carolina (Congdon and Gibbons, 1985) and Indiana (Clark et al., 2001). In central Florida, RCM increases in one, two, and three-egg clutches (9.7%, 12.4%, and 15.0%, respectively). Average RCM in South Carolina was 11.1%, and mean estimated RCM from three populations in Indiana ranged from 9.3 to 12.4%.

Florida populations represent an endpoint in a geographic trend for more southerly populations to have annual production of many small clutches of small eggs. The strategy of producing many small clutches could be strongly selected for, particularly in southern Florida, where a pronounced wet season could flood many clutches during very wet years.

Incubation and Hatching. — The incubation period ranges from 56 (Gad, 1987) to 132 days (Polder, 1979). Only Ernst (1986) provided a "natural" incubation period for *S. odoratus*, which in Pennsylvania ranged from 75–82 days (mean = 78.3; *n* = 32). Records of laboratory incubation periods from known sites are numerous and generally range between 60–101 days (Risley, 1933; Edgren, 1956; Iverson, 1977; Mitchell, 1985b; Dundee and Rossman, 1989; Mitchell, 1994; Palmer and Braswell, 1995; Schilde 2001; Debry, 2005; Thierfeldt and Höfler-Thierfelt, 2005). Because incubation temperatures influence length of incubation (Risley, 1933; Ewert, 1979), lack of temperature data for most of these studies makes it impossible to examine them for geographic patterns in incubation time. However, when controlled for temperature, incubation times are in general inversely related to latitude (Table 14-8). Details of embryonic development (Ewert, 1985) and hatching (Carr, 1952; Polder, 1979; Thierfeldt and Höfler-Thierfelt, 2005) exist for *S. odoratus*, and twinning (Ewert, 1971b; Gad, 1987) and kyphosis (Gad, 1987; Saumure, 2001; JBI, *pers. obs.*) have been recorded in this species.

Like incubation periods, most hatching dates are derived from captive conditions. In Florida a hatching egg was discovered on 12 August (Carr, 1952), and a single captive egg hatched on 5 July (Iverson, 1977). Outside of Florida captive hatching dates are during August–October (Edgren, 1956; Schlauch, 1969; Mitchell, 1985b; Cagle, in Dundee and Rossman, 1989; Palmer and Braswell, 1995). Natural hatching of *S. odoratus* occurs in late summer and fall (Eigenmann, 1896; Evermann and Clark, 1916; Ernst, 1986; Mitchell, 1988, 1994).

Table 14-8. Average incubation times in days for common musk turtle, *Sternotherus odoratus*, eggs from selected locations under different temperature regimes (Ewert, 1971a, 1979, 1985).

Location	22.5-25.0ºC	25.0-25.5ºC	27.4ºC	29.5-30.0ºC
Wisconsin	–	80.5	–	59.4
Tennessee	86.7	–	69.0	70.3
Alabama	–	90.0	–	65.0
Northern Florida	106.6	91.2	–	63.1

In South Carolina, hatchlings of *S. odoratus* overwinter in the nest (Gibbons, 1970; Gibbons and Nelson, 1978). Farther north, hatchlings are evident only in the fall (JBI, *pers. obs.*; Ernst, 1986; Mitchell, 1988). The discovery of dead embryos in eggs found in the spring in Michigan (Risley, 1933) and the inability of hatchlings to survive at -6.5°C in contact with vermiculite that contains ice-nucleating bacteria (Costanzo et al., 2000) corroborate the notion that overwintering is distinctly a phenomenon of southern populations and is contrary to Gadow's (1920; in Risley, 1933) statement that hatchlings of *S. odoratus* "apparently pass the winter months in the egg and hatch in the spring." Overwintering in the egg or as hatchlings in the nest has not been confirmed anywhere in Florida.

Upon emergence from the nest, hatchlings of *S. odoratus* are attracted to high humidity and move immediately to the nearest body of water, orienting toward large areas of illumination (Noble and Breslau, 1938). Hatchlings have extremely high rates of evaporative water loss (Costanzo et al., 2001), and in Florida constitute less of their fresh egg mass than do those from Wisconsin (Ewert, 1979). However, because most nests are in close proximity to water (see above), hatchlings generally are exposed to desiccating conditions for only short periods.

Hatching success data for *S. odoratus* are lacking throughout much of its range and do not exist for Florida populations; however, for 32 nests (104 total eggs) in Pennsylvania (Ernst, 1986), 25 were destroyed by predators, 2 desiccated, and only 16 of the remaining 20 eggs from 5 nests hatched successfully. Although the success rate of that cohort was low (15.4%), it is probably typical for small kinosternid turtles (Iverson, 1991b,c).

Sternotherus odoratus is subject to temperature-dependent sex determination (Vogt et al., 1982; Clark et al., 1986; Ewert and Nelson, 1991), whereby females predominate at extreme temperatures (e.g., 22.5 or 30.0°C) and males predominate at intermediate temperatures (e.g., 25°C). No evidence of geographic variation in this pattern has yet been identified.

Hatchlings. — Hatchling size of *S. odoratus* from north Florida is within the 17–26 mm CL range found elsewhere

(Risley, 1933; Mahmoud, 1969; Iverson, 1977; Ernst, 1986; Mitchell, 1985b, 1994; Palmer and Braswell, 1995).

POPULATION BIOLOGY

Density and Biomass. — In Florida, density estimates of *S. odoratus* have ranged from 106/ha in the Rainbow River in Marion County (Meylan et al., 1992) to 700/ha in a shallow pond near Gainesville in Alachua County (Iverson, 1982). These values are typical for small freshwater kinosternid and emydid turtle species (Iverson, 1982).

Sternotherus odoratus can be extremely abundant anywhere in its range. In lakes, population size estimates ranged from 80/ha in Indiana (Wade and Gifford, 1965; calculated by Iverson, 1982) to 149/ha in Alabama (Dodd, 1989), 174/ha in Missouri (Ford, 1999), and 79/ha (Holinka et al., 2003) and 194/ha (Mitchell, 1988) in Virginia. A creek in Oklahoma was estimated to have 50/ha (Mahmoud, 1969). In Pennsylvania, it can occur at abundances of 24/ha in ponds, marshes, and streams (Ernst, 1986). Densities of *S. odoratus* ranging from 8–22/ha occurred in small ponds in South Carolina (Congdon et al., 1986).

In Florida, estimates of standing crop biomass have ranged from 6.1 kg/ha in Rainbow River (Meylan et al., 1992) to 41.7 kg/ha near Gainesville (Iverson, 1982) and are similar to those of other carnivorous kinosternid turtles, but are generally greater than those for herbivorous turtles (Iverson, 1982). Estimates of biomass outside of Florida have ranged from 8.4 kg/ha in Indiana (Wade and Gifford, 1965; estimated by Iverson, 1982) to 16.3 kg/ha in Missouri (Ford, 1999; see also Mahmoud, 1969; Iverson, 1982; Mitchell, 1988; Dodd, 1989).

Population Structure. — Sex ratio varies across populations from strongly male-biased (Ontario and Florida, among others) to strongly female-biased (Table 14-9). Interpreting this variation is complicated by temperature-dependent sex determination in this species (see above), possible differential migration patterns between the sexes, possible differential mortality between the sexes, and the different ages and sizes at maturity (see above). The contradictory and inconsistent patterns of seasonal variation in sex ratio (Risley, 1933; Dodd, 1989; Edmonds and Brooks, 1996) underscore the local scale sensitivity of this phenomenon and the possibility of sampling bias. However, there may be a general trend from generally more male-biased populations in the north to those more generally unbiased or female-dominated in the south.

Recruitment varies widely among populations (Agassiz, 1857; Risley, 1933; Wade and Gifford, 1965; Mitchell, 1988; Dodd, 1989; Edmond and Brooks, 1996; Ford, 1999). Juveniles comprise from 3% of the population in Missouri (Ford, 1999) to 28.4% in Pennsylvania (Ernst, 1986). These data may well reflect a collecting bias against juveniles and hatchlings in the north; in Florida, juveniles can be captured by hand in mats of floating vegetation much more readily than in traps (JBI and WEM, *pers. obs.*). Only one study in Florida examined juvenile population composition: 13% of the males and 17% of the females were juveniles (Bancroft et al., 1983).

Survivorship. — Data on age-specific survival do not exist for *S. odoratus* in Florida. However, in Virginia, annual survivorship was high for recaptured juveniles (85.8%), adult males (84.1%), and adult females (84.2%; Mitchell, 1988). Estimated annual survivorship based on the age-class structure in that study suggested that females averaged 84.5%/yr and males, 78%/yr.

INTERSPECIFIC INTERACTIONS

Community Structure. — In Florida, the relative abundance of *S. odoratus* in the aquatic turtle community varies widely. In a central Florida lake it was the dominant turtle (Bancroft et al., 1983), whereas in the southern Everglades it is extremely rare (Dalrymple, 1988; Meshaka et al., 2000; WEM, *pers. obs.*). Still, in some southern Florida canals, *S. odoratus* was captured routinely and in numbers similar to those of *K. baurii* (Meshaka, 1988). In Rainbow Run *S. odoratus* was second in abundance to *S. minor* (Meylan et al., 1992). Much remains to be learned regarding the community dynamics of *S. odoratus.*

Diet and Feeding. — Common musk turtles are omnivorous, but seem to favor carnivory (particularly molluscivory). Ernst and Barbour (1972) reported that they feed on earthworms, leeches, clams, snails, crabs, crayfish, aquatic insects, fish eggs, minnows, tadpoles, algae, and parts of higher plants. In Michigan they feed on carrion (40% by volume), mollusks (23%), insects (17%), crayfish (6%),

Table 14-9. Variation in sex ratio among populations of common musk turtle, *Sternotherus odoratus* (listed in approximate order of increasing average annual temperatures). *small juveniles only; **subjected to significant road mortality of nesting females.

Location	*n*	% Male	Source
Ontario	420	72.1	Edmonds & Brooks, 1996
Michigan	255	30.3	Risley, 1933
Michigan	68	52.9	Gibbons, 1990
Northern Indiana	717	62.9	Smith & Iverson, 2002
Northern Indiana	188	58.5	Wade & Gifford, 1965; Wade, unpubl. data
Pennsylvania	146	57.3	Ernst, 1986
Illinois	51*	29.4	Tinkle, 1961
Illinois	226	41.2	Cagle, 1942
Indiana	292	58.2	Conner et al., 2005
Virginia	ca. 1596	43.9	Mitchell, 1988
Virginia	651	63.4	Holinka et al., 2003
Virginia	197	64.0	Smar & Chambers, 2005
Missouri	252	48.0	Ford, 1999
Oklahoma	233	50.6	Mahmoud, 1969
South Carolina	413	56.7	Gibbons, 1990
Alabama	113	26.3	Dodd, 1989
Alabama	–	< 50	Marion, in Dodd, 1989
Alabama	–	37.5	Prassack et al., 1992
Louisiana	86	33.3	Rayburn et al., 1989
Northern Florida	449	65.3**	Aresco, 2005a
Northern Florida	39	38.5	Aresco, 2005a
Northern Florida	62	64.5	Iverson, unpubl. data
Central Florida	3008	53.7	Bancroft et al., 1983
Southern Florida	28	35.7	Meshaka, 1988
“southern”	86	59.3	Tinkle, 1961

fish (6%), debris (4%), and plants (3%; Lagler, 1943). In Wisconsin, specimens examined by Vogt (1981) contained primarily mollusks and crayfish. In Indiana, Evermann and Clark (1916) observed them feeding on dead fish and cow dung. Although virtually all feeding is done underwater, Newman (1906) observed musk turtles crawling on land at dusk in northern Indiana and eating terrestrial slugs. In Pennsylvania, Surface (1908) found snails (in 50% of stomachs), crickets (25%), lepidopteran larvae (50%), and beetles (50%) in the diet, and Ernst (1986) observed musk turtles feeding (in no particular order) on algae, leeches, snails, crayfish, larval and adult insects, tadpoles and adult frogs, and dead fish. In Missouri, Ford (1999) stomach-flushed musk turtles and found unidentifiable material (55% by volume), algae (22%), plant material (11%), mollusks (11%), crayfish (8%), seeds (7%), insects (6%), and fish (1%); she also recorded crustaceans and spiders on occasion. In Oklahoma, Mahmoud (1969) reported that they feed on insects (46% by volume), mollusks (24%), aquatic vegetation (20%), crustaceans (5%), carrion (3%), and amphibians (1%). In Virginia, Mitchell (1994) recorded (in no particular order) seed pods and seeds, beetles, moths, dragonflies, crayfish, and snails. In North Carolina, Palmer and Braswell (1995) observed one individual feeding on a dead catfish and another that defecated snail shell fragments.

In central Florida, Bancroft et al. (1983) found that almost 20% of the diet of *S. odoratus* was plant material, with the seeds of pond lilies (*Nuphar luteum*) and eelgrass (*Vallisneria americana*) being the most common plant items (29.4% of ingested plant biomass). Other plants in the diet included (in decreasing order of abundance by biomass) vegetative parts of *Nuphar*, vegetative parts of *Vallisneria*, filamentous algae, water hyacinths (*Eichhornia*), Illinois pondweed, and hydrilla (*Hydrilla*). Of the 80% of the diet by biomass comprising animal matter, 44% was snails, 16% was lepidopteran insect larvae, 13% was tricopteran insect larvae, 9% was crustaceans, 3% was clams, and the remainder was unidentifiable.

Although musk turtles clearly feed purposely on the seeds of aquatic plants, other kinds of plant material in the diet may be the result of secondary ingestion while capturing animal prey. However, Ford (1999) suggested that *S. odoratus* may be important seed dispersers for aquatic macrophytes like *Ludwigia*. No study has been done relating food item availability versus food selectivity by musk turtles.

Berry (1975) examined stomach contents of *S. odoratus* in the Wakulla River (Wakulla Co.), Wacissa River (Jefferson Co.), and Horn Springs (Leon Co.) in Florida. He found that crustaceans made up 19.1% of the diet on average, plant material 9.0%, snails 4.3%, insect larvae 2.1%, clams 1.4%, fish 0.3%, adult insects 0.2%, and detritus or carrion 12.0%.

The only analysis of sexual differences in diet was that of Ford (1999) in Missouri, who found that females ate more grass seeds, *Ludwigia* seeds, crayfish, planorbid snails, fingernail clams, mayflies, beetles, and isopods; fewer *Ceratophyllum* seeds, water striders, and lepidopterans; and more animal matter overall than males did.

Mahmoud (1969) presented data on the seasonal variation in diet in this species, suggesting that turtles ingested significantly more vegetation and fewer insects in September than in May through August. Ford (1999) also found seasonal differences in the diet, with more seeds being consumed in September than in June–August, more vegetative (plant) matter in July–August, more crayfish in June, and more *Heliosoma* snails, Asian clams, and insects in June. Bancroft et al. (1983) also demonstrated seasonal variation in diet with fewer plants being consumed in spring and fewer tricopterans later in summer. Ernst (1986) observed feeding from mid-April to mid-September in Pennsylvania, but the species appears to feed year-round in southern Florida (WEM; *pers. obs*.).

Feeding trials in captivity (47 trials of 5 turtles) showed that *S. odoratus* in Oklahoma fed on snails in 132 of 235 trials (56%), dipteran larvae in 70 of 235 trials (30%), june bugs in 23 of 235 trials (10%), tadpoles in 10 of 235 trials (4%), and juvenile garter snakes in none of 235 trials. A live rat placed in an aquarium was killed and devoured by the *S. odoratus* inhabiting the tank (Newman, 1906). Mahmoud (1969) reported gut passage times of two to five days (mean = 3), when turtles were held at 20ºC, and five to eight days (mean = 7) at 15ºC.

Lagler (1943; repeated by Minton, 1972) suggested that because musk turtles prey so heavily on snails, *S. odoratus* may be important in reducing fish parasites for which snails are the hosts. Lagler (1943) also speculated that musk turtles might be important in dispersing the seeds of aquatic plants, although neither of these hypotheses has been tested.

In clear water, musk turtles can often be observed walking along the bottom with the head and neck extended as they probe the substrate with their snout (Mahmoud, 1969; JBI, *pers. obs*.). Although they can clearly use visual signals to detect prey items, the primary means of prey detection is probably olfactory. However, tactile stimuli via the chin and neck barbels are probably also important.

Dietary niche overlap between *S. odoratus* and *S. minor* may have bearing on the composition of the turtle community in the Rainbow River (Marion Co.) in Florida. In 1940, 1022 turtles of seven species (including *S. odoratus*) were captured in the Rainbow River, but not a single *S. minor* (Marchand, 1942, 1945). In the 1970s, both species were nearly equal in abundance (P. Meylan and JBI, unpubl. data). Somewhat subjectively, it seemed that *S. odoratus* primarily inhabited the shallower, slower, backwaters with abundant vegetative and organic substrates, whereas *S. minor* was more often in open water, on sandy or rocky substrates. Quantitative censusing in 1990 (Meylan et al., 1992) demonstrated that not only were *Sternotherus* species the most common species encountered, but that *S. minor* was 2.6 times more numerous than *S. odoratus.* Likewise, surveys during 1990–91 by Giovanetto (1992) revealed that *S. minor* was 2.2 times as abundant as *S. odoratus.* Apparently, *S. minor* was introduced into Rainbow River subsequent to 1940, after which time it rapidly colonized the river. Because abundances of *S. odoratus* also increased over that time (Meylan et al., 1992), a detrimental effect from syntopy seems unlikely. Analysis of gut contents and head morphology from museum specimens of *S. odoratus* before and after 1940 could possibly determine if any behavioral or anatomical adjustments occurred in response to the colonization of *S. minor*.

Predation. — *Sternotherus odoratus* is eaten by raccoons, foxes, skunks, large wading birds, water snakes (Mitchell, 1994), muskrats (Evermann and Clark, 1916), red-shouldered hawks (Ernst et al., 1994), bald eagles (Clark, 1982; Palmer and Braswell, 1995), alligators (Delany and Abercrombie, 1986; Delany et al., 1988; Delany 1990; JBI, *pers. obs.*), snapping turtles (Pritchard, 1989; Mitchell, 1994; Palmer and Braswell, 1995; Punzo and Alton, 2002), cottonmouths (Ernst and Barbour, 1972; Ernst et al., 1994), bullfrogs, and largemouth bass (Ernst and Barbour, 1972; Mitchell 1994). They also have been accidentally killed by clams (Plummer and Goy, 1997). Eggs of *S. odoratus* are eaten by scarlet snakes, kingsnakes, skunks, raccoons, herons, and crows (Ernst et al., 1994). However, eggs can sometimes hatch after being defecated by a kingsnake (Forks, 1979; Knight and Loraine, 1986).

The primary defense of *S. odoratus* is crypsis. Upon provocation underwater, individuals quickly swim away. Removed from water, some individuals withdraw into their shells, but most individuals of all size-classes vigorously defend themselves by biting and by scratching with their claws. Their surprisingly long neck and reduced plastron permit them to bite nearly to the level of their hind legs, and once they have bitten something, they are reluctant to release their grip. Regardless of their behavioral reaction to physical disturbance, alarmed individuals nearly always exude a pungent yellowish musk from the musk glands, adjacent to the bridge of the shell (Ehrenfeld and Ehrenfeld, 1973). The musk is comprised of four phenylalkonoic acids and several aliphatic acids (Eisner et al., 1977). The role of its musk other than in defense is unknown.

Parasites and Disease. — *Sternotherus odoratus* is parasitized by leptospiran bacteria (Glosser et al., 1974), protozoans (Evermann and Clark, 1916; Ernst and Ernst, 1979), nematodes (Ernst and Ernst, 1977; Platt, 1983), trematodes (Byrd, 1939; Hughes et al., 1941, 1942; Ernst and Ernst, 1977; Platt, 1988), and leeches (Curry and Kennedy, 1975; Ernst, 1986; Ryan and Lambert, 2005). The wide range of aquatic habitats used by this species in Florida warrants concern regarding parasite loads particularly in eutrophic and polluted retention ponds and canals.

At least nine species of algae have been recorded from the shells of this species (Wilson and Friddle, 1950; Edgren et al., 1953; Neill and Allen, 1954; Proctor, 1958; Dixon, 1960; Belusz and Reed, 1969; Mahmoud, 1969; Reilly, 1983; Ernst, 1986), and algal colonies have been recorded from more than 50% of individuals examined (Edgren et al., 1953; Ernst, 1986). Occasionally the shells of *S. odoratus* are pitted and eroded by some unknown pathogen. Shells of individuals from northern Indiana are pitted (JBI, unpubl. data) in the same manner described for *S. minor* in Florida (Jackson, 1965).

THREATS

Sternotherus odoratus was used for food (Adler, 1968; Rhodin, 1995) and possibly for medicinal and/or ceremonial purposes (Hoffmann, 1990) by prehistoric humans. Today, it faces a range and intensity of threats. Its highly aquatic habits and ability to inhabit nearly all kinds of freshwater habitats remains an advantage as long as these sites are not impacted by humans. For example, when a shallow, wooded, shrubby wetland (maximum total surface area only 900 m^2) on both sides of a road in southern Gainesville, Florida was drained in December 1971 to bury utility pipes, 62 adults were captured in an unbaited funnel trap in the 18 inch culvert that connected the two sites below the road (JBI, unpubl. data). This suggests that destruction of even the smallest wetlands can destroy significant populations of *S. odoratus*.

Significant mortality of females on roads during nesting forays has been documented in north Florida, and has been shown to alter sex ratios in adjacent wetlands (Aresco, 2005a,b). Recreational boating also takes an unknown toll on *S. odoratus* populations in larger lakes through propeller damage and/or death (Bancroft et al., 1983; JBI, *pers. obs.*). Reductions in shoreline vegetation (e.g., by grass carp) reduce cover for musk turtles, and Bancroft et al. (1983) demonstrated a decline in populations in central Florida when pondweed was reduced. In this connection, routine aquatic weed control in the extensive canals of southern Florida creates barren shorelines, no doubt less habitable by many organisms, including *S. odoratus*. Lastly, because this species is easily caught on hook and line (Babcock 1919; Williams, 1952; Mahmoud, 1969; Mitchell, 1988), populations can be negatively impacted in areas with high bait fishing intensity. For example, 1% of Pennsylvanian turtles (*n* = 204) had jaw wounds presumably caused by fish hooks (Ernst, 1986). Relatively few *S. odoratus* apparently are collected for the commercial pet trade.

Because this turtle is highly aquatic, found in a wide range of freshwater systems, secretive, and unattractive to the pet trade, it is likely to escape serious depletion throughout mainland Florida as long as wetlands and the adjacent uplands needed for nesting are protected.

STATUS

This species is listed as threatened in Iowa (Frank and Ramus, 1994), and protected in Vermont and Quebec (Mitchell, 1994), all of which lie along the northern limits of its geographic range. Certain states, including Illinois, Indiana, Kansas, Maryland, Massachusetts, Michigan, Missouri, Oklahoma, Pennsylvania, and Virginia limit the number a person can keep in captivity (Frank and Ramus, 1994; Mitchell, 1994). In addition, some states (Arkansas, Illinois, Indiana, Maine, Massachusetts, Missouri, Oklahoma, Pennsylvania, Rhode Island, and Virginia) prohibit the sale or trade of this species, although a permit to do so may be obtained in some cases (Frank and Ramus, 1994; Mitchell, 1994; JBI, *pers. obs*.).

CONSERVATION OPTIONS AND SOLUTIONS

As noted above, conservation of wetlands and adjoining uplands will insure the continued presence of this species in Florida. Public education about this abundant but secretive turtle could curtail needless killing by the fishing public.

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LITERATURE CITED

Adler, K.K. 1968. Turtles from archeological sites in the Great Lakes region. Michigan Archaeologist 14:147-163.

Agassiz, L. 1857. Contributions to the natural history of the United States of America, vol. 1, 2. Boston, MA: Little, Brown and Co., 452 pp.

Andrews, K.D., and Andrews, S.L. 1992. Life history notes. *Sternotherus odoratus* (stinkpot). Reproduction. Herpetological Review 23(4):116-117.

Aresco, M, J. 2005a. The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. Biological Conservation 123:37-44.

Aresco, M. J. 2005b. Mitigation measures to reduce highway mortality of turtles and other herpetofauna at a north Florida lake. Journal of Wildlife Management 69:549-560.

Babcock, H.L. 1919. The turtles of New England. Memoirs of the Boston Society of Natural History 8:323-431.

Bancroft, G. T., Godley, J. S., Gross, D. T., Rojas, N. N., Sutphen, D. A., and McDiarmid, R. W. 1983. The herpetofauna of Lake Conway: species accounts. U.S. Army Corps Engineers, Miscellaneous Papers, A-83-5. Army Engineer Waterways Experiment Station, Vicksburg, Miss. 354 pp.

Belusz, L.C., and Reed, R.J. 1969. Some epizoophytes on six turtle species collected in Massachusetts and Michigan. American Midland Naturalist 81:598-601.

Berry, J.F. 1975. The population effects of ecological sympatry on musk turtles in northern Florida. Copeia 1975:692-701.

Berry, J.F., and Shine, R. 1980. Sexual size dimorphism and sexual selection in turtles (order Testudines). Oecologia 44:185-191.

Byrd, E.E. 1939. Studies on the blood flukes of the family Spirorchidae. Part II. Revision of the family and description of new species. Journal of the Tennessee Academy of Science 14:116-161.

Cagle, F.R. 1937. Egg laying habits of the slider turtle (*Pseudemys troostii*), the painted turtle (*Chrysemys picta*), and the musk turtle (*Sternotherus odoratus*). Journal of the Tennessee Academy of Science 12:87-95.

Cagle, F.R. 1942. Turtle populations in southern Illinois. Copeia 1942:155-162.

Carr, A.F., Jr. 1940. A contribution to the herpetology of Florida. University of Florida, Biology Science Series 3:1-118.

Carr, A.F., Jr. 1952. Handbook of turtles. The turtles of the United States, Canada, and Baja California. Ithaca, NY: Cornell University Press, 542 pp.

Clark, P.J., Ewert, M.A., and Nelson, C.E. 1986. Physiological aspects of temperature dependent sex. Proceedings of the Indiana Academy of Sciences 95:519.

Clark, P.J., Ewert, M.A., and Nelson, C.E. 2001. Physical apertures as constraints on egg size and shape in the Common Musk Turtle, *Sternotherus odoratus*. Functional Ecology 15:70-77.

Clark, W.S. 1982. Turtles as a food source of nesting bald eagles in the Chesapeake Bay region. Journal of Field Ornithology 53:49-51.

Conant, R. 1951. The Reptiles of Ohio. Notre Dame, IN: University of Notre Dame Press, 284 pp.

Conant, R. 1958. A Field Guide to Reptiles and Amphibians of the United States and Canada East of the 100th Meridian. Boston, MA: Houghton Mifflin Co., 366 pp.

Conant, R., and Bailey, R.M. 1936. Some herpetological records from Monmouth and Ocean counties, New Jersey. Occasional Papers of the Museum Zoology University of Michigan (328):1-10.

Conant, R., and Berry, J.F. 1978. Turtles of the family Kinosternidae in the southwestern United States and adjacent Mexico: Identification and distribution. American Museum Novitates (2642):1-18.

Conant, R., and Downs, A. 1940. Miscellaneous notes on the eggs and young of reptiles. Zoologica, New York 25:33-48.

Congdon, J. D., and Gibbons, J.W. 1985. Egg components and reproductive characteristics of turtles: Relationships to body size. Herpetologica 41(2):194-205.

Congdon, J.D., Tinkle, D.W., and Rosen, P.C. 1983. Egg components and utilization during development in aquatic turtles. Copeia 1983:264-268.

Congdon, J. D., Greene, J. L., and Gibbons, J.W. 1986. Biomass of freshwater turtles: A geographic comparison. American Midland Naturalist 115:165-173.

Conner, C. A., Douthitt, B. A., and Ryan, T. J. 2005. Descriptive ecology of a turtle assemblage in an urban landscape. American Midland Naturalist 153:428-435.

Costanzo, J.P., Litzgus, J.D., Iverson, J.B. and Lee, R.E., Jr. 2000. Ice nuclei in soil compromise cold hardiness of hatchling painted turtles (*Chrysemys picta*). Ecology 81:346-360.

Costanzo, J.P., Litzgus, J.D., Iverson, J.B. and Lee, R.E., Jr. 2001. Cold-hardiness and evaporative water loss in hatchling turtles. Physiological and Biochemical Zoology 74:510-519.

Curry, M.G., and Kennedy, W.G. 1975. Louisiana turtle leeches with new host record. Proceedings of the Louisiana Academy of Science 38:124.

Dalrymple, G.H. 1988. The herpetofauna of Long Pine Key, Everglades National Park, in relation to vegetation and hydrology. In: Szaro, R., Severson, K.E., and Patton, D.R. (Eds.). Management of amphibians, reptiles, and small mammals in North America. U.S.D.A. Forest Service, General Technical Report RM-166, Fort Collins, Colorado, pp. 72-86.

Debry, A. 2005. Elevage et reproduction en captivité du Cinosterne odorant, *Sternotherus odoratus*. Manouria 8(26):6-9.

Delany, M.F. 1990. Late summer diet of juvenile American alligators. Journal of Herpetology 24:418-821.

Delany, M. F., and Abercrombie, C. L.1986. American alligator food habits in northcentral Florida. Journal of Wildlife Management. 50:348-353.

Delany, M.F., Woodward, A.R., and Kochel, I.H. 1988. Nuisance alligator food habits in Florida. Florida Field Naturalist 16:86-90.

Dixon, J.R. 1960. Epizoophytic algae on some turtles of Texas and Mexico. Texas Journal of Science 12:36-38.

Dodd, C.K., Jr. 1989. Population structure and biomass of *Sternotherus odoratus* (Testudines: Kinosternidae) in a northern Alabama lake. Brimleyana 15:47-56.

Dundee, H.A., and Rossman, D.A. 1989. The amphibians and reptiles of Louisiana. Baton Rouge, LA: Louisiana State University Press, 300 pp.

Dunn, E.R. 1918. A preliminary list of the reptiles and amphibians of Virginia. Copeia 53:16-27.

Dunson, W.A. 1986. Estuarine populations of the snapping turtle (*Chelydra*) as a model for the evolution of marine adaptations in reptiles. Copeia 1986:741-756.

Edgren, R.A. 1942. A nesting rendezvous of the musk turtle. Chicago Naturalist 5:63.

Edgren, R.A. 1949. Variation in the size of eggs of the turtles *Chelydra s. serpentina* (Linne) and *Sternotherus odoratus* (Latreille). Natural History Miscellanea 53:1.

Edgren, R.A. 1956. Egg size in the musk turtle, *Sternotherus odoratus* Latreille. Natural History Miscellanea 152:1-3.

Edgren, R. A. 1960. Ovulation time in the musk turtle, *Sternothaerus odoratus*. Copeia 1960(1):60-61.

Edgren, R.A., Edgren, M.K. and Tiffany, L.H. 1953. Some North American turtles and their epizoophytic algae. Ecology 34:733-740.

Edmonds, J.H. 1998. Population ecology of the stinkpot turtle (*Sternotherus odoratus*) in Georgian Bay, Ontario. Unpubl. data Master's Thesis, University of Guelph, Guelph, Canada.

Edmonds, J.H., and Brooks, R.J. 1996. Demography, sex ratio, and sexual size dimorphism in a northern population of common musk turtles (*Sternotherus odoratus*). Canadian Journal of Zoology 74:918-925.

Ehrenfeld, J.G., and Ehrenfeld, D.W. 1973. Externally secreting glands of freshwater and sea turtles. Copeia 1973:305-314.

Eigenmann, C.H. 1896. The inhabitants of Turkey Lake: Testudinata. Proceedings of the Indiana Academy of Sciences 5:262-264.

Eisner, T., Conner, W.E., Hicks, K., Dodge, K.R., Rosenberg, H.I., Jones, T.H., Cohen, M. and Meinwald, J. 1977. Stink of stinkpot turtle identified: ~phenylalkanoic acids. Science 196:1347-1349.

Ernst, C.H. 1968. Evaporative water-loss relationships of turtles. Journal of Herpetology 2:159-161.

Ernst, C.H. 1986. Ecology of the turtle, *Sternotherus odoratus*, in southeastern Pennsylvania. Journal of Herpetology 20:341-352.

Ernst, C.H., and Barbour, R.W. 1972. Turtles of the United States. Lexington, KY: University Press, Kentucky, 347 pp.

Ernst, C.H., and Ernst, E.M. 1977. Synopsis of helminths endoparasitic in native turtles of the United States. Bulletin of the Maryland Herpetological Society 13:1-75.

Ernst, C.H., and Ernst, E.M. 1979. Synopsis of protozoans parasitic in native turtles of the United States. Bulletin of the Maryland Herpetological Society 15:1-15.

Ernst, C. H., Barbour, R.W. and Lovich, J.E. 1994. Turtles of the United States and Canada. Washington, DC.: Smithsonian Institution Press, 578 pp.

Ernst, C H., Belfit, S.C., Sekscienski, S. W. and Laemmerhahl, A.F. 1997. The amphibians and reptiles of Ft. Belvoir and northern Virginia. Bulletin of the Maryland Herpetological Society 33(1):1-62.

Evermann, B.W., and Clark, H.W. 1916. The turtles and batrachians of the Lake Maxinkuckee region. Proceedings of the Indiana Academy of Sciences 1916:472-518.

Ewert, M.A. 1971a. A comparison of incubation periods of turtles of the western Great Lakes region. Herpetological Review 3(6):105.

Ewert, M.A. 1971b. Cover photo (twin stinkpots). International Turtle Tortoise Society Journal 5(5):cover.

Ewert, M.A. 1979. The embryo and its egg: Development and natural history. In: Harless, M., and Morlock, H. [Eds.]. Turtles: Perspectives and research, 333-413. , New York, NY: .John Wiley & Sons.

Ewert, M.A. 1985. Embryology of turtles. In: Gans, C., Billett, F., and Maderson, P. F. A. [Eds.]. Biology of the Reptilia, vol. 14, Development A, John Wiley & Sons, New York, pp. 75-267.

Ewert, M.A., and Nelson, C.E. 1991. Sex determination in turtles: Diverse patterns and some possible adaptive values. Copeia 1991:50-69.

Finneran, L.C. 1948. Reptiles at Branford, Connecticut. Herpetologica 4:123-126.

Ford, D. 1999. Foraging ecology and demography of *Sternotherus odoratus* in a southwestern Missouri population. Unpubl. data Master's Thesis, Southwest Missouri State University, Springfield, Missouri.

Forks, T. 1979. Kingsnake "lays turtle eggs." Bulletin of the Chicago Herpetological Society 14:119.

Frank, N., and Ramus, E. 1994. State, federal, and CITES Regulations for herpetologists. Pottsville, PA: N. G. Publishing, 377 pp

Gad, J. 1987. Die Zucht von *Sternotherus odoratus* (Latreille, 1801) und die dabei auftretenden Schildanomalien. Salamandra 23(1):1-9.

Gad, J. 1993. Untersuchungen zur Deckungswahl (Sichtschutz) der Schildkröten *Kinosternon subrubrum* und *Sternotherus odoratus*. Salamandra 29(1):1-5.

Gadow, H. 1920. Amphibians and Reptiles. Cambridge Natural History. Vol. 8. Second edition. New York, NY: MacMillan and Co., 410 pp.

Gibbons, J.W. 1970. Reproductive characteristics of a Florida population of musk turtles (*Sternotherus odoratus*). Herpetologica 26:268-270.

Gibbons, J.W. 1982. Reproductive patterns in freshwater turtles. Herpetologia 38:222-227.

Gibbons, J.W. 1987. Why do turtles live so long? Bioscience 37:262-269.

Gibbons, J.W. 1990. Sex ratios and their significance among turtle populations. In: Gibbons, J.W. (Ed.). Life History and Ecology of the Slider Turtle. Smithsonian Institution Press. Washington, D.C., pp. 171-182.

Gibbons, J.W., and Nelson, D.H. 1978. The evolutionary significance of delayed emergence from the nest by hatchling turtles. Evolution 32:297-303.

Gibbons, J.W., Greene, J. L. and Patterson, K.K. 1982. Variation in reproductive characteristics of aquatic turtles. Copeia 1982:776-784.

Gibbons, J.W., Greene, J.L., Congdon, J.D. 1983. Drought-related responses of aquatic turtles. Journal of Herpetology 17:242-246.

Giovanetto, A.L. 1992. Population ecology and relative abundance of sympatric freshwater turtles in the headwaters of two spring-fed rivers in western peninsular Florida. Unpubl. data doctoral dissertation, Florida Institute of Technology, 106 pp.

Gist, D.H., and Congdon, J.D. 1994. Onset of copulatory activities in turtles. Annual Meetings, HL/SSAR, University of Georgia, Athens.

Gist, D.H., and Jones, J.M. 1989. Sperm storage within the oviduct of turtles. Journal of Morphology 199:379-384.

Glosser, J., Sulzer, C.R., Eberhardt, M. and Winkler, W.G. 1974. Cultural and serologic evidence of *Leptospira interrogans* serotype *tarassovi* infection in turtles. Journal of Wildlife Distribution 10(4):429-435.

Graham, T.E., and Forsberg J.E. 1986. Clutch size in some Maine turtles. Bulletin of the Maryland Herpetological Society 22:146-148.

Graham, T.E., and Hutchinson, V.H. 1979. Turtle diel activity: Response to different regimes of temperature and photoperiod. Comparative Biochemistry and Physiology 63A:299-305.

Gray, J.E. 1825. A synopsis of the genera of reptiles and amphibia, with a description of some new species. Annals of Philosophy, new series 10:193-217.

Gross, D.T. 1982. Reproductive biology of the stinkpot, *Sternotherus odoratus*, in a central Florida lake system. Unpubl. data Master's Thesis, University of South Florida, Tampa.

Hankinson, T.L. 1908. Biological survey of Walnut Lake, Michigan. Report of the Geological Survey of Michigan 1907:157-288.

Harper, F. 1940. Some works of Bartram, Daudin, Latreille, and Sonnini, and their bearing upon North American herpetological literature. American Midland Naturalist 23:692-723.

Hay, W.P. 1902. A list of the batrachians and reptiles of the District of Columbia and vicinity. Proceedings of the Biological Society of Washington 15:121-145.

Hoffmann, C.R. 1990. People of the Fresh Water Lake. A prehistory of Westborough, Massachusetts. American University Student Series 11 (Anthropol. Sociol.) 47:1-304.

Holinka, A. M., Dave, R., and Chambers, R. M. 2003. Population ecology of musk turtles (*Sternotherus odoratus*) in a lake in Virginia. Chelonian Conservation and Biology 4:721-725.

Hughes, R.C., Higginbotham, J.W., and Clary, J.W. 1941. The trematodes of reptiles. Part II. Host catalogue. Proceedings of the Oklahoma Academy of Science 21:35-43.

Hughes, R.C., Higginbotham, J.W., and Clary, J.W. 1942. The trematodes of reptiles. Part I. Systematic section. American Midland Naturalist 27(1):109-134.

Iverson, J.B. 1977. Reproduction in freshwater and terrestrial turtles of north Florida. Herpetologica 33(2):205-212.

Iverson, J.B. 1982. Biomass in turtle populations: A neglected subject. Oecologia 55:69-76.

Iverson, J.B. 1991a. Phylogenetic hypotheses for the evolution of modern Kinosternid turtles. Herpetological Monographs 5:1-27.

Iverson, J.B. 1991b. Patterns of survivorship in turtles (order Testudines). Canadian Journal of Zoology 69:386-391.

Iverson, J.B. 1991c. Life history and demography of the yellow mud turtle, *Kinosternon flavescens*. Herpetologica 47(4):373-395.

Iverson, J.B. 1992. A revised checklist with distribution maps of the turtles of the world. Richmond, IN: Privately published, 374 pp.

Iverson, J.B. 1998. Molecules, morphology and mud turtle phylogenetics (family Kinosternidae). Chelonian Conservation Biology 3(1):113-117.

Iverson, J.B., and Ewert, M.A. 1991. Physical characteristics of reptilian eggs and a comparison with avian eggs. In: Deming, D.C. and Ferguson, M.W.J. (Eds.). Egg Incubation: Its Effects on Embryonic Development in Birds and Reptiles. Cambridge University Press, N.Y., pp. 87-100.

Jackson, C.G., Jr. 1965. Carapace erosion in the loggerhead musk turtle *Sternotherus minor minor* Agassiz. Herpetologica 20:279-281.

Jackson, D.C., Herbert, C.V., and Ultsch, G.R. 1984. The comparative physiology of diving in North American freshwater turtles. II. Plasma ion balance during prolonged anoxia. Physiological Zoology 57:632-640.

Jackson, J.F. 1988. Crevice occupation by musk turtles: Taxonomic distribution and crevice attributes. Animal Behavior 36:793-801.

King, P.D. 1996. Aquatic respiration of freshwater tutles (*Sternotherus odoratus, Clemmys guttata, Terrapene carolina*). Unpubl. data doctoral dissertation, North Carolina State University, Raleigh, 136 pp.

Kingsbury, B. A. 1993. Habitat use by the common musk turtle, *Sternotherus odoratus* in Crooked Lake, Indiana. Annual Meetings of the Indiana Academy of Sciences, Purdue University, West Lafayette. Abstract.

Knight, J.L., and Lorraine, R.K. 1986. Notes on turtle egg predation by *Lampropeltis getulus* (Linnaeus) (Reptilia: Colubridae) on the Savannah River Plant, South Carolina. Brimleyana 12:1-4.

Lagler, K.F. 1941. Fall mating and courtship of the musk turtle. Copeia 1941:268.

Lagler, K.F. 1943. Food habits and economic relations of the turtles of Michigan with special reference to fish management. American Midland Naturalist 29:257-312.

Latreille, P.A. 1801. Historie naturelle de reptiles, avec figures Déssinnées d´ après nature. Sonnini de Manoncourt, C. S., and Latreille, P. A. [Eds]. Vol. 1. Paris: Détérville, 280 pp.

Lindsay, R.V. 1965. Egg-laying habits of the musk turtle. Ontario Field Biologist 19:9-10.

Mahmoud, I.Y. 1967. Courtship behavior and sexual maturity in four species of Kinosternid turtles. Copeia 1967:314-319.

Mahmoud, I.Y. 1969. Comparative ecology of the kinosternid turtles of Oklahoma. Southwestern Naturalist 14(1):31-66.

Mahmoud, I.Y., and Klicka, J. 1972. Seasonal gonadal changes in kinosternid turtles. Journal of Herpetology 6:183-189

Marchand, L.J. 1942. A contribution to a knowledge of the natural history of certain freshwater turtles. Unpubl. data Master's Thesis, University of Florida, Gainesville.

Marchand, L.J. 1945. The individual range of some Florida turtles. Copeia 1945:75-77.

Marion, K.R., and McPherson, R.J. 1981. The female reproductive cycle of *Sternotherus odoratus* in central Alabama (Reptilia: Chelonia). Association of Southeastern Biologists Bulletin 28(2):95.

McPherson, R.J., and Marion, K.R. 1981a. Seasonal testicular cycle of the stinkpot turtle (*Sternotherus odoratus*) in central Alabama. Herpetologica 37:33-40.

McPherson, R.J., and Marion, K.R. 1981b. The reproductive biology of female *Sternotherus odoratus* in an Alabama population. Journal of Herpetology 15:389-396.

McPherson, R.J., and Marion, K.R. 1983. Reproductive variation between two populations of *Sternotherus odoratus* in the same geographic area. Journal of Herpetology 17:181-184.

McPherson, R.J., Boots, L.R., MacGregor, III, R., and Marion, K.R. 1982. Plasma steroids associated with seasonal reproductive changes in a multiclutched freshwater turtle, *Sternotherus odoratus*. General and Comparative Endocrinology 48:440-451.

Mendonca, M.T. 1987. Photothermal effects on the ovarian cycle of the musk turtle, *Sternotherus odoratus*. Herpetologica 43(1):82-90.

Mendonca, M.T., and Licht, P. 1986. Seasonal cycles in gonadal activity and plasma gonadotropin in the musk turtle, *Sternotherus odoratus*. General and Comparative Endocrinology 62(3):459-469.

Meshaka, W.E. 1988. Reproductive characteristics of South Florida *Sternotherus odoratus* and *Kinosternon baurii* (Testudines: Kinosternidae). Proceedings of the Arkansas Academy of Sciences 42:1988.

Meshaka, W.E. 1991. In erratum. Proceedings of the Arkansas Academy of Sciences, 44:136.

Meshaka, W.E., and Ashton, R.E. 2005. The Florida herpetofauna in a changing environment. In: Meshaka, W.E., and Babbitt (Eds.). Status and Conservation of Florida Amphibians and Reptiles. Melbourne, FL: Krieger Publ., pp. 3-22.

Meshaka, JR., W.E., Loftus, W.B., and Steiner, T.M. 2000. The herpetofauna of Everglades National Park. Florida Scientist 63(2):84-103.

Meylan, P.A., Stevens, C.A., Barnwell, M. E., and Dohm, E.D. 1992. Observations on the turtle community of Rainbow Run, Marion Co., Florida. Florida Scientist 55(4):219-228.

Minton, S. 1972. Reptiles and amphibians of Indiana. Indiana Academy of Sciences, Monographs 3:1-346.

Mitchell, J.C. 1985a. Variation in the male reproductive cycle in a population of stinkpot turtles, *Sternotherus odoratus*, from Virginia. Copeia 1985(1):50-56.

Mitchell, J.C. 1985b. Female reproductive cycle and life history attributes in a Virginia population of stinkpot turtles, *Sternotherus* *odoratus*. Copeia 1985(4):941-949.

Mitchell, J.C. 1988. Population ecology and life histories of the freshwater turtles *Chrysemys picta* and *Sternotherus odoratus* in an urban lake. Herpetological Monographs 4:40-61.

Mitchell, J.C. 1994. The Reptiles of Virginia. Washington, D. C.: Smithsonian Institution Press, 352 pp.

Moll, E.O. 1979. Reproductive cycles and adaptations. In: Harless, M. and Morlock, H. [Eds.]. Turtles: Perspectives and Research. John Wiley & Sons, New York. pp. 305-331.

Moll, E.O., and Williams, K.L. 1963. The musk turtle *Sternothaerus odoratus* from Mexico. Copeia 1963:157.

Nagle, R.D., Burke, V.J., and Congdon, J.D. 1998. Egg components and hatchling lipid reserves: Parental investment in kinosternid turtles from the southeastern United States. Comparative Biochemistry and Physiology B 120:145-152.

Neill, W.T., and Allen, E.R. 1954. Algae on turtles: Some additional considerations. Ecology 35:581-584.

Newman, H.H. 1906. The habits of certain tortoises. Journal of Comparative Neurobiology and Psychology 16:126-152.

Nickerson, M. A. 2000. Testudines: *Sternotherus odoratus* (Common Musk Turtle): Aerial basking. Herpetological Review 31:238-239.

Noble, G.K., and Breslau, A.M. 1938. The senses involved in the migration of young fresh-water turtles after hatching. Journal of Comparative Psychology 25:175-193.

Olexa, A. 1969. Breeding of common musk turtles *Sternotherus odoratus* at Prague Zoo. International Zoo Yearbook. 9:28-29.

Palmer, W.M., and Braswell, A.L. 1995. Reptiles of North Carolina. Chapel Hill, NC: University of North Carolina Press, 412 pp.

Platt, T.R. 1983. Redescription of *Capillaria serpentina* Hardwood, 1932, (Nematoda: Trichuroidea) from freshwater turtles in Virginia. Canadian Journal of Zoology 61(9):2185-2189.

Platt, T.R. 1988. Phylogenetic analysis of the North American species of the genus *Hapalorhynchus*, 1922 (Trematoda: Spirochiidae) blood-flukes of freshwater turtles. Journal of Parasitology 74(5):870-874.

Plummer, M.V., and Goy, J.W. 1997. *Sternotherus odoratus* (common musk turtle. Mortality. Herpetological Review 28(2):88.

Polder, R. 1979. De kweek van *Sternotherus odoratus*. Aquariumwereld 31(1):6-9.

Powell, R., and Phillips, S. 1984. *Sternotherus odoratus* (stinkpot). Reproduction. Herpetological Review 15:51.

Prassack, S.L., Sauge, J.B., and Guyer, C. 1992. Skewed sex ratios and sexual dimorphism in a population of musk turtles (*Sternotherus odoratus*). Society for the Study of Amphibuians and Reptiles, 35th Ann. Meet. Abstracts, p. 75.

Pritchard, P.C.H. 1989. The alligator snapping turtle: Biology and conservation. Milwaukee, WI: Milwaukee Public Museum, 104 pp.

Proctor, V. W. 1958. The growth of *Basicladia* on turtles. Ecology 39:634-645.

Punzo, F., and Alton, L. 2002. Evidence for the use of chemosensory cues by the alligator snapping turtle, *Macroclemys temminckii*, to detect the presence of musk and mud turtles. Florida Scientist 65:134-138.

Rayburn, L.A., Fontenot, C. and Palis, J. 1989. Population ecology of the stinkpot turtle, *Sternotherus odoratus*, in an urban pond. Proceedings of the Louisiana Academy Science 52:70.

Reilly, S.M. 1983. *Sternotherus odoratus* (stinkpot). Algal relationships. SSAR Herpetological Review 14(3):76

Reynolds, S.L., and Seidel, M.E. 1983. Morphological homogeneity in the turtle *Sternotherus odoratus* (Kinosternidae) throughout its range. Journal of Herpetology 17(2):113-120.

Rhodin, A.G.J. 1995. Archaeological turtle bone remains from Concord Shell Heap. Bulletin of the Massachusetts Archaeological Society 56(2):71-82.

Risley, P.J. 1930. Anatomical differences in the sexes of the musk turtle, *Sternotherus odoratus* (Latreille). Papers of the Michigan Academy of Science, Arts and Letters 11:445-464.

Risley, P.J. 1933. Observations on the natural history of the common musk turtle, *Sternotherus odoratus* (Latreille). Papers of the Michigan Academy of Science, Arts and Letters 17:685-711.

Risley, P.J. 1934. The activity of the coelomic (germinal) epithelium of the male musk turtle, *Sternotherus odoratus* (Latreille). Journal of Morphology 56:59-99.

Risley, P.J. 1938. Seasonal changes in the testis of the musk turtle, *Sternotherus odoratus* L. Journal of Morphology 63:301-317.

Root, R.W. 1949. Aquatic respiration in the musk turtle. Physiological Zoology 22:172-178.

Ryan, T. J., and Lambert, A. 2005. Prevalence and colonization of *Placobdella* on two species of freshwater turtles (*Graptemys geographica* and *Sternotherus odoratus*). Journal of Herpetology 39:284-287.

Sanderson, R.A. 1970. Notes on a communal nesting site of *Sternotherus odoratus*. Bulletin of the Maryland Herpetological Society 6:81-82.

Saumure, R. A. 2001. Kyphosis in a musk turtle (*Sternotherus odoratus*) from Ontario, Canada. Chelonian Conservation and Biology 4:159.

Schlauch, F.C. 1969. Eggs of a stinkpot. Intern at. Turtle and Tortoise Society Journal 3 (5):25.

Schilde, M. 2001. Schlammschildkröten: *Kinosternon*, *Sternotherus*, *Claudius* und *Staurotypus*. Münster, Germany: Natur und Tier Vierlag, 133 pp.

Schmidt, K.P. 1953. A check list of North American amphibians and reptiles. Sixth edition. Chicago, IL: University of Chicago, 280 pp.

Seidel, M.E., Reynolds, L., and Lucchino, R.V. 1981. Phylogenetic relationships among musk turtles (genus *Sternotherus*) and genic variation in *Sternotherus odoratus.* Herpetologica 37:161-165.

Seidel, M.E., Iverson, J.B., and Adkins, M.D. 1986. Biochemical comparisons and phylogenetic relationships in the family Kinosternidae (Testudines). Copeia 1986:285-294.

Smar, C. M., and Chambers, R. M. 2005. Homing behavior of musk turtles in a Virginia lake. Southeastern Naturalist 4:527-532.

Slavens, F.L., and Slavens, K. 1994. Reptiles and Amphibians in Captivity: Breeding-Longevity and Inventory. Seattle. WA: Slaveware, 533 pp.

Smith, G.R., and Iverson, J.B. 2002. Sex ratio of common musk turtles *(Sternotherus odoratus*) in a north-central Indiana lake: A long-term study. American Midland Naturalist 148:185-189.

Smith, G.R., and Iverson, J.B. 2004. Diel activity patterns of the turtle assemblage of a northern Indian lake. American Midland Naturalist 152:156-164.

Smith, H.M., and Larson, K.R. 1974. The generic name of the North American musk turtles. Great Basin Naturalist 34:42-44.

Smith, H.M., and Smith, R.B. 1979 [1980]. Synopsis of the herpetofauna of Mexico, Vol. 6, Guide to Mexican turtles. Bibliographic addendum III. North Bennington, VT: John Johnson, 1044 pp.

Snider, A.T., and Bowler, J.K. 1992. Longevity of reptiles and amphibians in North American collections, second edition. Society for the Study of Amphibian and Reptiles, Herpetological Circular (21):1-40.

Stejneger, L.H. 1923. Rehabilitation of a hitherto overlooked species of musk turtle of the southern states. Proceedings of the United States National Museum 62(6):1-3.

Stone, P.A., Dobie, J.L., and Henry, R.P. 1992a. Cutaneous surface area and bimodal respiration in soft-shelled (*Trionyx spiniferus*), stinkpot (*Sternotherus odoratus*), and mud turtles (*Kinosternon* *subrubrum*). Physiological Zoology 65:311-330.

Stone, P.A., Dobie, J.L., and Henry, R.P. 1992b. The effect of aquatic O_2 levels on diving and ventilatory behavior in soft-shelled (*Trionyx spiniferus*), stinkpot (*Sternotherus odoratus*), and mud turtles (*Kinosternon subrubrum*). Physiological Zoology 65:331-345.

Surface, H. A. 1908. First report on the economic features of the turtles of Pennsylvania. Zoology Bulletin of the Division of Zoology, Pennsylvania Department of Agriculture 6:105-196.

Thierfeldt, S., and Höfler-Thierfeldt, S. 2005. Continuous breeding of the Common Musk Turtle *Sternotherus odoratus* (Latreille, 1801) and development of hatchlings. Radiata 14:12-22.

Thomas, E.S., and Trautman, M.B. 1937. Segregated hibernaculum of *Sternotherus odoratus* (Latreille). Copeia 1937:231.

Tinkle, D.W. 1961. Geographic variation in reproduction, size, sex ratio and maturity of *Sternotherus odoratus* (Testudinata: Chelydridae). Ecology 42(1):68-76.

Tuberville, T.D., Gibbons, J.W., and Greene, J.L. 1996. Invasion of new aquatic habitats by male freshwater turtles. Copeia 1996(3):713-715.

Ultsch, G.R. 1985. The viability of Nearctic freshwater turtles submerged in anoxia and normoxia at 3 and 10° C. Comparative Biochemistry and Physiology 81A:607-611.

Ultsch, G.R. 1988. Blood gases, hematocrit, plasma ion concentrations, and acid-base status of musk turtles (*Sternotherus odoratus*) during simulated hibernation. Physiological Zoology 61:78-94.

Ultsch, G.R., and Cochran, B.M. 1994. Physiology of northern and southern musk turtles (*Sternotherus odoratus*) during simulated hibernation. Physiological Zoology 67(1):263-281.

Ultsch, G.R., Herbert, C.V., and Jackson, D.C. 1984. The comparative physiology of diving in North American freshwater turtles. 1. Submergence tolerance, gas exchange, and acid-base balance. Physiological Zoology 57(6):620-631.

Vermersch, T.G. 1992. Lizards and turtles of south-central Texas. Austin, TX: Eakin Press, 170 pp.

Vogt, R.C. 1981. Natural History of Amphibians and Reptiles of Wisconsin. Milwaukee, WI: Milwaukee Public Museum, 205 pp.

Vogt, R.C., Bull, J.J., McCoy, C.J., and Houseal, T.W. 1982. Incubation temperature influences sex determination in kinosternid turtles. Copeia 1982:480-482.

Wade, S.E., and Gifford, C.E. 1965. A preliminary study of the turtle population of a northern Indiana lake. Proceedings of the Indiana Academy of Sciences 74:371-374.

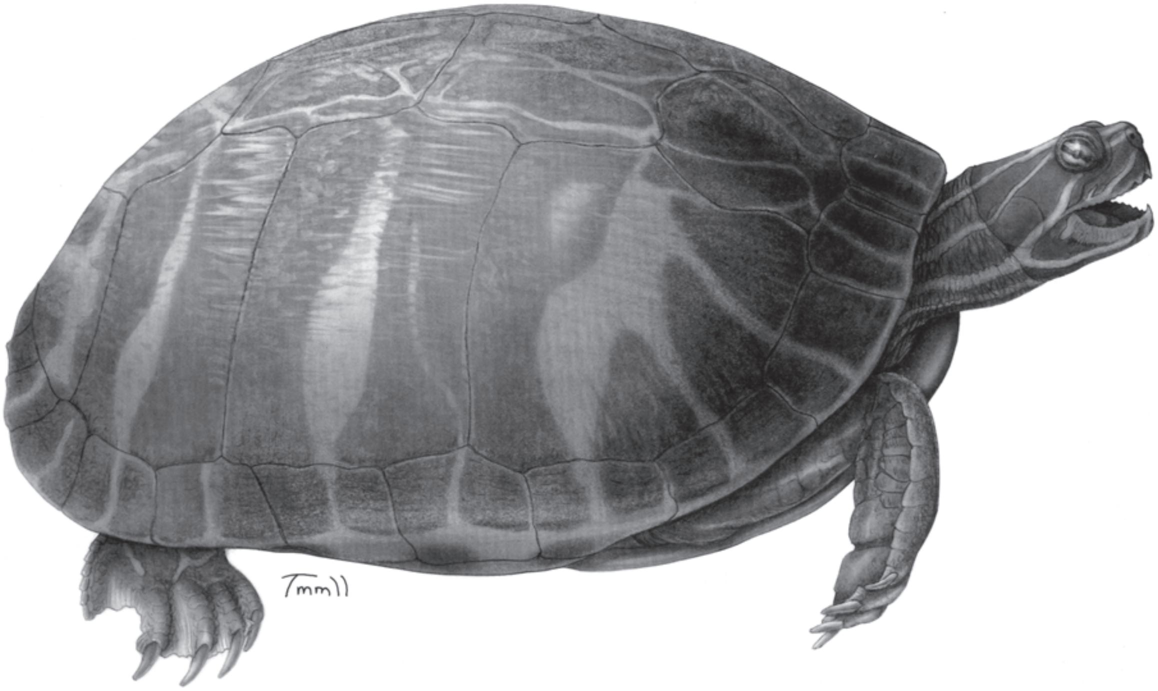
Walker, D., Nelson, W.S., Buhlmann, K.A., and Avise, J.C. 1997. Mitochondrial DNA phylogeography and subspecies issues in the monotypic freshwater turtle *Sternotherus odoratus*. Copeia 1997:16-21.

Wilkinson, L. R., and Gibbons, J. W. 2005. Patterns of reproductive allocation: Clutch size and egg size variation in three freshwater turtles. Copeia 2005:868-879.

Williams, J.E. 1952. Homing behavior of the painted turtle and musk turtle in a lake. Copeia 1952:76-82.

Wilson, K.W., and Friddle, S.B. 1950. The herpetology of Hardy County, West Virginia. American Midland Naturalist 43:165-172.

Zug, G.R. 1971. American musk turtles, *Sternothaerus* or *Sternotherus*? Herpetologica 27:446-449.



Florida Red-Bellied Turtle, *Pseudemys nelsoni* (Emydidae).
Drawing by Susan Trammell.

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Introduction to the New World Pond Turtles: Family Emydidae

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This family of turtles is represented in Florida by more species than any other. It includes box turtles (*Terrapene*), spotted turtles (*Clemmys*), chicken turtles (*Deirochelys*), map turtles (*Graptemys*), diamondback terrapins (*Malaclemys*), sliders (*Trachemys*), and cooters (*Pseudemys*). Seven of 18 Florida genera and 10 of 25 Florida species belong to this family. "Pond turtles" is a poor common name for the members of this group since they inhabit a wide variety of freshwater and terrestrial habitats from large rivers to desert.

Content. — This is the largest and most diverse turtle family in the New World. Its members are currently treated as 12 genera and about 36 species, more than one-quarter of which occur in Florida.

Relationships. — The concept of the family Emydidae has changed significantly in the past 20 years. Before the work of Hirayama (1985), the Emydidae was considered to include all of the pond turtles, New World and Old World. This broadly conceived Emydidae was recognized as having two major components, the Emydinae (or largely New World pond turtles) and the Batagurinae (or largely Old World pond turtles) (McDowell, 1964). Hirayama's observation that land tortoises (Testudinidae) are more closely related to batagurines than to emydines required a reclassification of the pond turtles. The old Emydinae became the Emydidae and now includes 11 genera of North American pond turtles plus one genus (*Emys*) from Europe and adjacent Asia. The old Batagurinae became the Bataguridae that now includes about 30 Old World genera and one in the New World (*Rhinoclemmys*). In the last few years, the family name Geoemydidae has been considered to have priority over the name Bataguridae and is now used for the Old World pond turtles.

Gaffney and Meylan (1988) suggested recognizing two subfamilies within the restricted Emydidae: the Emydinae for *Emys*, *Clemmys*, *Terrapene*, and *Emydoidea*, and the Deirochelyinae for *Deirochelys*, *Graptemys*, *Malaclemys*, *Trachemys*, *Pseudemys*, and *Chrysemys*. The genus *Clemmys* has since been broken up into three genera—*Clemmys*, *Glyptemys*, and *Actinemys* (Holman and Fritz, 2001).

Geologic Distribution. — Hadrianus, a land tortoise, reported from the Willwood Formation of Wyoming (Hutchison, 1980), provides a minimum age estimate of 52 million years for the split between the Emydidae and the geoemydid/ testudinid lineage. The oldest known emydid turtle (about 50 million years old) is represented by a fossil from the early Eocene of Ellesmere Island, Canada (Estes and Hutchison, 1980). Thus, there is good evidence that the lineage leading to modern emydids is more than 50 million years old.

Geographic Distribution. — The family is largely restricted to North America, with only a few species entering Mexico and further south. Members of one genus, *Trachemys*, have dispersed into the West Indies and through South America as far as Argentina (Seidel, 2002). The single Old World representative, *Emys*, is found throughout much of Europe and eastward into Russia, the Near East, and North Africa.

Status. — This is a large and diverse family and many species are quite common. However, some terrestrial and semiaquatic forms, most notably *Glyptemys muhlenbergii* and *Terrapene coahuila,* are threatened with extinction. Among the more highly aquatic forms, those in the greatest danger are species with the most restricted geographic ranges. Several species in the genus *Graptemys*, including the two Florida species, have limited distributions. In some cases they are limited to a single drainage basin and a single catastrophic event could be devastating for these species. A major concern for Florida's emydids is the fact that turtles in the rest of the world are becoming scarce due in large part to unsustainable consumption. As they do, those cultures that consume turtles on a regular basis are likely to increase harvest and export pressure on the more common members of this family in the U.S., and especially in Florida.

LITERATURE CITED

Estes, R. and Hutchison, J.H. 1980. Eocene lower vertebrates from Ellesmere Island, Canadian Arctic Archipelago. Palaeogeography, Palaeoclimatology, Palaeoecology 30:325-347.

Gaffney, E.S. and Meylan, P.A. 1988. A phylogeny of turtles. In: Benton, M.J. (Ed.). The Phylogeny and Classification of the Tetrapods, Volume1: Amphibians, Reptiles, Birds. Clarendon Press, Oxford, pp. 157-219.

Hirayama, R. 1985. Cladistic analysis of batagurine turtles (Batagurinae: Emydidae: Testudinoidea): a preliminary result. Studia Geologica Salmanticensia, Studia Palaeocheloniologica 1:141-157.

Holman, J.A. and Fritz, U. 2001. A new emydine species from the Middle Miocene (Barstovian) of Nebraska, USA with a new generic arrangement for the species of *Clemmys* sensu McDowell (1964) (Reptilia: Testudines: Emydidae). Zoologische Abhandlungen 51:331-354.

Hutchison, J.H. 1980. Turtle stratigraphy of the Willwood Formation, Wyoming: preliminary results. University of Michigan Museum of Paleontology Papers in Paleontology 24:115-118.

McDowell, S.B. 1964. Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae. Proceedings of the Zoological Society of London 143:239-279.

Seidel, M.E. 2002. Taxonomic observations on extant species and subspecies of slider turtles, genus *Trachemys*. Journal of Herpetology 36:285-292.

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Clemmys guttata – Spotted Turtle

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Summary. – The spotted turtle, *Clemmys guttata,* is the only species in Florida that has small yellow spots on a black carapace. It is the rarest freshwater turtle in Florida, with fewer than 50 verifiable records of occurrence. The earliest records were considered to be escaped captives, but regular occurrences in five different areas of the state away from human population centers suggest that this species is native to much of the northern half of peninsular Florida. The little that we know about the spotted turtle in Florida is considered in light of studies of this species from the northeastern U.S. and Canada where it is relatively well-studied. As is the case elsewhere, in Florida this species appears to use a variety of ephemeral and permanent wetland types and seems to occur with regularity in wetland complexes. Elsewhere in its range it is well-known to move between wetland types and adjacent uplands with seasonal regularity. Most observations of this species in Florida have occurred between March and May and nearly all are observations of individuals crossing roadways. Other states that are on the periphery of the range of this species have given it protected status. It is argued that Florida should do likewise. The protection of small wetlands, both permanent and ephemeral, will be essential to the future of this species in Florida.

Conservation Status. – FNAI Global - G5 (Demonstrably Secure), State - S3 (Rare, Local, or Vulnerable); ESA Federal - Not Listed; State - Not Listed; CITES - Not Listed; IUCN Red List - VU (Vulnerable).

Species Recognition. — This is the only turtle in Florida that has a small dark black carapace (to 124 mm carapace length [CL] in Florida) with one or more small yellow spots on each carapacial scute (Fig. 15-1). The carapace is fairly smooth and has no keels. The unhinged plastron is mostly yellow or yellow-orange with a black mark of variable size on each scale (Fig. 15-2). Older individuals may have a plastron that is mostly black. The skin of the head and legs is black with yellow to yellow orange markings. These light markings usually include a large irregular orange blotch on the side of the neck just behind the head, a slightly smaller blotch behind the eye, and stripes on the medial surface of the forearm. Hatchlings typically have one spot per scute on the carapace and the number of spots increases with size (Laemmerzahl, 1990). Spotted turtles are sexually dimorphic: males have a tan or brown chin, brown eyes, a concave plastron, and longer, thicker tails with the cloaca distal to the carapace margin, whereas females have a yellow chin, yellow or orange eyes, a flat plastron, and a shorter, thinner tail with the cloaca proximal to the carapacial margin (Berry and Meylan, 1992; Ernst et al. 1994).

Taxonomic History. — This distinctive species was named *Testudo guttata* (Schneider, 1792) on the basis of a specimen apparently from Philadelphia. The name *Clemmys guttata* has been stable since it was first used by Strauch (1862). Although the name *C. guttata* has been used consistently, there have been important recent taxonomic changes in the genus *Clemmys*. Although four North American species (*C. guttata*, *C. marmorata*, *C. insculpta*, *and C. muhlenbergii*) have long been treated as a natural group, several studies have suggested that these four species may not be each other's closest relatives (Bickham et al., 1996; Burke et al., 1996; Feldman and Parham, 2001, 2002; Holman and Fritz, 2001). The results of these studies provide additional evidence about interrelationships among the members of the subfamily Emydinae, to which *C. guttata* belongs, and a new taxonomy for this group has been proposed (Holman and Fritz, 2001). It places *C. insculpta* and *C. muhlenbergii* in the genus *Glyptemys*, and *C. marmorata* in the genus *Actinemys*. This new taxonomy does not change the name of the spotted turtle, because *C. guttata* is the type species of the genus *Clemmys*. Thus, the names *Clemmys* and *guttata* are permanently bonded.

No significant geographic variation is known in the morphology of *C. guttata* (Lammerzahl, 1990) and no subspecies have been proposed. Geographic variation in the genetics of the species is under study (C. Callahan, *pers. comm.*).

DISTRIBUTION

Geographic Distribution. — The spotted turtle occurs in the southern Great Lakes region from as far west as northeastern Illinois, across the lower peninsula of Michigan, northern Indiana, and northern Ohio, western Pennsylvania, western New York, southern Ontario, and southern Quebec. It also occurs along the Atlantic Coastal Plain from Maine through Georgia and into central Florida (Ernst, 1972; Iverson and Etchberger, 1989; Iverson, 1992; Ernst et al., 1994; Barnwell et al., 1997). The range of this species appears to be discontinuous with isolated populations occurring in many states within the range, including Florida.

Figure 15-1. Adult spotted turtle, *Clemmys guttata,* from Seminole Co., Florida. Photo by Barry Mansell.

It has been suggested that records of spotted turtles in Florida were the result of escapees or introductions (Neill, 1954; Ernst, 1972; Ashton and Ashton, 1985; Hipes et al., 2000). However, a significant number of records now exist for widely separate and remote areas (Fig. 15-3) which suggests that the species' distribution in Florida is more likely relictual rather than a result of releases (Barnwell et al., 1997). In fact, almost no records exist for areas with large human populations (only Jacksonville, Sanford, and Gainesville), unlike the case of *Trachemys scripta elegans*, which is introduced in Miami, Tampa, St. Petersburg, Jacksonville, and Pensacola. Locality records of spotted turtles near Jacksonville and Gainesville occur in drainage basins that also have records from more remote rural locations. Multiple records for this species in several remote natural areas, such as St. Marks National Wildlife Refuge, Green Swamp, Mallory Swamp, and Osceola National Forest, also argue for a natural occurrence in Florida.

Figure 15-2. Plastron of a spotted turtle, *Clemmys guttata,* from Clinch Co., Georgia. Photo by Dick Bartlett.

The distribution of the spotted turtle in Florida is not very well known. The distribution of 28 vouchered records available in 1996 was reviewed by Barnwell et al (1997), and fewer than 50 records are now known. These records indicate an overall distribution from Wakulla Co. in the eastern panhandle to Nassau Co. in northeast Florida, and northern Polk Co. in central Florida. However, the distribution of this species in Florida is certainly not continuous. Herpetological sampling in intervening areas has been sufficient to suggest that this species occurs in isolated pockets throughout this relatively large area.

Most museum records for Florida are from the greater St. John's River basin, as far upstream (south) as Seminole and Volusia counties. Records from the Green Swamp in Polk Co., and Lake Weir, Marion Co., can also be considered to represent St. John's River system records because a major tributary of the St. John's, the Oklawaha River, historically drained the east side of the Green Swamp and still drains the Lake Weir area. Records from western Putnam Co. and adjacent Alachua Co. are in or near the drainage of Orange Creek, a tributary to the Oklawaha River. Additional populations occur in the St. Marks Wildlife Refuge, in Mallory Swamp (Lafayette Co.), along the upper Suwannee River, and along the St. Mary's River (Nassau Co.). Between these sites are large areas from which no spotted turtle records exist despite significant herpetological sampling.

Ecological Distribution. — Throughout its range, this species occupies a wide variety of wetland habitats, including vernal ponds, swamps, small streams, bogs, marshes, wet pastures, and early and late successional stages of wet forests. In a quantitative study of spotted turtle habitat use in Massachusetts (Milam and Melvin, 2001), seasonal or vernal pools and wetlands with emergent vegetation were used significantly more often than expected based on availability of habitat. However, spotted turtles do not remain in just one of these habitats throughout the year. There are regular shifts

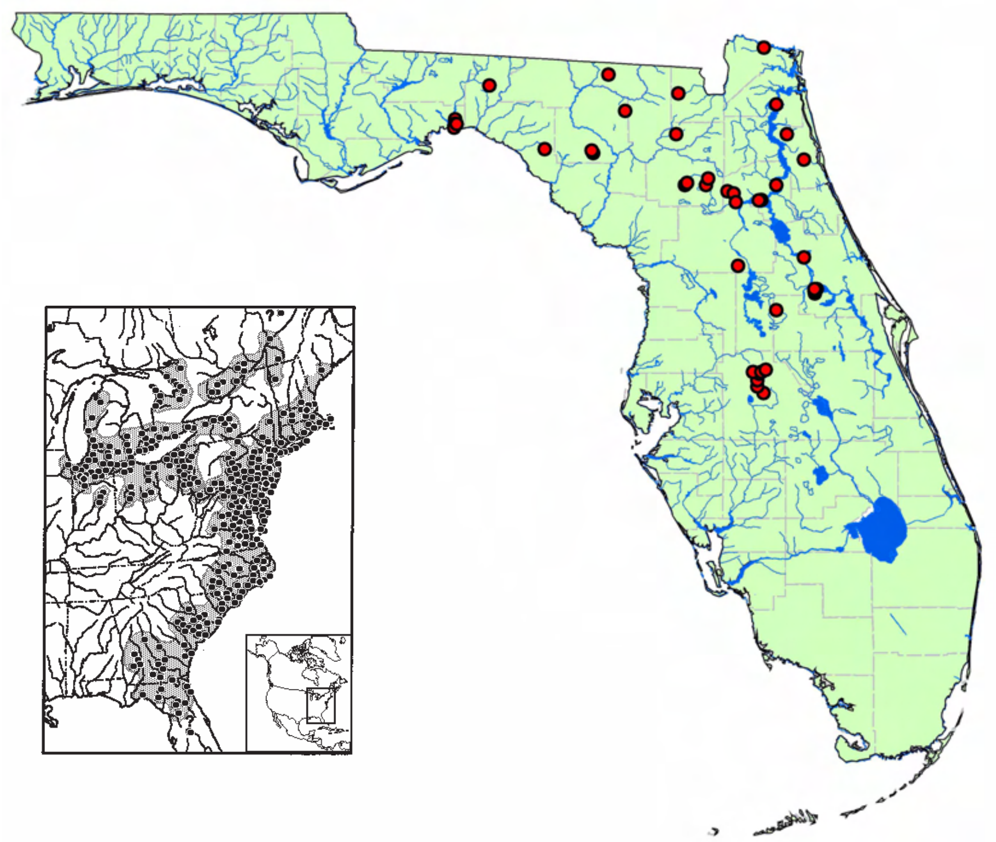

Figure 15-3. Distribution records for the spotted turtle, *Clemmys guttata,* from Florida. Inset: distribution records from entire range of *C. guttata* (adapted from Iverson, 1992; distribution in inset map not current for Florida as presented here).

between habitat types depending on season and activity (Litzgus and Brooks, 2000).

In Florida, the spotted turtle seems to be largely restricted to wooded swamps within areas of pine flatwoods (Berry and Meylan, 1992), although some records from the St. Marks NWR are near salt marsh (Berry and Gidden, 1973). Nearly all known Florida specimens were collected on roads, either alive or as road kills. Adjacent habitats from which these specimens may have come have been described as "a series of cypress strand systems and bay swamps", a "mixed hardwood wetland," and a "bay swamp" (Barnwell et al., 1997). Collection notes for other Florida specimens include: "roadside ditch with shallow water in slash pine" (UF 78842), "sphagnaceous bottomland forest along stream" (UF 66717), "pine flatwoods, pond cypress dome, roadside ditch" (UF 88491), and "low coastal marshland" (Berry and Gidden, 1973). Plant species occurring at these sites include cabbage palm, sweet bay, water oak, maple, sweet gum, and slash pine. This species has been reported from mud flats on Lake Apopka and Lake Woodruff (T. Gross *pers. comm.* to Barnwell et al., 1997) but no vouchers exist for these records. Elsewhere in the southern U.S., the habitat of this species has been described as "black-water cypress swamps, coastal plain wetlands, sinkhole ponds, and pine flatwoods ponds (Buhlman and Gibbons, 1998). Graham (1995) described the habitat in two study sites with high population density (Cedar Swamp, Massachusetts, and Carroll Island, Maryland) as "vast and heterogeneous wetland habitats." Each of these sites at which this species was abundant consisted of several hundred acres of mixed wetlands.

HABITAT RELATIONS

Annual Activity Cycle. — Ernst (2001) considered *C. guttata* to be the most aquatic of the eastern "*Clemmys*" species, suggesting that it spends most of its annual activity season in water. However, it seems to be largely limited to water less than half a meter in depth and at all sites where it has been studied in detail, it makes considerable seasonal shifts that include a variety of terrestrial habitats (Ward et al., 1976; Graham, 1995; Behler, 1996; Litzgus and Brooks, 2000; Milam and Melvin, 2001). Where the species is well studied in the northern part of its range, it occupies flooded fields and woodlands or temporary ponds after emerging from hibernation. It usually remains in these temporary wetlands during spring and early summer but often leaves them and enters aestivation sites when the wetlands warm up or dry out as summer progresses. At this time, longer terrestrial movements were generally observed, including travel to aestivation sites and/or nesting sites (Perillo, 1997; Litzgus and Brooks, 2000).

Spotted turtles may enter aestivation as early as June and may remain until August of the same summer (Graham, 1995), or they may not reemerge until the following spring (Ernst, 1982). Aestivation takes place in a variety of sites

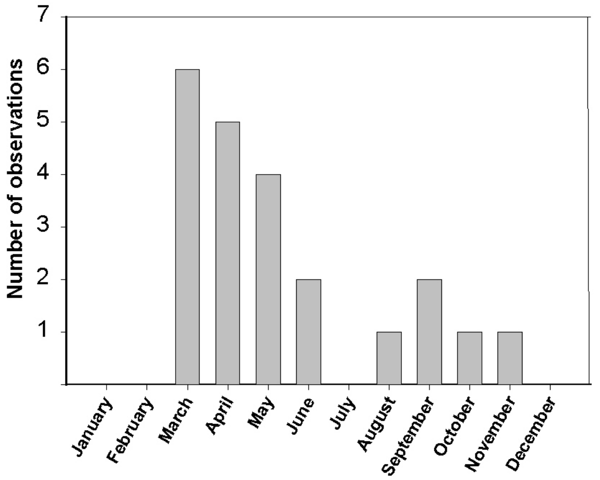

Figure 15-4. Number of observations by month for the spotted turtle, *Clemmys guttata,* from Florida (data are from museum records and field notes).

including muskrat burrows, pools of flowing water, overgrown fields, flooded woodlands under thick leaf litter, and upland forests (Ernst, 1976; Ernst et al., 1994; Perillo, 1997; Milam and Melvin, 2001). In Maryland and Massachusetts, spotted turtles have been observed to aestivate terrestrially under leaf litter and vegetation or in forms in meadows. These individuals then moved to aquatic hibernation sites in the fall (Ward et al., 1976; Graham, 1995; Litzgus and Brooks, 2000; Milam and Melvin, 2001). Spotted turtles are known to migrate moderate distances to hibernation sites and to hibernate communally (Netting, 1936; Ernst, 1976; Behler, 1996; Lewis and Ritzenthaler, 1997; Litzgus et al., 1999). Hibernacula include soft bottoms of streams (Ernst, 1982), edges of small pools (Ward et al., 1976), muskrat burrows (Bloomer, 1978), flooded woodlands (Behler, 1996), rock caves, and sphagnum hummocks (Litzgus et al., 1999). In all of these sites, hibernation occurs under at least 10 cm of water. Communal hibernacula are known to serve up to 34 spotted turtles at one time, with some individuals using the same site during multiple winters (Lewis and Ritzenthaler, 1997; Litzgus et al., 1999).

This species has a relatively short activity season, even in the temperate parts of its range (Lovich, 1988; Ernst et al, 1994). It is most active in early spring in Florida (Berry, 1978) and elsewhere. Half of the spotted turtles encountered in Florida for which there are data for month of collection ($n = 21$), were found in March or April; 67% were found between March and May (Fig. 15-4). Elsewhere, most encounters also occurred from March to May: 73% in North Carolina (Palmer and Braswell, 1995), 89% in Ohio (Conant, 1951), and 92% in Maryland (Ward et al., 1976).

Spotted turtles are typically active only by day (except for nesting females). They are active at air temperatures as low as 2ºC in Ontario (Litzgus and Brooks, 2000). In Pennsylvania, females begin basking at air temperatures as low as 6ºC and both sexes have been seen feeding at water temperatures of about 15ºC (Ernst, 1976, 1982). They are apparently not active at temperatures above 32ºC (Ernst, 1976; Kiviat, 1978). Lovich (1988) determined that activity level peaks when temperatures are between 13.1 and 18.0ºC. Spotted turtles have been observed to be active beneath ice in shallow water (Ernst, 1982) and thus might be expected to be active in Florida throughout the winter. In South Carolina, they have been observed entering Carolina bays in March and were thought to have been coming from terrestrial hibernation sites (D. Scott *pers. comm*. to Ernst et al., 1994).

The annual peak of activity varies geographically for this species. Lovich (1988) has convincingly shown that populations in South Carolina have an activity peak earlier in the year (March) than populations found further north which may not become active until May (Haxton and Berrill, 2001). In South Carolina, basking occurs as early as February (J. Litzgus, *pers. comm.*). If this trend extends into Florida, it might be predicted that spotted turtles in Florida would be active in winter (January–March). However, dates of collection of this species in Florida (Fig. 15-4) indicate a pattern similar to that seen in South Carolina, with peak activity in March and April. Thus, it may not be temperature alone that determines the activity level of this species. If both temperature and rainfall determine activity, the typical dryness of Florida winters may explain the absence of winter records for this species in Florida. Fall records could be explained by high rainfall associated with tropical storms.

The daily activity cycle of this species varies seasonally where it has been studied in detail. In Pennsylvania, during early spring, spotted turtles appear to be most active at midday, but as spring turns into summer they are active earlier and earlier in the morning and then show little activity during the hottest parts of the summer (Ernst, 1976).

Movements and Home Range. — Normal daily movements are generally not extensive (Ernst, 1976), but during the mating season males travel extensively and are known to travel at least 250 m from water. Ernst (1970a) and Behler (1996) reported remarkable homing ability in this species. However, Behler (1996) also reported long distance movements that appear to have been natural translocations between populations.

The home range of this species has been studied in Pennsylvania (Ernst, 1970a), Ohio (Lewis and Faulhaber, 1999), and Massachusetts (Graham, 1995; Milam and Melvin, 2001). During 1965–67 adult *C. guttata* in southeastern Pennsylvania had a home range of about 0.54 ha (Ernst, 1970a) based on mark-recapture data. Lewis and Faulhaber (1999) studied home range in Clark Co, Ohio, using radiotelemetry. In their study, 27 spotted turtles were followed for a total of 36 turtle years; they found that 95% of the locations occurred within an average area of 1.79 ha. The home ranges were always centered on some aquatic habitat such as a stream, ditch, or fen, but also included fields, shrubby areas, and other non-aquatic habitats. Lewis and Faulhaber (1999) found no significant differences in home range size between genders or before and after reproductive activity. Both genders made extended movements of up to 1.5 km outside of their home range during all months from April to September. Milam and Melvin (2001) used radio-telemetry to follow 26 turtles for a total of 37 turtle years and found a mean annual home range of 3.5 ha at two sites in Massachusetts. They, too, found no significant difference between sexes, although females tended to have larger home ranges and tended to move farther to hibernacula.

Terrestrial Activity. — This species makes extensive use of terrestrial habitats (Ernst, 1970a, 1976; Ward et al., 1976; Lovich, 1990; Palmer and Braswell, 1995; Behler, 1996; Litzgus and Brooks, 2000; Milam and Melvin, 2001). Spotted turtles regularly move overland between wetlands and may aestivate terrestrially during times of low water. In a radio-telemetry study of this species conducted in coastal South Carolina, two adult males were tracked for periods of 41 and 9 days (Lovich, 1990) during March and April. The two males moved a total of 2.75 and 1.84 km, respectively. They each occupied three different aquatic habitats, moving overland between them (Lovich, 1990). The results of this brief study provide strong preliminary evidence that adult male spotted turtles in the south may act as "transients" moving overland from wetland to wetland. The reason for this springtime behavior in these adult males was hypothesized to be the need to maximize reproductive fitness by finding as many mates as possible during the breeding season. Perillo (1997) also found that males in a Connecticut study site traveled between wetlands more often than females during spring months when mating took place.

GROWTH AND REPRODUCTION

Growth. — Although studies of the growth and reproductive biology of the spotted turtle are now underway in the southern portion of its range (Litzgus and Mousseau, 2003; J. Litzgus, *pers. comm.*), the observations provided below are based on published data from Ontario, Pennsylvania, Rhode Island, and other northern localities. How these patterns might differ latitudinally has not been determined.

A study of growth rates in this species in Rhode Island (Graham, 1970) suggested that they grow an average of about 7.5 mm per year for the first seven years of life, with a range of 4.9 to 10.6 mm per year. The growth rate decreases each year for the first five years or so and then increases slightly before sexual maturity is achieved. At sexual maturity, growth slows or stops. Males and females appear to grow at the same rate (Litzgus and Brooks, 1998a). Ernst (1976) pointed out that in Pennsylvania most growth occurs during just three months of the year, April through June, and that growth rates can be higher (up to 17.5 mm per year) than that seen in Rhode Island. In Ontario, spotted turtles take 11 or 12 years to mature and do so at a slightly larger size than in other populations (Litzgus and Brooks, 1998a).

Size at Maturity. — No sexual size dimorphism is apparent in this species. The smallest mature female observed by Ernst and Zug (1994) from a study site in Pennsylvania was 85.0 mm plastron length (PL) and, based on growth annuli, was estimated to be 8 years old. But at least one female larger than this size was judged to be immature. Other small but mature females were estimated to be 8 or 9 years old. Based on the presence of sperm, Ernst and Zug (1994) identified an 82.1 mm, 8-year-old male as the smallest mature male in their study. Ernst has followed individuals of both sexes in the field in Pennsylvania for more than 30 years.

Reproductive Cycles. — Spermatogenesis in this species has been described only from Pennsylvania, where it peaks in mid- to late summer. Mature sperm remain in the epididymides over winter for spring matings (Ernst and Zug, 1994.). This appears to fit the "post-nuptial" reproductive pattern common for emydid turtles (Meylan et al., 2002), although fall mating has also been observed (Milam and Melvin, 2001). Females in Pennsylvania were found to have enlarged ovarian follicles in April, May, and June, but shelled eggs were only observed during May (Ernst and Zug, 1994). Females in South Carolina have shelled eggs in April–June and nested from mid-May to mid-July (Litzgus and Mousseau, 2003). Females in Ontario have shelled eggs only in June (Litzgus and Brooks, 2000).

Courtship and Mating. — Courtship and mating occur earlier in warmer climates, from early March to mid-May in Pennsylvania (Ernst, 1976; Ernst and Zug, 1994), April to May in Indiana (Pope, 1939), and late May to June in Ontario (Chippindale, 1989, Litzgus and Brooks 1998b, 2000). Males appear to be more active during the courtship season, apparently searching for mates. At least one-third of the known records for Florida are of adult males found on roads between March and June. In South Carolina, males were observed to move through and explore Carolina bays in early spring (Lovich, 1990; D. Scott *pers. comm.* to Ernst et al., 1994). Unless these are turtles returning from hibernation sites, it seems likely that these males travel extensively in the early spring in search of females. In North Carolina, males have been observed fighting in a shallow floodplain pool in mid-March (Palmer and Braswell, 1995).

Courtship occurs in shallow water and on adjacent land and courting pairs may cover distances as large as 50 m (Ernst et al., 1994). Mating typically takes place in the water, and mating aggregations of up to 16 individuals are known (Ernst, 1967, 1970b). Mating aggregations have also been observed in Ontario and South Carolina (J. Litzgus, *pers. comm.*).

Nesting. — Outside of Florida, nests have been recorded from May to July. They are dug in full sunlight in a variety of habitats from open grass tussocks (Ernst, 1970b) to the tops of rotten logs in swamp forest (J. Litzgus, unpubl. data), to soil patches on rocky outcrops (Litzgus and Brooks, 1998b). The nesting process takes from 45 minutes to 8 hrs. Females in Ontario wandered 50 m or more from water in their search for nest sites and spent up to a week on land prior to egg laying (Litzgus and Brooks, 1998b). Females at two sites in Massachusetts traveled an average of 249 m overland before nesting (Milam and Melvin, 2001). There are no data on nesting by this species in Florida.

Clutch Size and Eggs. — The eggs of spotted turtles are elliptical, roughly 30 mm long and 16 mm wide, and have a flexible shell (Ernst and Zug, 1994). They are usually laid in clutches of 3 to 5 eggs with an average of 3.6 eggs for a Pennsylvania population and also for a sample of 12 nests from North Carolina (Ernst, 1976; Ernst and Zug, 1994; Palmer and Braswell, 1995). Larger females produce larger clutches (Ernst, 1970b, 1976, Ernst and Zug, 1994; Litzgus and Brooks, 1998b). In Ontario, where females are generally larger than in other populations, a single clutch can include as many as 7 eggs with the average being about 5 (Litzgus and Brooks 1998b). It seems likely that not all adult females in a population reproduce every year. Litzgus and Brooks (1998b) reported that an average of 58% of adult females reproduced each year at their study site in Ontario.

Clutch Frequency. — Ernst (1976) reported that for the spotted turtle in Pennsylvania, there is no evidence that more than one clutch per year is laid. However, in a later study of the same population (Ernst and Zug, 1994), it was suggested that one late clutch (July) could have been a second clutch for the year. Litzgus and Mousseau (2003) have since found that wild populations of spotted turtles in South Carolina can produce up to 3 clutches per year, and have an annual clutch frequency of 1.2 clutches per year.

Incubation and Hatching. — Incubation in Pennsylvania takes 70–83 days (Ernst, 1970b), but some hatchlings may overwinter in the nest (Ernst, 1975). Sex determination in this species is temperature dependent (Ewert and Nelson, 1991), with cooler temperatures producing males. Hatchlings are about 30 mm long and usually have at least one spot per carapacial scute (Ernst, 1970b).

POPULATION BIOLOGY

Density and Biomass. — In a 3.2 ha Pennsylvania marsh, spotted turtles varied in density from 39.5 to 79.1 turtles/ ha over a 7-yr period (Ernst, 1976). This translates to a biomass of 4.3 to 8.7 kg/ha (Iverson, 1982). At other study sites, densities have been much lower. Graham (1995) provided data from five sites at which density varied from 0.94 (Illinois) to 10.6 (New York) turtles/ha. Milam and Melvin (2001) reported densities of 2.4 and 8.0 turtles/ha of wetland at two sites in Massachusetts. The paucity of records in Florida, even in areas that are relatively well sampled (St. Marks NWR, Ocala National Forest, Osceola National Forest, Green Swamp), suggests that this species occurs at very low densities in this state.

Population Structure. — The structure of a Pennsylvania population was well documented by Ernst (1976). It appeared to be female biased at 1.46:1 females to males. About one-third (32.3 %) of the spotted turtles encountered were juveniles.

INTERSPECIFIC INTERACTIONS

Community Structure. — At Ernst's (1976) study site in Pennsylvania, spotted turtles made up only 10.2% of the turtle fauna. The most common turtle species was *Chrysemys picta* (76.3% of captures). *Sternotherus odoratus*, *Chelydra serpentina*, *Terrapene carolina*, *Glyptemys insculpta*, and *G. muhlenbergii* were also present in the marsh but were less abundant than spotted turtles.

Diet and Feeding. — Spotted turtles are omnivorous and actively forage in shallow water (Ernst, 1976). Although they will eat filamentous algae and cranberries, they appear to eat more animal matter than plants. Animal prey includes aquatic insect larvae, small crustaceans, snails, amphibian larvae, and fish (Ernst, 1976; Ernst et al., 1994). At some sites spotted turtles consume large numbers of larval insects and larval amphibians that become abundant in temporary vernal ponds soon after they fill (Graham, 1995; Milam and Melvin, 2001).

Predation. — Spotted turtles often show signs of predation attempts; 17.9% of adults in a Pennsylvania population, and 31% in an Ohio population, had some kind of serious injury such as missing limbs, or shell damage (Ernst, 1976; Lovich, 1989). Known predators of spotted turtles and their eggs include raccoons, skunks, and eagles (Ernst et al., 1994). Ernst (1976) considered the raccoon to be a primary predator of spotted turtles in southeastern Pennsylvania with predation rates on this species being higher than that for the more aquatic painted turtle (*Chrysemys picta*). Lovich (1989) also cited a large raccoon population as a serious threat to spotted turtles in a protected area in Ohio.

THREATS

Documented Threats. — Buhlman and Gibbons (1998) suggested that *C. guttata* is imperiled, and Ernst (2001) considered the four species of "*Clemmys*" to be the most threatened turtles in North America. Ernst suggested that the four species (see taxonomic history above) share the significant problem that they occur in discrete, isolated populations. Habitat fragmentation, alteration, and destruction can eliminate the habitat used by these populations and also reduce the ability of individuals to move between populations. Draining of wetlands and flooding of wetland corridors by damming destroy habitat for these species (Lovich, 1989; Berry and Meylan, 1992; Palmer and Braswell, 1995). The construction of drainage ditches to dry out wetlands of various types, and the construction of dams that flood wetland habitat, have both probably resulted in habitat loss for *C. guttata* in Florida.

Buhlman and Gibbons (1998) cited urban development and destruction of wetlands for silviculture and agriculture as threats to this species on the coastal plain of Virginia. Lovich (1989) and Lewis and Faulhaber (1999) cited loss of wetland habitat, over-collection, and increased predation by raccoons as major causes of decline of this species in Ohio. Behler (1996) suggested that spotted turtle numbers have declined due to habitat alteration and fragmentation, increased predation from raccoons and coyotes, and collection for the exotic pet industry. Lewis and Faulhaber (1999) implied that early successional stages of wetlands are important to this species and that succession and encroachment by exotics may make remaining wetland habitat less suitable.

This species makes extensive use of terrestrial areas adjacent to wetlands. The activities that occur in those uplands can have important consequences for survivorship of the population. In areas where agricultural fields are adjacent to wetlands, aestivating and migratory animals are subject to injury from farm machinery. In a study in Pennsylvania, injuries from mowers were evident in a number of individuals (Ernst, 1976).

The spotted turtle and its close relatives are very popular in the pet trade (Ernst, 2001). However, this species seems to be so rare in Florida that few if any from Florida are likely to reach the pet trade each year. Enge (1993) did not list this species as one which entered the pet trade from Florida during the two-year period that the trade in reptiles and amphibians was monitored. However, this species is being collected from the wild in other southern states. Buhlman and Gibbons (1998) reported that 543 were taken in North Carolina in a single year. Litzgus reports one collector has removed at least 300 from South Carolina in recent years (J. Litzgus, *pers. comm.*).

Although the spotted turtle is so rare in Florida that the pet trade probably has little or no impact, habitat destruction (such as the flooding of the Oklawaha River Basin by Rodman Pool) has almost certainly reduced the habitat available to this species.

Potential Threats. — Clemmys guttata is at the edge of its range in Florida. In the past it was questioned whether or not this species is in fact native to Florida. However, there are now nearly 50 vouchered records in Florida and a certain consistency in their distribution. It seems clear that spotted turtle populations in Florida are isolated from one another, and, judging by the frequency with which this species is encountered, it does not seem that any of these populations is particularly large or dense. Occurrence in small and widely dispersed populations, in habitats that are subject to modification (draining, logging, succession), puts this species at risk. This risk is compounded by the fact that spotted turtles make overland movements between aquatic habitats at regular intervals.

Our lack of understanding of the terrestrial movements of this wetland species in the south means that we do not have the knowledge necessary to provide adequate management plans for the species, even in publicly held lands where it stands the best chance for long-term survival (e.g., St. Marks NWR, Osceola National Forest, Ocala National Forest, Green Swamp). The importance of open habitats and early successional stages of flooded woodlands to this species elsewhere in its range suggests that forestry management strategies might be identified that could benefit the spotted turtle in Florida. Succession is definitely a problem for this species (Lovich, 1989; Graham, 1995). The use of fire to suppress succession has been specifically mentioned as a management option for spotted turtles in Massachusetts (Graham, 1995), and is already known to be a valuable management tool for flatwoods in Florida (Abrahamson and Hartnett, 1990).

STATUS

The spotted turtle was listed as "Rare" by the Florida Committee on Rare and Endangered Plants and Animals in 1978 (Berry, 1978) and again in 1992 (Berry and Meylan, 1992). It is listed as "G5/S3?" in Hipes et al. (2000). G5 refers to its global status, which is considered to be demonstrably secure, while S3? refers to the state status. Apparently the S3 status, "rare, restricted or otherwise vulnerable to extinction", was questioned by Hipes et al. (2000). S2 status is defined as "imperiled, or six to 20 occurrences". The S2 status would better reflect the current situation for spotted turtles in Florida, since it is known from far fewer than 20 populations within the state, and none of these are of sufficient size that this species can be observed or captured with any regularity.

The spotted turtle is listed as "special concern" in Canada, and The Nature Conservancy considers it to be Critically Imperiled (Illinois, Vermont, West Virginia), Imperiled (Indiana), or Vulnerable (Delaware, District of Columbia, Florida, Georgia, Maine, Massachusetts, Michigan, New Hampshire, Ohio, and Virginia) in 14 of the 22 United States in which it occurs (USFWS, 2000) . Several authors have suggested that spotted turtle numbers are declining (Lovich, 1989; Behler, 1996), and Ernst (2001) cautioned that the four species of the genus "*Clemmys*" could disappear unless a more concerted effort is made to protect them. Although spotted turtles are likely to become extirpated in other states (Illinois) before they do so in Florida, the possibility that this species might disappear from Florida must be considered. Protection of land on which this species is known to occur is not sufficient to guarantee its survival. Because of its semiterrestrial lifestyle, management plans for protected areas must take the specific needs of this species into consideration. It seems clear that mismanagement of suitable habitat has led to a decline in this species in a protected area at the Cedar Bog Memorial Site in Ohio (Lovich, 1989). As long as we are uncertain of this species' needs in Florida, it is in jeopardy.

The spotted turtle is listed as threatened at the northern limits of its distribution in the state of Maine (McCollough, 1997). Records in Maine, although uncommon, appear to be more frequent than they are in Florida. Fourteen new observations of this species were made from 1990 to 1995, and a survey of 2500 wetlands during the same period yielded about 90 new site occurrences (USFWS, 2000). As in Florida and elsewhere, populations in Maine appear to be disjunct. In Maine, three large population centers for spotted turtles were identified, and planning is underway to develop wetlands protection strategies for these areas. The strategies include acquisition of, or conservation easements for, key wetland complexes, improved state wetland permit review, unified management goals for federal, state land local and use, and an increase in environmental education (McCollough, 1997). Additionally, wetlands smaller than 10 acres are now protected in Maine. This should help to protect the spotted turtle in that state. A similar program in Florida would greatly benefit the spotted turtle.

It appears that at most sites, spotted turtles require both permanent wetlands for hibernation and temporary wetlands for access to seasonally abundant food supplies (insects and amphibian larvae) in the spring and early summer. They also use adjacent upland sites for aestivation and nesting. Thus, the conservation of complex wetland systems with adjacent uplands is a likely requirement for the survival of this species in Florida.

CONSERVATION OPTIONS AND SOLUTIONS

The long-term survival of this species in Florida appears to depend on the conservation of heterogeneous wetland systems. Berry and Meylan (1992) suggested that this species would be best conserved in Florida by preservation and restoration of wooded wetlands. They specifically mentioned restoration of the Oklawaha River along which a series of historical records exist. The impoundment formed by the damming of this river (Rodman Reservoir) south of Palatka eliminates habitat for this semiterrestrial species. Restoration of a floodplain corridor would be more likely to allow movement of individuals of this species along the historic Oklawaha River floodplain.

Dredging and impoundment are clearly problematic for this species because it is not a lake-dwelling species. In a conservation area in Ohio, these practices are thought to have contributed to a marked decline in the number of spotted turtles (Lovich, 1989). Recommendations compiled by the USFWS (2000) to promote the recovery of this species include wetland restoration and connection, creation of wetland complexes, conservation of sufficient adjacent habitat for nesting and aestivation, control of succession, control of invasive exotic plants, and maintenance of high water quality. Milam and Melvin (2001) suggested expanding protection of uplands around clusters of seasonal pools (temporary wetlands) that are associated with similarly buffered, more permanent wetlands with emergent vegetation.

In portions of its range, the number of spotted turtles entering the pet trade appears to be a significant problem. Although Florida is not a likely source for spotted turtles because of their rarity, it is very likely to be a major exporting state for national and international trade. In order to monitor the level of this trade in Florida, a use and trade monitoring system, like that employed from 1990 to 1992 (Enge, 1993) should be reinstated. Furthermore, the laws protecting the spotted turtle in Florida should be changed so that it cannot be collected from the wild. This should be done, not because large numbers are known to be taken from Florida, but so that spotted turtles taken elsewhere cannot be said to have come legally from Florida. As long ago as 1990, biologists were in agreement that stopping trade in the three eastern species of "*Clemmys*" was a necessary step for their survival (Stearns et al., 1990). As states throughout the range of this species protect it from collection, Florida should not be the last to do so.

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LITERATURE CITED

Abrahamson W.G. and Hartnett, D.C. 1990. Pine flatwoods and dry prairies. In: Myers, R.L. and Ewel, J.J. Ecosystems of Florida, University of Central Florida Press, Orlando, pp. 103-149.

Ashton, R.E., and Ashton, P.S. 1985. Handbook of reptiles and amphibians of Florida, Part two, Lizards, turtles and crocodilians. Windward Publishing.

Barnwell, M.E., Meylan, P.A., and Walsh, T. 1997. The spotted turtle (*Clemmys guttata*) in Central Florida. Chelonian Conservation and Biology 2:405-408.

Behler, J.L. 1996. Spying on spotties. Wildlife Conservation. October, 1996.

Berry, J.F. 1978. Spotted Turtle. In: McDiarmid, R.W. (Ed.) Rare and Endangered Biota of Florida. Vol. 3. Amphibians and Reptiles. University Press of Florida, pp. 47-49.

Berry, J.F., and Gidden, C.S. 1973. The spotted turtle in Florida and southern Georgia. Florida Scientist 36(2-4):198-200.

Berry, J.F., and Meylan, P.A. 1992. Spotted turtle (*Clemmys guttata*). In: Moler, P.E. (Ed.) Rare and Endangered Biota of Florida, Vol. III. Amphibians and Reptiles. University Press of Florida, pp.191-195.

Bickham, J.W., Lamb, T., Minx, P., and Patton, J.C. 1996. Molecular systematics of the genus *Clemmys* and the intergeneric relationships of emydid turtles. Herpetologica 52:89-97.

Bloomer, T.J. 1978. Hibernacula congregating in the *Clemmys* genus. Journal of the Northern Ohio Association of Herpetologists 4:37-42.

Buhlmann, K.A., and Gibbons, J.W. 1998. Imperiled aquatic reptiles of the southeastern United Sates: Historical review and current conservation status. In: Benz, G., and Collins, D.E. (Eds.). Conference on Aquatic Fauna in Peril: The Southeastern Perspective. Southeast Aquatic Research Institute, Lenz Design & Communication, Decatur, GA, pp. 201-232.

Burke, R.L., Leuteritz, T.E., and Wolf, A.J. 1996. Phylogenetic relationships of emydine turtles. Herpetologica 52(4):572-584.

Chippendale, P. 1989. Courtship and nesting records for spotted turtles, *Clemmys guttata*, in the Mer Bleue Bog, southeastern Ontario. Canadian Field Naturalist 103: 289-291.

Conant, R. 1951. The reptiles of Ohio. University of Notre Dame Press, Notre Dame, Indiana.

Enge, K.M. 1993. Herptile use and trade in Florida, Florida Game and Fresh Water Fish Comm. Nongame Wildlife Program Final Performance Report. Tallahassee, FL, 102 pp.

Ernst, C.H. 1967. A mating aggregation of the turtle *Clemmys guttata*. Copeia 1967:473-474.

Ernst, C.H. 1970a. Home range of the spotted turtle, *Clemmys guttata* (Schneider). Copeia 1970:391-393.

Ernst, C. H. 1970b. Reproduction in *Clemmys guttata*. Herpetologica 26:228-232.

Ernst, C.H. 1972. *Clemmys guttata*. Catalogue of American Amphibians and Reptiles 124:1-2.

Ernst, C.H. 1975. Growth of the spotted turtle, *Clemmys guttata*.

Journal of Herpetology 9:313-318.

Ernst, C.H. 1976. Ecology of the spotted turtle, *Clemmys guttata* (Reptilia, Testudines, Testudinidae), in southeastern Pennsylvania. Journal of Herpetology 10:25-33.

Ernst, C.H. 1982. Environmental temperatures and activities in wild spotted turtles, *Clemmys guttata*. Journal of Herpetology 16:112-120.

Ernst, C.H. 2001. An overview of the North American turtle genus *Clemmys* Ritgen, 1828. Chelonian Conservation and Biology 4:211-216.

Ernst, C.H., and Zug, G.R. 1994. Observations on the reproductive biology of the spotted turtle, *Clemmys guttata*, in southeastern Pennsylvania. Journal of Herpetology 28:98-102.

Ernst, C.H., Lovich, J.E., and Barbour, R.W. 1994. Turtles of the United States and Canada. Smithsonian Institution Press.

Ewert, M.A., and Nelson, C.E. 1991. Sex determination in turtles: diverse patterns and some possible adaptive values. Copeia 1991:50-69.

Feldman, C.R., and Parham, J.F. 2001. Molecular systematics of Emydine turtles. Linnaeus Fund Research Report. Chelonian Conservation and Biology 4:224-228.

Feldman, C.R., and Parham, J.F. 2002. Molecular phylogenetics of emydine turtles: taxonomic revision and the evolution of shell kinesis. Molecular Phylogenetics and Evolution 22:388-398.

Graham, T.E. 1970. Growth rate of the spotted turtle, *Clemmys guttata*, in southern Rhode Island. Journal of Herpetology 4:87-88.

Graham, T.E. 1995. Habitat use and population parameters of the spotted turtle, *Clemmys guttata*, a species of special concern in Massachusetts. Chelonian Conservation and Biology 1:207-214.

Haxton, T., and Berrill, M. 2001. Seasonal activity of spotted turtles (*Clemmys guttata*) at the northern limit of their range. Journal of Herpetology 35(4): 606- 614.

Hipes, D., Jackson, D.R., Nesmith, K., Printiss, D., and Brandt, K. 2000. Field guide to the rare animals of Florida. Florida Natural Areas Inventory, Tallahassee.

Holman, J.A., and Fritz, U. 2001. A new emydine species from the Middle Miocene (Barstovian) of Nebraska, USA, with a new generic arrangement for the species of *Clemmys* sensu McDowell (1964) (Reptilia: Testudines: Emydidae). Zoologische Abhandlungen 51:331-354.

Iverson, J.B. 1982. Biomass in turtle populations: a neglected subject. Oecologica 55: 69-76.

Iverson, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, Indiana: Privately printed, 363 pp.

Iverson, J.B., and Etchberger, C.R. 1989. The distributions of the turtles of Florida. Florida Sci. 52(2):119-144.

Kiviat, E. 1978. Vertebrate use of muskrat lodges and burrows. Estuaries 1:196-200.

Laemmerzahl, A.F. 1990. Variation in the spotted turtle, *Clemmys guttata*. Master's thesis, George Mason University, Fairfax, Virginia.

Lewis, T.L., and Ritzenthaler, J. 1997. Characteristics of hibernacula use by spotted turtles, *Clemmys guttata*, in Ohio. Chelonian Conservation and Biology 2:611-615.

Lewis, T.L., and Faulhaber, C.A. 1999. Home ranges of spotted turtles (*Clemmys guttata*) in southwestern Ohio. Chelonian Conservation and Biology 3:430-434.

Litzgus, J.D., and Brooks, R.J. 1998a. Growth in a cold environment: body size and sexual maturity in a northern population of spotted turtles, *Clemmys guttata*. Canadian Journal of Zoology 76:773-782

Litzgus, J.D., and Brooks, R.J. 1998b. Reproduction in a northern population of *Clemmys guttata*. Journal of Herpetology 32:252-259.

Litzgus, J.D., and Brooks, R.J. 2000. Habitat and temperature selection of *Clemmys guttata* from a northern population. Journal of Herpetology 34(2):178-185.

Litzgus, J. D., and Mousseau, T. A. 2003. Multiple clutching in southern spotted turtles, *Clemmys guttata*. Journal of Herpetology 37:17-23.

Litzgus, J.D., Costanzo, J.P., Brooks, R.J., and Lee, R.E. 1999. Phenology and ecology of hibernation in spotted turtles (*Clemmys guttata*) near the northern limit of their range. Canadian Journal of Zoology 77(9):1348-1357.

Lovich, J.E. 1988. Geographic variation in the seasonal activity cycle of spotted turtles, *Clemmys guttata*. Journal of Herpetology. 22:482-485.

Lovich, J.E. 1989. The spotted turtles of Cedar Bog: historical analysis of a declining population. In: Glotzhober, R.C., Kochman, A., and Schultz, W.T. (Eds.). Proceedings of Cedar Bog Symposium II, Ohio Historical Society, Columbus, Ohio, pp. 23-28.

Lovich, J.E. 1990. Spring movement patterns of two radio-tagged male spotted turtles. Brimleyana 16:67-71.

McCollough, M. 1997. Status and conservation of turtles in Maine. In: Tyning, T.F. (Ed.). Status and Conservation of turtles of the Northeastern United States. Minnesota: Serpent's Tale, pp. 7-11.

Meylan, P.A., Schuler, R.A., and Moler, P. 2002. Spermatogenic cycle of the Florida softshell turtle, *Apalone ferox*. Copeia 2002:779-786.

Milam, J.C., and Melvin, S.M. 2001. Density, habitat use, movements and conservation of spotted turtles (*Clemmys guttata*) in Massachusetts. Journal of Herpetology 35:418-427.

Neill, W.T. 1954. Ranges and taxonomic allocations of amphibians and reptiles in the southeastern United States. Publications of the Research Division of Ross Allen's Reptile Institute 1(7):75-96.

Netting, M.G. 1936. Hibernation and migration of the spotted turtle, *Clemmys guttata.* Copeia 1936:112.

Palmer, W.M. and Braswell, A.L. 1995. Reptiles of North Carolina. University of North Carolina Press. Chapel Hill.

Perillo, K.M. 1997. Seasonal movements and habitat preferences of spotted turtles (*Clemmys guttata*) in north Central Connecticut. Chelonian Conservation and Biology 2:445-447.

Pope, C.H. 1939. Turtles of the United States and Canada. Alfred A. Knopf. Inc. New York.

Schneider, J.G. 1792. Beschreibung un Abbildung einer neuen Art von Wasserschildkröte. Schriften der Gesellschaft Naturfoorschender Freunde zu Berlin 10:259-283.

Stearns, B., Collins, D., and Herman, D. 1990. *Clemmys* protection resolution. Herpetological Review 21:77.

Strauch, A. 1862. Chelonologishe Studien. Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg, Ser. 7, 5:1-196.

U.S. Fish and Wildlife Service. 2000. Proposal 11.37 to the Eleventh Meeting to the Conference of the Parties to the Convention on International Trade in Endangered Species of Wild Fauna and Flora: Inclusion of *Clemmys guttata* in Appendix II. United States Fish and Wildlife Service, Arlington, VA.

Ward, F.P., Hohmann, C.J., Ulrich, J.F., and Hill, S.E. 1976. Seasonal microhabitat selections of spotted turtles (*Clemmys guttata*) in Maryland elucidated by radioisotope tracking. Herpetologica 32:60-64.

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Terrapene carolina – Eastern Box Turtle

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SUMMARY. – The Eastern box turtle, *Terrapene carolina*, is one of two terrestrial turtles found in Florida. The high-domed shell with a hinged plastron that can completely enclose the turtle makes this species familiar both to Florida residents and visitors. Two subspecies, the Florida box turtle, *T. c. bauri*, and the Gulf Coast box turtle, *T. c. major*, are found predominantly within Florida. Historically, four subspecies have been identified as occurring in Florida, although it is unlikely that non-hybridized Eastern box turtle, *T. c. carolina*, and three-toed box turtle, *T. c. triunguis*, occur within the state. Box turtles are found throughout Florida in a wide variety of habitats, including coastal floodplains, grasslands, marshes, and mesic forests. Box turtles are omnivorous but there is no quantitative information on diet. Box turtles mature at approximately 5–8 yrs of age, and adult females produce an average of approximately 8 eggs per year. While often perceived as "common", the population status of box turtles is not well understood, but population studies in geographically distributed areas indicate that population densities range from 4.8 to 16.4 individuals/ha in suitable habitat. Juvenile turtles appear rare in many populations and the sex ratio of adults varies geographically from 53–61% male. Fire and predators that consume eggs and hatchlings are important sources of mortality. The role of disease, including upper respiratory tract disease, needs more study. Although not a current threat to Florida *Terrapene*, domestic and international trade likely contributed to the depletion of populations in the past. Box turtles are listed on Appendix II of CITES and commercial collecting is banned within Florida. Inasmuch as a great amount of box turtle habitat has been developed or fragmented many populations may be in peril.

CONSERVATION STATUS. – FNAI Global - G5 (Demonstrably Secure), State - S5 (Demonstrably Secure); ESA Federal - Not Listed; State - Not Listed; CITES - Appendix II; IUCN Red List - NT (Near Threatened).

Species Recognition. — The most distinctive features of *Terrapene carolina* are its hinged plastron and high-domed carapace. The carapace is keeled and has its highest point behind the plastral hinge. Males typically have a concave posterior plastron, whereas this area is flat or slightly convex in females. The toes of *T. carolina* bear strong claws that are thicker in males than females and are partially webbed; hind feet have three or four toes. *Terrapene c. major* attains a carapace length (CL) of more than 21 cm, although CL is rarely greater than 16 cm in the other subspecies and their hybrids. Size and coloration vary considerably among individual box turtles, even within a subspecies or geographic region.

North American subspecies can be distinguished on the basis of size, coloration, and a variety of morphological characters (reviewed by Ernst and McBreen, 1991b; Dodd, 2001). The Florida box turtle, *Terrapene carolina bauri* (Figs. 16-1 through 16-4), has a dark brown to black carapace with bright yellow radiating lines, and variable (low to extreme) flaring of the posterior marginals. Hind feet typically have three or four toes, and some individuals even have three toes on one foot and four on the other (Minx, 1992; Dodd, 2001). *Terrapene c. carolina,* the Eastern box turtle (Fig. 16-5), typically has a relatively short, broad carapace with bright patterning of yellow, red, or orange on a dark background, little or no flaring of the rear marginals, and four toes on each hind foot. *Terrapene c. major,* the Gulf Coast box turtle (Figs. 16-6 through 16-9), is the largest and most variable in color pattern of the North American subspecies, and generally shows weak patterning on the carapace, flaring of the posterior marginals, and four toes on the hind feet. Adult males often have large white blotches on the side of the head. The three-toed box turtle, *T. c. triunguis* (Fig. 16-10), which probably occurs in Florida only as an intergrade, is normally dully colored with a tan or olive background with relatively little patterning by lighter pigments. The highest point of the carapace is more posterior than in other subspecies, and adult size is on average smaller than in other subspecies (Ernst and McBreen, 1991b; Bartlett and Bartlett, 1999; Dodd, 2001). The largest reported *T. c. bauri* is a male of 187 mm CL from Sanibel Island (Pritchard, 1980); the largest *T. c. major* reported is 216 mm CL (Conant and Collins, 1991).

Hatchlings of *T. carolina* are very low-domed compared to adults. In all subspecies the adult shell pattern is not well developed at hatching (Figs. 16-11, 16-12). Still, hatchlings of *T. c. bauri* are much more vivid than those of the other box turtles within Florida, with bright yellow

Figure 16-1. Adult Florida box turtle, *Terrapene carolina bauri,* from Lee Co., Florida. Photo by Dick Bartlett.

markings along the lateral junctures of marginals, the sides of the head and neck, and along the dorsal crest of the shell (Dodd, 2001). Hatchlings retain the egg caruncle, used to help open the tough egg shell, for a period of days to weeks after hatching.

Taxonomic History. — Originally described as *Testudo carolina* by Linnaeus (1758), North American box turtles were reassigned to the genus *Terrapene* by Merrem (1820). *Terrapene bauri* and *T. major* both were described by Taylor (1895). Stejneger and Barbour (1917) were the first authors to use the trinomial *T. c. carolina* to indicate the nominate subspecies, whereas the trinomials for the Gulf Coast and Florida Box Turtles (*T. c. major* and *T. c. bauri)* were both first used by Carr (1940). Ernst and McBreen (1991a) and Dodd (2001) provided a complete synonymy of the genus and its various subspecies. Use of the English common name "Eastern box turtle" is applied both to the species *T. carolina* and to the subspecies *T. c. carolina* (Crother, 2000). The Spanish common name is *tortuga carolina*.

The genus *Terrapene* currently includes four extant species distributed across two-thirds of the lower 48 United

Figure 16-2. Plastral views of adult male (left) and adult female (right) Florida box turtle, *Terrapene carolina bauri,* from Volusia Co., Florida. Photo by Peter May.

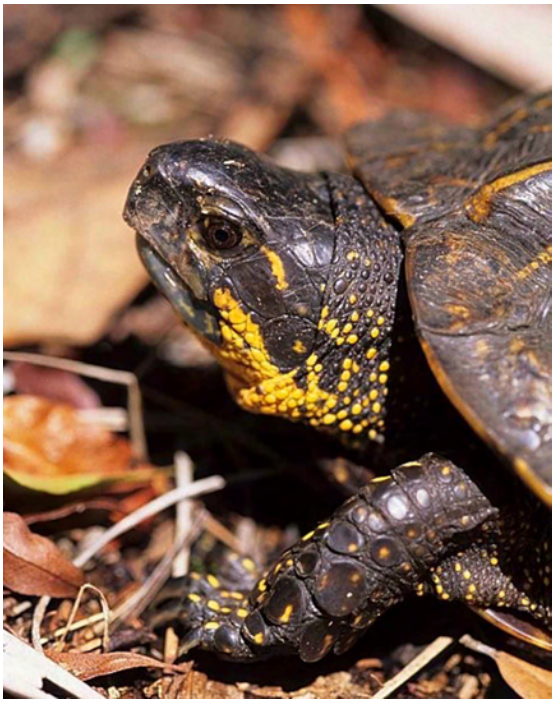

Figure 16-3. Florida box turtle, *Terrapene carolina bauri*, from Volusia Co., Florida. Photo by Peter May.

Figure 16-4. Adult female Florida box turtle, *Terrapene carolina bauri*, from Highlands Co., Florida. Photo by Robert T. Zappalorti.

States and as far south as the Yucatan Peninsula and Nayarit in Mexico: *T. carolina* (eastern US and Atlantic Coast of Mexico), *T. ornata* (central and near western US and adjacent Mexico), *T. coahuila* (Coahuila, Mexico), and *T. nelsoni* (coastal Sonora to Nayarit, Mexico). Eastern box turtles extend as far north as extreme southern Maine, Ontario, and central Michigan.

Terrapene carolina includes six extant subspecies, four of which (*T. c. carolina*, *T. c. triunguis*, *T. c. major*, and *T. c. bauri*) occur in the United States, and two (*T. c. mexicana* and *T. c. yucatana*) that are restricted to Mexico (Ernst and McBreen, 1991b; Dodd, 2001). The subspecies *T. c. bauri* and *T. c. major* have been suggested as distinct species at one time or another (Ward, 1980; Minx, 1996; Dodd, 2001), and Bentley and Knight (1998) suggested that *T. c. major* and the Pleistocene *T. c. putnami* also are conspecific. Phylogenetic analyses of morphology demonstrated that the Mexican *T. coahuila* is the basal taxon of the Carolina Group and indeed of all currently known *Terrapene* (Minx, 1996; reviewed by Dodd, 2001).

Confusing the taxonomy and systematics of the genus even further, especially in Florida, is the complicated fossil history of box turtles within the state. The genus *Terrapene* first appeared in the Miocene (ca. 15 million years before present) of Nebraska. The earliest Floridian fossils (originally described as *T. antipex*) were found in Pliocene deposits (5–1.9 million years before present) from Columbia, Pinellas, Polk, and Hardee counties. In Pleistocene deposits (1.9 million to 10,000 years before present), six species (*putnami, canaliculata, antipex, formosa, innoxia, singletoni*) have been described from Florida, although all seem to be variants of a single large (now referred to *putnami*) and a single small species (now referred to *bauri*). Dodd (2001) reviewed the complicated taxonomy of fossil Florida box turtles.

Because of the extent of variation within each of the recognized subspecies, and intergradation between them, delineating the exact range of each is difficult. Blaney (1971) commented with respect to box turtles of the Apalachicola region that due to the broad zones of intergradation that exist between the various subspecies, individuals of that area may appear typical of a particular subspecies or be intermediate in appearance between two subspecies. Minx (1996) suggested that only three of the four subspecies (*carolina*, *bauri*, and *major*) occur in Florida. However, the influence of intergradation between *triunguis*, *major*, *carolina*, and *bauri* may be seen in populations throughout the middle and western panhandle and along contact zones between *bauri* and *carolina* near the Georgia–Florida border. It seems unlikely that there are any "pure" populations of *carolina* or *triunguis* within Florida, but only a genetic analysis can provide conclusive evidence.

DISTRIBUTION

Geographic Distribution. — The range of *T. carolina* includes the eastern U.S. from southern Maine to the Florida

Figure 16-5. Adult female box turtle from Jackson Co., Florida, showing Eastern box turtle (*Terrapene carolina carolina*) characteristics. Photo by Matt Aresco.

Figure 16-6. Adult male Gulf Coast box turtle, *Terrapene carolina major*, from Liberty Co., Florida. Photo by Dick Bartlett.

Figure 16-7. Plastral view of adult male Gulf Coast box turtle, *Terrapene carolina major*, from Liberty Co., Florida. Photo by Dick Bartlett.

Figure 16-8. Adult Gulf Coast box turtle, *Terrapene carolina major*, Gulf Coast box turtle, from Liberty Co., Florida. Photo by Barry Mansell.

Keys, west to Michigan, Illinois, eastern Kansas, Oklahoma, Texas, and several states in Mexico (Dodd, 2001). Individuals have been found far outside this range in many different types of habitats. Due to the popularity of box turtles as pets and their transport to and release in areas outside of their native range, the exact boundaries of its distribution are uncertain. Even prior to European colonization, American Indians apparently also carried box turtles or their shells to distant locations.

Box turtles are found throughout Florida (Fig. 16-13) (Iverson and Etchberger, 1989). In a survey of Florida specimens of box turtles in North American museum collections, Dodd and Franz (1993) found that only four Florida counties were not represented by specimens (Hardee, Hendry, Martin, and Union); this situation has not changed in the years hence. All of these counties are surrounded by counties in which box turtles are found, so their absence from these counties almost certainly reflects collection bias rather than gaps in their distribution. Specimens have also been collected from many of the Florida Keys all the way south to Key West (Duellman and Schwartz, 1958; Lazell, 1989).

The precise boundaries of the ranges of the North American subspecies and their occurrence in Florida need further investigation. Carr (1940, 1952), Ernst et al. (1994), and Conant and Collins (1991) recognized only *bauri* and *major* in Florida. Ashton and Ashton (1985) and Bartlett and Bartlett (1999) indicated that characteristics of *carolina* may occur in populations in the extreme northeast of Florida, and that characteristics of *triunguis* may occur in northern panhandle populations. However, neither of these latter field guides unambiguously states that true *triunguis* or *carolina* occur within the state, nor do they present original data.

Figure 16-9. Adult male Gulf Coast box turtle, *Terrapene carolina major*, from Liberty Co., Florida. Photo by Dick Bartlett.

Questions of distribution relate back to the questions of taxonomy mentioned previously, especially within the northern parts of the state near the Georgia border, and westward through the panhandle. Various authors have treated the distribution differently. Minx (1996) indicated that all box turtle populations in northern peninsular Florida were intergrades between *carolina* and *bauri*; within the panhandle, he suggested that there is extensive intergradation between *major* and adjacent *carolina* and *bauri* in areas of contact (although his map indicates only *major* within the Florida panhandle). Ernst et al. (1994), Bartlett and Bartlett (1999), and Minx (1996) all suggested that the Florida distribution of *T. c. major* only included the panhandle region; Conant and Collins (1991) showed the range extending eastward only to about Taylor County, with regions of intergradation between *T. c. major* and *T. c. triunguis* in the northern half of the panhandle. These authors go on to state that the rest of the state was inhabited solely by *T. c. bauri*, with regions of intergradation with *T. c. carolina* near the Georgia border eastward from approximately Columbia County. Ashton and Ashton (1985), on the other hand, indicated that *T. c. major* inhabited the southern half of the panhandle and occurred in the coastal counties of the peninsula along the Gulf of Mexico south to Collier County, which is now known to be incorrect. These latter authors mapped the distribution of *T. c. carolina* as extending well into northern Florida, but with the peninsula mostly inhabited by *T. c. bauri*. Clearly, the ranges and taxonomic affinity of northern Florida box turtle populations needs further study, and currently available field guides do not adequately reflect subspecific (or phenotypic) distributional patterns.

Ecological Distribution. — *Terrapene carolina* is probably the most terrestrial of the emydid turtles, and is gener-

Figure 16-10. Male box turtle from Calhoun Co., Florida, showing influence of three-toed box turtle (*Terrapene carolina triunguis*) including amber carapace color and unflared peripheral bones. Photo by Kenny Krysko.

ally considered to be a woodland species across most of its range (Ernst et al., 1994; Dodd, 2001), although *T. c. major* is commonly associated with marsh habitats (Carr, 1940; Blaney, 1971). Carr (1940) recorded that the Gulf Coast box turtle was commonly found in streams in flatwoods and hammocks, but that the Florida box turtle was rarely seen in water. Habitats used can vary, although they are typically characterized as moist or humid, and may include coastal floodplains, meadows, and pastures or grasslands in addition to forested (especially flatwoods and upland and mesophytic hammocks) habitats (Carr, 1940; Ernst et al., 1994; Dodd, 2001). Population studies of *T. c. triunguis* at prairie-woodland ecotones in Arkansas and on *T. c. bauri* in grassy sea oats meadows on Egmont Key at the mouth of Tampa Bay revealed extensive use of grasslands in late spring and early fall (and winter on Egmont Key), when temperatures were moderate and moisture levels were high. At other times of year, the turtles restricted their activity to forest habitat, where they buried in the leaf litter to avoid high temperatures and low humidity (Reagan, 1974; Dodd et al., 1994). Bogert and Cowles (1947) measured the rate of water loss of one individual of *T. c. bauri* from Highlands County, Florida, and found it to be similar to that of the terrestrially adapted gopher tortoise, *Gopherus polyphemus.*

In Florida, box turtles are rather generalized in habitat requirements, and are found in a variety of forested and open habitats. The consistent environmental attribute usually associated with suitable box turtle habitat is high relative humidity (Dodd et al., 1994). In south Florida and the Keys, *T. c. bauri* is most abundant in xeric habitats (which includes sandy scrub, pine forest and pine rocklands), less common in mesic (oak, cabbage palm, and tropical hammocks) and “alternohygric” (cypress flats and prairies) habitats, and nearly absent from hygric (cypress heads and sink ponds), halohygric (salt marsh, mangrove [but see Verdon, 2004]), and “edificarian-ruderal” (man-made) habitats (Duellman and Schwartz ,1958; Verdon, 2004). At one time, box turtles were thought to be absent from the Everglades, although one of us (CKD) photographed this subspecies on the elevated roadbed leading to Mahogany Hammock.

Elsewhere in south and central Florida, *T. c. bauri* prefers damp woods or glades (Dickson, 1953), flatwoods, and upland and mesophytic hammocks (Carr, 1940, 1952; Abrahamson and Hartnett, 1990). *Terrapene c. bauri* may reach its greatest abundance in limestone flatwoods (Carr, 1940, 1952) and on offshore islands, such as the highly altered habitats on Egmont Key (Langtimm et al., 1996; Dodd, 1997a, 1998, 2001). Babbitt and Babbitt (1951) found a high density of *T. c. bauri* in a burned over area in Dade County that was described only as “thick undergrowth” on a limestone ridge prior to burning. Florida box turtles are rare in the “high pine” uplands of the state.

Ashton and Ashton (1985) listed habitat associations of each of the four subspecies of *T. carolina* that they recognized in Florida. They indicated that *T. c. carolina* was common in pine flatwoods, mesic hammock, and farms/fields/disturbed areas and human habitations/golf courses/trash piles, and uncommon in longleaf pine-turkey oak habitats (sandhills). *Terrapene c. bauri* was described as common in the same four habitats as that of *T. c. carolina,* and rare in sand pine-rosemary scrub. *Terrapene c. major* was common in pine flatwoods and uncommon in salt marsh

Figure 16-11. Hatchling Florida box turtle, *Terrapene carolina bauri,* from Alachua Co., Florida. Photo by Dick Bartlett.

Figure 16-12. Post-hatchling Gulf Coast box turtle, *Terrapene carolina major*, from Liberty Co., Florida. Photo by Dick Bartlett.

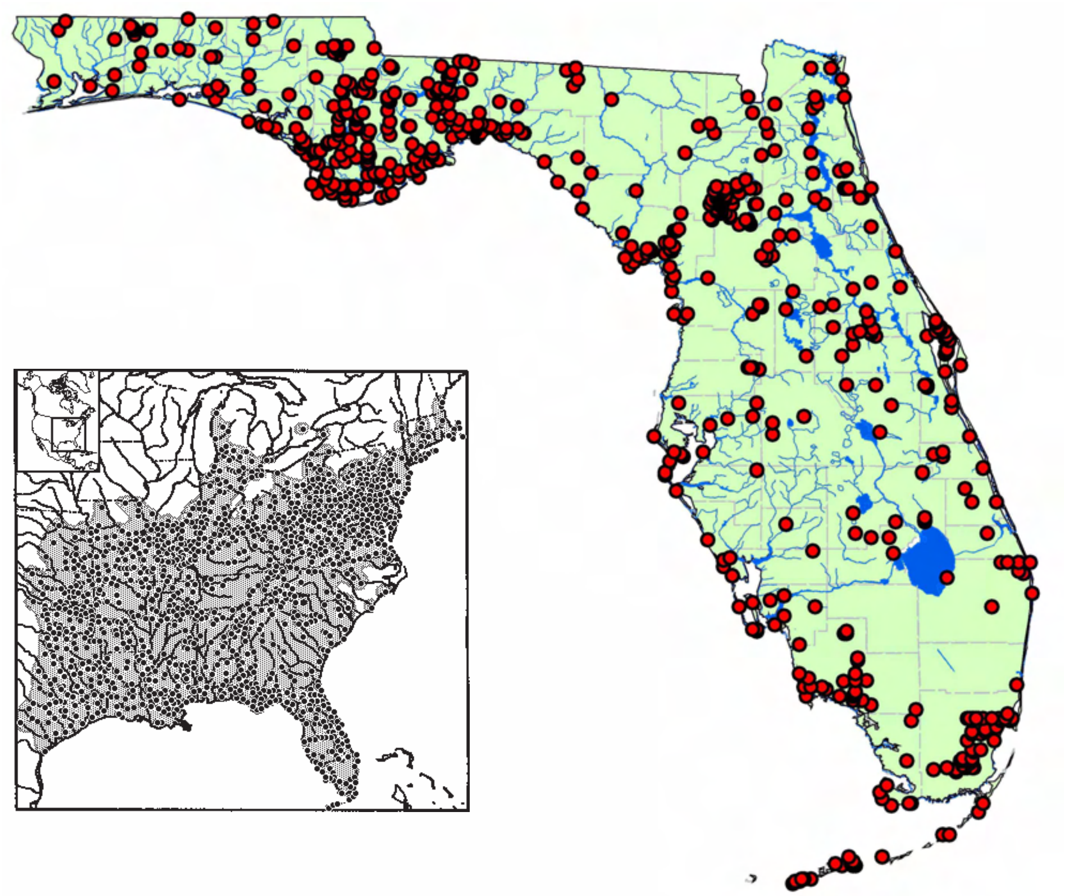

Figure 16-13. Available distribution records for the box turtle, *Terrapene carolina*, from Florida. Inset: distribution records from U.S. range of *T. carolina* (adapted from Iverson, 1992; distribution in inset map not current for Florida as presented here).

and coastal dunes beaches and dunes, whereas *T. c. triunguis* was considered common in mesic hammock and temperate deciduous forest and uncommon in pine flatwoods and longleaf pine-turkey oak.

Quantitative data on habitat use of box turtles in Florida are mostly lacking. Published information on the ecology of Florida box turtles prior to the 1990s consists mainly of anecdotal or descriptive information with little or no quantitative data (Carr, 1940; Allen and Neill, 1952; Blaney, 1971; Lazell, 1989). The numerous studies of Dodd and his colleagues on *T. c. bauri* on Egmont Key, a 180 ha island at the mouth of Tampa Bay, are the most comprehensive source of data on habitat use and ecological characteristics of Florida box turtles (Dodd et al., 1994, 1997; Dodd and Franz, 1996; Langtimm et al., 1996; Dodd, 1997a, b, 1998, 2001, 2003; Hamilton, 2000; Jennings, 2003; Devaux, 1993). Dodd et al. (1994) found these turtles most frequently in human altered habitat (lawns) or former hammock that was highly modified by the presence of invasive nonindigenous species (*Schinus terebinthifolius* and *Casuarina equisetifolia).*

A central Florida population of *T. c. bauri* studied by Pilgrim et al. (1997) was primarily found in an isolated 8 ha palm-oak hammock surrounded by *Spartina-Cladium* floodplain marsh. Individual turtles monitored by radiotelemetry in this population made extensive forays from the hammock into the surrounding marsh, where they remained on occasion for weeks at a time. In the Keys, recent work by Verdon (2004) has led to additional information on habitat use. She found telemetered box turtles in pine rockland forest (87% of 1884 sightings), lawns (7.8%), and in wetlands (5.5%), with the remainder on roads and in mangrove, on approximately 12 ha of Big Pine Key. Her study was conducted for one year in all months. On Egmont Key, an extensive study (Hamilton, 2000; Jennings, 2003) of juvenile Florida box turtles showed that the smaller size classes preferred the cooler, mesic interior portions of the island rather than the more exposed patches of open scrub, sea oats meadows, and lawns. A canopied forest habitat structure is important in helping juveniles maintain favorable thermal and moisture preferences, especially during Florida's hot summers.

HABITAT RELATIONS

Activity. — Activity patterns of box turtles vary significantly over their range, especially with respect to the occurrence and duration of the period of winter dormancy. Box turtles from more northern parts of the range in the eastern United States may be active only between March and April to October and November (Ernst et al., 1994; Dodd, 2001), but in peninsular Florida they are active year-round. At least on Florida's peninsula and keys, box turtles do not become dormant or undertake extended periods of summer inactivity, although temporal patterns of activity of adults during the day may shift between seasons (Dodd et al., 1994; Verdon, 2004). Pilgrim et al. (1997) found box turtle activity in Volusia County, Florida, during all months of the year, with greatest activity levels in fall and spring. Peaks of activity were also associated with extensive flooding of their hammock habitat.

On Egmont Key, activity occurs when air temperature exceeds 17ºC, and seems to be associated with high humidity (> 66%) (Dodd et al., 1994). Adult males and females do not differ in activity patterns, and both sexes show a seasonal shift from bimodal activity with peaks in morning and afternoon when temperatures are high to activity peaking during the middle part of the day during cooler months (Dodd et al., 1994). Radiotelemetry of *T. c. bauri* in Volusia County revealed that no turtles were active when air temperature was below 14ºC, and highest levels of activity were found when air temperatures were between 26 and 30ºC, when more than 60% of turtles located were out of cover and active (Farrell and May, unpubl. data). On more southern Big Pine Key, however, activity occurred between air temperatures of 18 and 36ºC, and at relative humidities between 41 and 86% (Verdon, 2004); turtles favored warm temperatures with high rainfall for activity.

Like adults, juvenile activity is bimodal during the warmer part of the summer and fall months; more activity occurs in the morning than in the afternoon. For juveniles, temperature may play a more important role in initiating activity than moisture. Activity in juveniles occurs more often in areas with lower soil and ambient temperatures and higher humidities than in surrounding areas, and activity (based on distance moved by thread-trailed animals) is not influenced by environmental factors, including rainfall (Hamilton, 2000; Jennings, 2003). Presumably these correlations reflect juvenile preference for dense habitat structure and avoidance of direct sun and open habitats.

Movements and Home Range. — Two of us (PGM, TMF) have studied movement patterns of *T. c. bauri* in Volusia County since October 1996, and have monitored the movements of 15 individuals for periods ranging from 1–24 months. Individual turtles show tremendous variability in the scope of their movements. We monitored the movements of 7 turtles for periods exceeding 11 months, with samples ranging between 35 and 81 relocations per individual. This sample included 6 males and 1 female, so it is difficult to make generalizations about gender-related differences in movement patterns. However, the single female moved much more extensively than the males. Her home range size, estimated by the minimum convex polygon method, was 30.96 ha, with a length of 1015 m and width of 558 m, measured over a period of 11 months and including 55 relocations. CKD has also observed straight-line movements of >1 km among *T. c. bauri* on Egmont Key. The six Volusia County males had home ranges averaging only 2.8 ha (SD = 1.18; range = 0.98–3.94), with mean lengths and widths of 304 and 153 m respectively. These males were tracked for an average of 17 months each (SD = 5.7) and 63 relocations each (SD = 16.6).

We initially thought box turtles in our population restricted their activity primarily to the interior of an 8 ha mesic hammock (Pilgrim et al., 1997), but radiotelemetry indicated that not all individuals do. Some turtles, including the single female, made regular transits between areas of focused activity in the hammock to secondary activity areas several hundred meters into the surrounding *Spartina-Cladium* marsh. The female typically spent several weeks in marsh habitat before returning to the hammock. Excursions from the hammock appeared to be most closely related to periods of drought when available standing water in the hammock disappeared. However, some turtles have shown extremely restricted home ranges confined entirely to the hammock habitat; perhaps significantly, the home range of these turtles typically includes low-lying areas within the hammock, where standing water or significant subsurface moisture is most likely to be found. More reliable conclusions about movement patterns, and particularly differences between males and females, will require larger samples of both sexes.

Although our intent has been to monitor similar numbers of male and female turtles, females have proven more difficult to monitor for long periods, mostly for unknown reasons. Transmitter failure has occurred in at least a couple of females, but it is possible that females in our population are simply more mobile and their extensive home ranges often take them beyond the range of our tracking capability. Irrespective of male-female differences, our initial results from this small sample suggest that central Florida box turtles may differ significantly from northern subspecies with respect to spatial requirements, and that these differences in activity areas are quite likely directly related to the habitat and resource characteristics in which the turtles are found.

There are two published reports on home range size in Florida box turtles. On Big Pine Key, Verdon (2004) tracked 12 adult Florida box turtles (9 males, 3 females) at both natural and disturbed sites for a period of a year. Based on 426 captures the mean home range was 1.4 ha using the minimum convex polygon method, 1.8 ha using the 95% kernel method, 2 ha using the 95% Jerich-Turner method, and 129.9 m using the maximum diameter method. Mean daily travel was significantly greater in the wet season than in the dry season (30.2 m vs. 9.2 m). Home ranges of northern populations are generally no more than about 200 m in diameter. *Terrapene c. carolina* home ranges vary from a maximum diameter of < 228 m in New York to a mean diameter of 74 m in Tennessee. Most straight-line maximum linear distances are between means of 97–213 m, but there is considerable geographic variation and the techniques used to obtain the measurement vary considerably (Dodd, 2001). Due to differences in habitats, the home ranges of Florida box turtles may be quite different, even among habitats and geographic areas.

On Egmont Key, a study tracking 58 thread-trailed juvenile box turtles (Hamilton, 2000; Jennings, 2003) recorded distances traveled from 0–200 m within a 24-hr period (mean 60.3 m), although daily movements < 100 m were common. Trail tortuosity was measured for 50 juveniles: 45% of trails were mostly linear, 22% were horseshoe-shaped, and 33% were concentrated extensively within a particular area, although usually returning near the point of origin. In addition, there was considerable among-juvenile variation in the tortuosity of the movement patterns. Clearly, juveniles on Egmont Key, at least, travel complex paths and are very active, rather than remaining entirely under cover or within one location for an extensive period of time.

GROWTH AND REPRODUCTION

Growth. — Growth of *T. c. bauri* was estimated from museum specimens by Ernst et al. (1998), who found their growth pattern to be typical for an emydine turtle. Growth is rapid in juveniles but slows after maturity (which they estimated to occur at 12–13 yrs), and nearly ceases entirely by 16 (females) or 17 (males) yrs of age. Dodd (1997a; unpubl. data), in contrast, monitored known-age animals in a long-term marked population and determined that male *T. c. bauri* at Egmont Key matured at 5–6 yrs and females at 7–8 yrs. Given the potential sources of bias in estimating maturity from museum specimens, Dodd's estimates are likely to be more reliable, at least for the turtles of Egmont Key. Ernst et al.'s (1998) museum data showed that during their first year, Florida box turtles grew by about 27% per year, similar to rates reported for *T. c. carolina.* By 8 yrs of age, growth by male *T. c. bauri* had slowed to 6% per year and to 5.4% per year in females. At 13 yrs of age, growth rate had decreased to about 2% per year in both sexes. Based on recapture data from Egmont Key turtles, Dodd (1997a) suggested that males grow faster and mature earlier than females. Males are generally recognizable by their plastral concavity by their fifth or sixth year of age, whereas females are typically 7 or 8 yrs of age before they can be reliably assigned to gender. Once mature, growth may halt completely. Dodd (unpubl. data) has followed a number of turtles on Egmont Key for more than 12 years, during which time no measurable growth has been noted.

Sexual Dimorphism. — Tails of males and females are dimorphic; male tails are usually longer and thicker than those of females, with the vent positioned more posterior (Carr, 1952; Ernst and McBreen, 1991b; Dodd, 2001). Males also tend to be larger than females (Pilgtrim et al., 1997), and have larger rear legs and shorter hind foot claws than females (Carr, 1952; Dodd, 2001). Male *T .c. bauri* typically have broader posterior portions of the plastron relative to similar-sized females, due to broad, outwardly flaring marginals (Pilgrim et al., 1997). Differences in eye color are not apparent between male and female *T. c. bauri* as they are in most other subspecies of *T. carolina*. Intergrades in northern Florida and *T. c. major* seem to retain the reddish eye color trait in males, with females predominantly having brown eyes. However, there is considerable variation. Male *T. c. major* also often have a blotch or extensive white patches on the side of the head; females lack these blotches.

Mating Season / Mating Behavior. — Timing of reproductive activities appears quite variable in Florida. Dodd (2001) noted that courtship could occur virtually at any time during the activity season, and provided an extensive description of courtship and mating. Ernst et al. (1994) stated that copulation occurs between March and October, whereas Dickson (1953) noted year-round mating activity in his captive box turtles. In Volusia and Hillsborough counties, copulation or pre-copulatory behaviors have been observed between July and November, with the majority of copulations occurring in September and October (Dodd and Farrell, unpubl. data). Shelled eggs are apparent in the oviducts beginning in late March, but most oviposition probably occurs between mid-April and July (Dodd, 1997b). Dickson (1953) reported that captive females dug nest holes in all months of the year.

Nesting Behavior. — Nesting typically begins in late afternoon, often after rains, and nest site selection tends to be fairly specific. Females seem to prefer slightly elevated, open sites that have adequate exposure but are protected from flooding, and they will sometimes leave their home range to find suitable oviposition sites (Jackson, 1991; Ernst et al., 1994; Dodd, 2001). Incubation period is dependent on temperature, and requires temperatures between 22 and 34ºC (Dodge et al., 1978; Dimond, 1985) for successful hatching. The normal incubation period is between 70 and 80 days, depending upon incubation temperature, although hatching may occur in as little as 45 days under laboratory conditions (Dickson, 1953; Jackson, 1991; Ernst et al., 1994; Dodd, 2001).

Sex determination in box turtles is largely temperature-dependent. Ewert et al. (2004) reported that clutches incubated at constant temperatures between 22.5 and 25ºC produced 60–71% males; 26 to 27ºC produced 82–86% males; 28ºC produced 46% males; and > 29ºC produced all females. Thus, there is considerable variation in the sex ratio of the offspring of Florida box turtles, even when incubation temperatures are held constant. In contrast, Indiana *T. carolina* have much higher percentages of males produced at all temperatures below ca. 28.5ºC (Ewert et al., 2004).

Clutch Size and Frequency. — The mean clutch size is 2.4 (mode = 2) eggs for *T. c. bauri* on Egmont Key, with individual clutches ranging between 1 and 5 (Dodd, 1997b). Mean clutch size did not vary among months or years. Data on frequency of clutches showed considerable variability between individual females; some females showed evidence of producing 2 or 3 clutches per year, whereas other females apparently produced only a single clutch, and some females may have produced no clutches. These data present a different picture of reproductive potential in box turtles than those observed in *T. c. major* (Tucker et al., 1978; Jackson, 1991). Tucker et al. (1978) dissected female turtles and counted eggs, preovulatory follicles, and enlarged follicles to estimate clutch size and frequency. They concluded that the mean clutch size for these turtles was around 2.7 eggs, and that individual females oviposited between 2 and 5 clutches per year. Their estimated annual reproductive output was between 7.26 and 9.25 eggs/female. A single female *T .c. major* kept in captivity and offered supplemental food produced between 1 and 3 clutches/year, ranging from 1 to 5 eggs/clutch, at intervals of 23–30 days (Jackson, 1991). The reproductive potential in Florida turtles may be similar to that for box turtles in more northern areas by producing more clutches per year, albeit with fewer eggs per clutch. In northern *T. carolina*, clutch size can vary from 1 to 11, although 4–5 eggs is the normal clutch size, and only one clutch is usually oviposited per year (Ernst et al., 1994; Dodd, 2001). Dodd (1997b) suggested that food resources might limit annual clutch size and frequency in the Egmont Key population he studied.

The most complete data on reproductive output and frequency in wild box turtles come from Dodd (1997b), who radiographed 515 *T. c. bauri* from Egmont Key between 1992 and 1995. Shelled eggs were found from March through August in females ranging from 124–153 mm CL. Between 2% and 54% of the turtles radiographed were gravid in any single month, with an overall mean of 27%. The fewest gravid turtles occurred, as might be expected, at the beginning and end of the reproductive season.

POPULATION BIOLOGY

Density and Biomass. — Although frequently referred to as “common” throughout its range, quantitative studies on the population biology and ecology of box turtles are mostly limited to northern populations (Dodd et al., 1994) and are of questionable relevance to Florida box turtles. Studies by Dodd, Franz, and colleagues on *T. c. bauri* on Egmont Key (Dodd et al., 1994, 1997; Dodd and Franz, 1996; Langtimm et al., 1996; Dodd, 1997a, b, 1998, 2001, 2003; Hamilton, 2000; Jennings, 2003; Dodd and Griffey, 2004, 2005), Farrell, May, and students on *T. c. bauri* in central Florida (Pilgrim et al., 1997), Verdon on Big Pine Key (Verdon, 2004; Verdon and Donnelly, 2005), and Ernst and colleagues on museum specimens of *T. c. bauri* (Ernst et al., 1995, 1998) are the only sources of extensive data on behavior and population biology of Florida’s box turtles. Box turtle populations are currently also being studied at the Central Florida Zoo in Seminole County (S. Decresie, *pers. comm.*), at Boyd Hill Nature Center in Pinellas County (G. Heinrich, *pers. comm.*), and in south Florida around Florida Bay (G. Mealey, *pers. comm.*), although no published data on these populations are available as of this writing.

Population densities for box turtles can be quite high, although data on Florida populations are scarce. Langtimm et al. (1996) calculated densities of *T. c. bauri* on Egmont Key of 14.9 individuals/ha (adults only) and 16.4 individuals/ha (adults + juveniles). These estimates may not be representative of the whole island because the authors restricted their analysis to turtles at the southern end of the island. Similarly, Pilgrim et al. (1997) estimated a population density of 16.3 individuals/ha in central Florida. Verdon and Donnelly (2005) estimated a density of 4.8 to 10.2 individuals/ha *T. c. bauri* on Big Pine Key. These estimates are within the range of densities reported for other populations of *T. carolina* that have varied from 2.7 individuals/ha in *T. c. carolina* in Indiana to more than 20 individual/ha in *T. c. carolina* in Tennessee and *T. c. triunguis* in Missouri (Dodd, 2001).

Dodd (1998) estimated the biomass of box turtles on Egmont Key to be between 5 and 8 kg/ha. He cautioned that estimates of biomass (and density) are often confounded by the definition used, but noted that standing crop biomass of *T. c. bauri* exceeded similar estimates for mainland *T. c. carolina* and *T. c. triunguis*. Although lower than biomass estimates obtained for some aquatic turtles, the magnitude of these estimates suggests that box turtles may have a significant impact on community energy budgets. Though island population densities are sometimes higher than those of comparable mainland populations (Dodd, 1998), Pilgrim et al. (1997) estimated density at their mainland study site in Volusia County to be nearly identical to that of the Egmont Key population.

Population Structure. — Whereas densities of the three best-studied populations were relatively similar, population structure varies significantly, particularly with respect to juvenile density. Juveniles (< 120 mm CL) comprised 26.5% of the Egmont Key sample (Dodd, 1997b), 13.3% of the Central Florida zoo sample (S. Decresie, *pers. comm.*), 7.5 % of the Big Pine Key sample (Verdon and Donnelly, 2005), and only 3% of the Volusia county population (Pilgrim et al., 1997), suggesting major differences in recruitment between the populations. Juvenile turtles are notoriously difficult to find, however, and are usually underrepresented in samples (Dodd, 1997a). Sex ratios also differ among sites; the Egmont Key population was 61% male (Dodd, 1997a), the Central Florida Zoo population was 56% male (S. Decresie, *pers. comm.*), the Big Pine Key population was 57% male (Verdon and Donnelly, 2005), and the Volusia County population was 53% male (the only population that did not differ significantly from 1:1; Pilgrim et al., 1997). All studies showed similar patterns of sexual dimorphism, with males larger in CL than females. *Terrapene c. bauri* differs from some northern subspecies of box turtles in this respect. Female *T. c. triunguis* were larger than males in Oklahoma (St. Clair, 1998) and in a compilation of road-killed individuals in North Carolina populations of *T. c. carolina* (Stuart and Miller, 1987). Differences in patterns of dimorphism suggest that key aspects of the biology of box turtles may vary significantly over their geographic range, emphasizing that conservation decisions about Florida box turtles should be based on data from Florida populations.

Survivorship. — Box turtles are renowned for their potential longevity, although it is mostly unknown how many turtles in the wild reach their maximum potential life span. There are reports of turtles living in the wild for over 100 yrs, though some studies have shown that few individuals live beyond 30–40 yrs (Ernst et al., 1994). The box turtles of Egmont Key are estimated to have quite high (> 93%) weekly survivorship rates (Langtimm et al., 1996).

INTERSPECIFIC INTERACTIONS

Diet and Feeding. — Box turtles are omnivorous and highly opportunistic in their feeding behavior (Dodd, 2001). Young turtles are often carnivorous, but the importance of other food categories seems to increase with age. There is no evidence, however, of major shifts between the diets of juveniles and adults (Dodd, 2001). The list of foods that box turtles have been observed taking is vast, but includes vertebrates and invertebrates (especially snails), fungi, and a variety of plant parts, including fruits, roots, stems, and seeds (Ernst et al., 1994; Dodd, 2001). Carrion will also be taken on occasion. Dodd et al. (1994) found that cockroaches procured while plowing through leaf litter were a major element of the diet of Egmont Key box turtles, and that they travel to and congregate around fruiting plants such as sea grape (*Coccoloba uvifera)* and prickly pear (*Opuntia* sp.) to feed on ripening fruits. Because of their omnivorous diet, Florida box turtles may be important as seed dispersers and passage through their digestive tract may enhance germination by some plant species (Liu et al., 2004).

Predation. — Box turtle nests are preyed upon by a wide variety of mammalian, avian, and reptilian predators (Ernst et al., 1994; Dodd, 2001). Scarlet snakes (*Cemophora coccinea)* seem to be particularly effective at finding nests (Dickson, 1953). Once hatched, juveniles are susceptible to predation by many of the same species that attack nests, and especially by fire ants (Mount, 1981; Montgomery, 1996). The characteristic ability of adults to completely withdraw into their shells seems to protect them from most large predators, although feral hogs have been observed to crush and eat adults (Ernst et al., 1994). Franz and Dodd (1993) reported that a single raccoon on Egmont Key killed 26 adult and juvenile box turtles before it was removed from the island. Adult turtles frequently show evidence of punctures and trauma to both the carapace and plastron, some of which may be due to the efforts of predators (Dodd et al., 1997).

Fire has likely affected box turtles in Florida at least since the Pleistocene, and possibly as early as the Pliocene, based on an analysis of fossil shells in the Florida Museum of Natural History (D. Ehret, *pers. comm.*). A major source of mortality and injury in some Florida box turtle populations results from their habitation of fire-adapted communities, such as pine flatwoods, scrub, prairies, and marshes. Ernst et al. (1995), in a study of museum specimens, found the incidence of probable fire damage to *T. c. bauri* specimens (30%) to be much higher than in any other subspecies (> 5%), emphasizing the importance of fire to some populations. They found that fire damage was not independent of carapace length in their sample, perhaps suggesting that fire does not affect individuals randomly. In that regard, Hamilton (2000) found that juveniles used more mesic habitats than adults, which might expose them to fire less often. The importance of fire is quite likely habitat-specific, as the incidence of fire damage in Egmont Key turtles was only 3.5% (Dodd et al., 1997). Box turtles have impressive abilities to survive severe damage and regenerate damaged carapacial tissue (e.g., Rose, 1986; Dodd, unpubl. data), but many turtles do not survive the effects of intense ground fire. In their sample of 60 box turtles collected from a recently burned Dade County site, Babbitt and Babbitt (1951) found that at least 10 of the animals had succumbed to fire damage, and one of us (CKD) has found dead box turtles immediately after a prescribed fire on St. Marks National Wildlife Refuge. Allen and Neill (1952) stated “In almost any burned area one can see the whitened shells of box turtles that were caught in the path of the flames. Occasionally one finds a turtle that managed to survive the blaze with only the loss of the outer layer of the shell.”

Parasites and Disease. — Eye and respiratory diseases may be frequent in box turtles from northern populations, especially in early spring following warm, wet winters (Ernst et al., 1994). Individuals of *T. c. bauri* from the Volusia County population have been observed to display symptoms of respiratory infection on several occasions, including eyes swollen or swollen shut, nostrils clogged or with copious mucous flow, and wheezing respiration. One symptomatic individual in May 1997 was diagnosed positive for *Mycoplasma agassizi* (D. Brown, *pers. comm.*), the causative agent for upper respiratory tract disease (URTD) that has plagued gopher tortoise conservation efforts (Brown et al., 1994, Mushinsky et al., this volume). URTD previously had been diagnosed only in the genera *Geochelone* and *Gopherus* (Jacobson et al., 1991). Dodd (2001) provided a comprehensive summary of parasites and diseases affecting *Terrapene*.

Abscesses affecting the inner ear of box turtles are not uncommon, and have been associated with the presence of organochlorines, poor nutrition (especially in captivity), deficiency in Vitamin A, and unusual weather conditions during winter dormancy (Dodd and Griffey, 2004). On Egmont Key, 26 turtles with aural abscesses were found immediately after an unusually wet winter, the only time such abscesses were observed during a 12-year study. Treated turtles appeared to recover; some turtles appeared to recover naturally; and some turtles with abscesses were later found dead. Although it is unclear what the long-terms effects of this disease would be on wild populations, aural abscesses certainly impair feeding and make the turtle more prone to predation, since the turtles cannot withdraw the head into the shell in severe cases and are otherwise very lethargic (Dodd and Griffey, 2004). The prevalence of aural abscesses in box turtles in Florida is unknown.

THREATS

Probably the most widespread single factor threatening box turtle populations is the continued growth of the human population and concomitant destruction or disturbance of natural habitat (Dodd and Griffey, 2005). Florida’s human population increased from 1.7 million to 14.1 million between 1936 and 1995 (Kautz, 1998), and continues to grow. Habitats important to box turtles have shown corresponding declines, with forests shrinking by 22% and herbaceous wetlands by 51% during the same time period. On the other hand, urban lands have increased by 632% during this time (Kautz, 1998). The development and conversion of natural landscapes to highly altered human-dominated communities poses several distinct threats to box turtle populations.

Outright destruction of habitat results in death or displacement of turtle populations inhabiting those areas, although turtles remaining in undeveloped habitats may also suffer population threats due to nearby development. Habitat fragmentation, especially by roads, leads to a decrease in size of populations in remnant habitat islands and alters population structure, and increases their vulnerability to extirpation or decline due to stochastic factors (Gibbs and Shriver, 2002; Marchand and Litvaitis, 2004; Steen and Gibbs, 2004; Aresco, 2005). Areas of natural habitat remaining near human-modified habitats may also experience increases in populations of predators such as raccoons and dogs, which are among the few predators capable of preying on adult box turtles. Loss of genetic diversity may also ensue from decreases in population size. Although there are cases where human-modified habitats may provide some benefits to box turtle populations (for example, heavy use of lawn areas by the Egmont Key box turtles), use of these areas may subject turtles to higher levels of mortality from road kills and trauma inflicted by lawn mowers. Finally, fragmentation of habitat by urbanization and development may restrict access of box turtle populations to key resources such as water during dry periods or suitable oviposition sites not found within islands of preserved habitat.

Optimism regarding the future of Florida's box turtles comes from their use of a wide range of habitat types and, in particular, their use of flatwood habitats that are the target of wetland preservation programs. In addition, viable populations occur on many federal, state, and conservation organization-owned lands (Dodd and Griffey, 2005). In addition to Egmont Key, Lake Woodruff, and Key Deer National Wildlife Refuges (where the studies of Dodd, May, Farrell, and Verdon have taken place), box turtles occur on many public lands in Florida, such as St. Marks National Wildlife Refuge and the Kennedy Space Center (Bury and Luckenbach, 1980; Seigel et al., 2002). Survey projects have been taken on certain State Parks and Wildlife Management Areas (Enge and Wood, 1998) and in Everglades National Park (Meshaka et al., 2000; G. Mealey, unpubl. data). Unfortunately, much information is as yet unpublished. When box turtle distributional records are presented, they usually represent the results of somewhat temporally limited surveys using drift fences, or as checklists (e.g., Meshaka et al., 2000; Seigel et al., 2002). This makes it very difficult to determine whether box turtles reside in substantial numbers on public lands, although such an assumption seems reasonable with regard to large land holdings that encompass diverse mesic habitats.

Box turtle populations existing in fire-maintained ecosystems are a source of concern. Especially in the wake of the devastating wildfires that affected extensive areas of peninsular Florida during the summer of 1998, there is considerable public and political interest in instituting a more consistent and conscientious program of prescribed burns in appropriate habitats. Dodd et al. (1994) have cautioned against the use of controlled burns in areas where they are not clearly a part of the natural disturbance regime. Even in areas where they are indicated, burns should be conducted in a manner so as to minimize potential catastrophic effect on box turtles.

In addition to directly causing mortality, fire can also negatively impact box turtle populations by a) reducing ground and low level vegetative cover, lowering the high humidity levels that box turtles apparently require by opening up habitats to sunshine and desiccating winds, and by b) reducing leaf litter and its associated invertebrate fauna, which may be a major food source for the turtles (Dodd et al., 1994). Because of fuel buildup between burns, initial burns in areas that have not burned recently are likely to be particularly severe. Dodd et al. (1994) suggested that burns should only be conducted during winter during periods of low wind speed and high humidity, and that they should be planned to minimize impact on fruiting plants that may be an important food source; these recommendations only applied to Egmont Key, however, and were specifically tailored to that location only after extensive population studies and consideration of the extent of fuel. If box turtle populations are substantial, small plots should be burned on Egmont Key, and should be timed to occur during or immediately after periods of cold temperature, when box turtle surface activity is likely to be minimal. In contrast, Verdon (2004) recommended burning during the wet season in order to minimize adverse impacts to box turtles in pine rockland habitats on the Florida Keys, especially for first fires.

A related concern for some populations is the removal of non-native vegetation. Egmont Key box turtles rely heavily on habitats dominated by invasive plant species (such as *Schinus terebinthifolius* and *Casuarina equisetifolia*), and outright removal of these plant communities may have serious negative consequences to box turtle populations by altering habitat structure (Dodd et al., 1994; Dodd and Griffey, 2005). Efforts to eradicate non-native plant species should be accompanied by concurrent establishment of native species such as oaks and cedars that will provide habitat structure similar to that provided by the species being removed.

For some oviparous Florida reptiles such as kingsnakes, introduced fire ants (*Solenopsis invicta*) have been linked to population declines (Mount, 1981; Tennant, 1997; Allen et al., 2004). Montgomery (1996) documented predation by fire ants on *T. c. triunguis* in Texas, and cited several anecdotal accounts of fire ant predation on eggs and young of a variety of turtles and other reptiles. Because box turtles are quite specific in nest site selection, and nest sites are often located in relatively elevated and open habitat, box turtle nests and hatchlings may be exposed to an increased risk of predation, even in turtle populations of closed, mesic habitats where there is little overlap between fire ants and the major activity areas of adult turtles. The impact of fire ant predation on eggs and young deserve greater attention, particularly in areas where recruitment of juveniles to the adult population appears to be nearly non-existent (Pilgrim et al., 1997).

Heinrich (1996) has addressed another source of concern for box turtle populations that occur in areas near high human population densities. In his study population in Pinellas County, more than 10% of the 143 turtles marked within Boyd Hill Nature Park belonged to non-native subspecies. Presumably, these are turtles from other parts of the species' range that have been released from captivity. The effects of genetic introgression from turtles adapted to vastly different habitat and climatic conditions are unknown, but Heinrich has labeled this threat as "gene-pool pollution", and since 1994 has been removing non-native subspecies from his study population. Dodd (unpubl. data) also has noted the presence of box turtle subspecies in areas where they should not occur naturally.

As emphasized by Dodd and Franz (1993, 1996), development of effective strategies of conservation and management of box turtle populations in Florida must be preceded by collection of reliable quantitative data from the areas of concern. Not only are monitoring protocols necessary to determine population trends, but in addition, sound management plans require collection of specific life-history data from regions with populations in question. The use of data on reproductive output from other areas may be misleading, and even where such data exist, they are not sufficient to estimate local population parameters. In addition to clutch size and frequency, reliable population modeling requires a number of other kinds of data, including proportion of females reproducing, age-specific reproductive parameters, egg viability and survivorship, and effects of resource availability on reproductive characteristics (Dodd, 1997a, 2001). Similarly, behavioral data such as habitat selection and home range behavior from other regions of the species' range may be inapplicable for management decisions regarding Florida populations (Pilgrim et al., 1997). Until these basic questions about status of Florida box turtle populations and their specific natural history and life-history parameters are addressed, management and conservation plans for Florida's box turtles will be inadequate.

STATUS

The conservation status of box turtles is unknown due to the lack of reliable historical data on natural populations. Dodd and Franz (1993) discussed the problems associated with determining current status and distribution patterns of species widely regarded as "common" without careful monitoring protocols. Although there are data indicating long term population declines in many northern parts of the box turtle's range (Stickel, 1978; Schwartz et al., 1984; Williams and Parker, 1987; Hall et al., 1999), no such data exist for Florida populations, and the discontinuous and highly biased nature of collection of museum specimens renders any conclusions from that source regarding population trends highly questionable.

In 1995, all North American box turtles were listed under Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), indicating serious concern about population trends throughout the range of all species of *Terrapene*. This was due in part to the large international trade in North American box turtles; an estimated 81,000 box turtles (including *T. carolina* and *T. ornata)* were exported between 1990 and 1993 (Dodd, 1995). Although CITES listing does not supersede state or national laws and regulations concerning collection and commercial trade in listed species, it does afford some protection to the affected species. Specifically, exportation of listed species requires permitting by the U.S. Fish and Wildlife Service's Office of CITES Management Authority, which specifies conditions of transport for any exported animals. Prior to approving export of a CITES Appendix II listed species, the Management Authority of that country must ensure that take will not adversely impact native populations.

CONSERVATION OPTIONS AND SOLUTIONS

Because of the paucity of population data on Florida box turtles, the existence and/or severity of population declines in the state is difficult to assess. Consequently, the impact of known threats to long term population viability is speculative. Currently, Florida box turtles are probably under little threat from legal collection; state non-game wildlife regulations limit possession of box turtles to two per person, and purchase, sale or possession for sale of box turtles is prohibited. Nonetheless, individual collection even in small numbers may pose a threat to specific turtle populations located in areas of high human visitation (Dodd et al., 1994), and collection by out-of-state individuals occurs frequently and with unknown effects on populations. Because of the potential for illegal commercial activity, particular vigilance should be paid by enforcement personnel in areas where box turtle populations and high human visitation coincide, especially on state and federal lands and areas deemed habitat sensitive, and collection violations should be dealt with severely.

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LITERATURE CITED

Abrahamsom, W. G., and Hartnett, D. C. 1990. Pine flatwoods and dry prairies. In: Myers, R.L. and Ewel, J.J. (Eds.). Ecosystems of Florida. University of Central Florida Press, Orlando, pp. 103-149.

Allen, C. R., Epperson, D.M. and Garmestani, A.S. 2004. Red imported fire ant impacts on wildlife: a decade of research. American Midland Naturalist 152:88-103.

Allen, R., and Neill, W.T. 1952. The box turtles. Florida Wildlife 5(9):16, 38.

Aresco, M. J. 2005. The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. Biological Conservation 123:37-44.

Ashton, R. E., Jr., and Ashton, P. S. 1985. Handbook of reptiles and amphibians of Florida. Part two: lizards, turtles and crocodilians. Windward Publ., Inc., Miami, Florida.

Babbitt, L. H., and Babbitt, C. H. 1951. A herpetological study of burned-over areas in Dade County, Florida. Copeia 1951:79.

Bartlett, R.D., and Bartlett, P.B. 1999. A field guide to Florida reptiles and amphibians. Gulf Publishing Co., Houston, Texas.

Bentley, C. C., and J. L. Knight. 1998. Turtles (Reptilia: Testudines) of the Ardis Local Fauna Late Pleistocene (Rancholabrean) of South Carolina. Brimleyana 25: 3-33.

Blaney, R.M. 1971. An annotated check list and biogeographic analysis of the insular herpetofauna of the Apalachicola region, Florida. Herpetologica 27: 406-430.

Bogert, C.M., and Cowles, R.B. 1947. Moisture loss in relation to habitat selection in some Florida reptiles. American Museum Novitates 1358:1-34.

Brown, M., Schumacher, I., Klein, P.A., Harris, K., Correll, T., and Jacobson, E. 1994. *Mycoplasma agassizii* causes upper respiratory tract disease in the desert tortoise. Infection and Immunology 62: 4580-4586.

Bury, R. B. and Luckenbach, R.A. 1980. Field study of box turtles and other herpetofauna, St. Marks National Wildlife Refuge, Florida. Appendix II in St. Marks National Wildlife Refuge: Forestry Management and Non-Game Wildlife, Final Report. U. S. Fish and Wildlife Service, Gainesville, Florida.

Carr, A. F., Jr. 1940. A contribution to the herpetology of Florida. University of Florida Publications in Biological Science 3:1-118.

Carr, A. F., Jr. 1952. Handbook of turtles; the turtles of the United States, Canada, and Baja California. Comstock Publ. Assoc., Ithaca, N.Y., 542 pp.

Conant, R., and Collins, J. T. 1991. A field guide to amphibians and reptiles of eastern and central North America. Third edition, expanded. Houghton Mifflin Co., Boston.

Crother, B. I. 2000. Scientific and standard English names of amphibians and reptiles of North America north of Mexico, with comments regarding confidence in our understanding. Society for the Study of Amphibians and Reptiles, Herpetological Circular No. 29.

Devaux, B. 1993. L'île des tortues. La Tortue 23:4-9.

Dickson, J. R., III. 1953. The private life of the box turtle. Everglades Natural History 1:58-62.

Dimond, M.T. 1985. Some effects of temperature on turtle egg incubation. In: Suresh, C.G., and Srivastava, C.B.L. (Eds.). Recent advances in developmental biology of animals. Indian Society for Developmental Biology, Poona, pp. 35-39.

Dodd, C.K., Jr. 1995. North American box turtles (*Terrapene*) listed under CITES Appendix II. Box Turtle Newsletter 2: 1-3.

Dodd, C.K., Jr. 1997a. Population structure and the evolution of sexual size dimorphism and sex ratios in an insular population of Florida box turtles (*Terrapene carolina bauri*). Canadian Journal of Zoology 75: 1495-1507.

Dodd, C.K., Jr. 1997b. Clutch size and frequency in Florida box turtles (*Terrapene carolina bauri*): implications for conservation. Chelonian Conservation and Biology 2: 370-377.

Dodd, C.K., Jr. 1998. Biomass of an island population of Florida box turtles (*Terrapene carolina bauri*). Journal of Herpetology 32: 150-152.

Dodd, C.K., Jr. 2001. North American Box Turtles. A Natural History. Univ. Oklahoma Press, Norman, Oklahoma.

Dodd, C. K., Jr. 2003. Etude sur la Tortue-boîte de Floride (*Terrapene carolina bauri*) à Egmont Key, Floride. Manouria 20:26-34.

Dodd, C.K., Jr., and Franz, R. 1993. The need for status information on common herpetofaunal species. Herpetological Review 24: 47-50.

Dodd, C.K., Jr. and Franz, R. 1996. The life-history and conservation biology of an island population of Florida box turtles *Terrapene carolina bauri*. In: Proceedings of the International Congress of Chelonian Conservation, Editions SOPTOM, Gonfaron, France, pp. 247-249.

Dodd, C. K., Jr. and Griffey, M. L. 2004. Aural abscesses on Florida box turtles are associated with abnormally wet winters. Herpetological Review 35:233-235.

Dodd, C.K., Jr., and Griffey, M. L. 2005. The conservation of box turtles on public lands in Florida. In: W. E. Meshaka Jr. and K. J. Babbitt (Eds.), Status and Conservation of Florida Amphibians and Reptiles. Krieger Publ., Malabar, Florida.

Dodd, C.K., Jr., Franz, R., and Smith, L.L. 1994. Activity patterns and habitat use of box turtles (*Terrapene carolina bauri*) on a Florida island, with recommendations for management. Chelonian Conservation and Biology 1: 97-106.

Dodd, C.K. Jr., Franz, R., and Johnson, S.A. 1997. Shell injuries and anomalies in an insular population of Florida box turtles (*Terrapene carolina bauri*). Herpetological Natural History 5: 66-72.

Dodge, C.H., Dimond, M.T., and Wunder, C.C. 1978. Effect of temperature on the incubation time of eggs of the eastern box turtle (*Terrapene carolina carolina* Linne). In: Henderson, G.E., (Ed.). Proceedings of the Florida and Interregional conference on sea turtles. Florida Marine Research Publications No. 33, pp. 8-11.

Duellman, W. E., and Schwartz, A. 1958. Amphibians and reptiles of southern Florida. Bulletin of the Florida State Museum, Biological Sciences 3:181-324.

Enge, K.M. 1997. A standardized protocol for drift-fence surveys. Technical Report 14, Florida Game and Fresw Water Fish Commission, Tallahassee, 68 pp.

Enge, K. M., and Wood, K.N. 1998. Herpetofaunal surveys of the Big Bend Wildlife Management Area, Taylor County, Florida. Florida Scientist 61: 61-87.

Ernst, C. H., and McBreen, J. F. 1991a. *Terrapene* Merrem. Box turtles. Catalogue of American Amphibians and Reptiles 511: 1-6.

Ernst, C.H., and McBreen, J.F. 1991b. *Terrapene carolina* (Linnaeus). Eastern Box Turtle. Catalogue of the American Amphibians and Reptiles 512: 1-13.

Ernst, C.H., Lovich, J.E, and Barbour, R.W. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington, D.C.

Ernst, C.H., Boucher, T.P., Sekscienski, S.W., and Wilgenbusch, J.C. 1995. Fire ecology of the Florida box turtle, *Terrapene carolina bauri*. Herpetological Review 26: 185-187.

Ernst, C.H., Wilgenbusch, J.C, Boucher, T.P., and Sekscienski, S.W. 1998. Growth, allometry and sexual dimorphism in the Florida box turtle, *Terrapene carolina bauri.* Herpetological Journal 8: 72-78.

Ewert, M.A., Etchberger, C. R., and Nelson, C. E. 2004. Turtle sex-determining modes and TSD patterns, and some environmental correlates. In: N. Valenzuela and V.A. Lance (Eds.), Temperature-dependent Sex Determination in Vertebrates. Smithsonian Books, Washington, D.C., pp. 21-32.

Franz, R., and Dodd, C.K., Jr. 1993. Raccoon predation on Florida box turtles at Egmont Key, Hillsborough County, Florida. Florida Scientist 56 (Suppl.1): 23.

Gibbs, J. P., and Shriver, W.G. 2002. Estimating the effects of road mortality on turtle populations. Conservation Biology 16: 1647-1652.

Hall, R. J., Henry, P. F. P., and Bunck, C. M. 1999. Fifty-year trends in a box turtle population in Maryland. Biological Conservation 88: 165-172.

Hamilton, A.M. 2000. Evidence for ontogenetic shifts in box turtles: activity patterns, movements, and use of microenvironments and habitats by juvenile *Terrapene carolina bauri* on Egmont Key, Florida. M.S. thesis, Univ. Florida, Gainesville.

Heinrich, G. 1996. Box turtle study and conservation effort in Pinellas County, Florida. Box Turtle Research and Conservation Newsletter 4: 12.

Iverson, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately printed, 363 pp.

Iverson, J.B., and Etchberger, C.R. 1989. The distributions of the turtles of Florida. Florida Scientist 52: 119-144.

Jackson, D. 1991. Multiple clutches and nesting behavior in the Gulf Coast box turtle. Florida Field Naturalist 19: 14-16.

Jacobson, E.R., Gaskin, J.M., Brown, M.B., Harris, R.K., Gardiner, C.H., LaPointe, J.L., Adams, H.P., and Reggiardo, C. 1991. Chronic upper respiratory tract disease of free-ranging desert tortoises, *Xerobates agassizii.* Journal of Wildlife Disease 27: 296-316.

Jennings, A.H. 2003. Daily and seasonal activity patterns and movements of juvenile box turtles (*Terrapene carolina bauri*) on Egmont Key, Florida. Chelonian Conservation and Biology 4:578-587.

Kautz, R.S. 1998. Land use and land cover trends in Florida 1936-1995. Florida Scientist 61:171-187.

Langtimm, C.A., Dodd, C.K., Jr., and Franz, R. 1996. Estimates of abundance of box turtles (*Terrapene carlina bauri*) on a Florida island. Herpetologica 52: 496-504.

Lazell, J. D. 1989. Wildlife of the Florida Keys. A Natural History. Island Press, Washington, D.C.

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum is, synonymis, locis. 10th ed. Vol. 1. L. Salvius, Stockholm.

Liu, H., Platt, S. G., and Borg, C. K. 2004. Seed dispersal by the Florida box turtle (*Terrapene carolina bauri*) in pine rockland forests of the lower Florida Keys, United States. Oecologia 138: 539-546.

Marchand, M. N., and J. A. Litvaitis. 2004. Effects of habitat features and landscape composition on the population structure of a common aquatic turtle in a region undergoing rapid development. Conservation Biology 18: 758-767.

Merrem, B. 1820. Tentamen systematis amphiborum (versuch eines Systems der Amphibien). Johann Cristian Krieger, Marburg.

Meshaka, W. E., Jr., Loftus, W. F., and Steiner, T. 2000. The herpetofauna of Everglades National Park. Florida Scientist 63: 84-103.

Minx, P. 1992. Variation in phalangeal formulae in the turtle genus *Terrapene*. Journal of Herpetology 26: 234-238.

Minx, P. 1996. Phylogenetic relationships among the box turtles, genus *Terrapene.* Herpetologica 52: 584-597.

Montgomery, W.B. 1996. Predation by the fire ant, *Solenopsis invicta,* on the three-toed box turtle, *Terrapene carolina triunguis.* Bulletin of the Chicago Herpetological Society 31: 105-106.

Mount, R. H. 1981. The red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae), as a possible serious predator of some native southeastern vertebrates: direct observations and subjective impressions. Journal of the Alabama Academy of Science 52: 71-78.

Pilgrim, M.A., Farrell, T.M., and May, P.G. 1997. Population structure, activity, and sexual dimorphism in a central Florida population of box turtles, *Terrapene carolina bauri.* Chelonian Conservation and Biology 2: 483-488.

Pritchard, P.C.P. 1980. Record size turtles from Florida and South Amerika (sic). Chelonologica 1(3): 113-123.

Reagan, D.P. 1974. Habitat selection in the three-toed box turtle, *Terrapene carolina triunguis.* Copeia 1974: 512-527.

Rose, F.L. 1986. Carapace regeneration in *Terrapene* (Chelonia: Testudinidae). Southwestern Naturalist 33: 357-361.

Schwartz, E.R., Schwartz, C.W., and Kiester, A.R. 1984. The three-toed box turtle in central Missouri, Part II: A nineteen-year study of home range, movements and population. Publications of the Missouri Department of Conservation, Terrestrial Series 12: 1-29.

Seigel, R., Smith, R.B., Demuth, J., Ehrhart, L.M., and Snelson, F. F., Jr. 2002. Amphibians and reptiles of the John F. Kennedy Space Center, Florida: a long-term assessment of a large protected habitat (1975-2000). Florida Scientist 65: 1-12.

St. Clair, R. C. 1998. Patterns of growth and sexual size dimorphism in two species of box turtles with environmental sex determination. Oecologia 115: 501-507.

Steen, D. A., and Gibbs, J. P. 2004. Effects of roads on the structure of freshwater turtle populations. Conservation Biology 18: 1143-1148.

Stejneger, L., and Barbour, R. 1917. A check list of North American amphibians and reptiles. Harvard Univ. Press, Cambridge, Massachusetts.

Stickel, L. 1978. Changes in a box turtle population during three decades. Copeia 1978: 221-225.

Stuart, M.D., and Miller, G.C. 1987. The eastern box turtle, *Terrapene c. carolina* (Testudines: Emydidae), in North Carolina. Brimleyana 13: 123-131.

Taylor, W.E. 1895. The box turtles of North America. Proceedings U.S. National Museum 17:573-588.

Tennant, A. 1997. A Field Guide to the Snakes of Florida. Gulf Publishing Co, Houston.

Tucker, J. K., Funk, R. S., and Paukstis, G. L. 1978. Reproductive potential of the Gulf Coast box turtle *Terrapene carolina major*. Bulletin of the Maryland Herpetological Society 14:23-28.

Verdon, E. 2004. Activity patterns, habitat use, and movements of the Florida box turtle (*Terrapene carolina bauri*) in the Florida Keys. M.S. thesis, Florida International Univ., Miami.

Verdon, E., and Donnelly, M.A. 2005. Population structure of Florida box turtles (*Terrapene carolina bauri*) at the southernmost limit of their range. Journal of Herpetology 39:572-577.

Ward, J. P. 1980. Comparative cranial morphology of the freshwater turtle subfamily Emydinae: an analysis of the feeding mechanisms and systematics. Ph.D. diss., North Carolina State University, Raleigh.

Williams, E.C., and Parker, W.S. 1987. A long term study of a box turtle population at Allee Memorial Woods, Indiana, with emphasis on survivorship. Herpetologica 43 328-335.

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Deirochelys reticularia – Chicken Turtle

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Summary. – The chicken turtle, *Deirochelys reticularia*, is a medium-sized, highly predaceous emydid turtle that frequents ephemeral shallow waters of the southeastern U.S. Coastal Plain. It is seldom associated with permanent lakes, streams, or rivers. The species is carnivorous throughout life and feeds principally on aquatic insects and crayfish, and occasionally amphibian larvae. Individuals acquire large fat stores while feeding and spend long dry periods quiescent in terrestrial refugia, most often in forested habitats. The Florida nesting season occurs mainly during the fall and winter. The eggs have arrested development in advance of cool weather. This chill-dependent embryonic diapause results in long periods of time that the eggs are in the nest. Population densities tend to be naturally low, which may be well suited to broad areas of isolated or weakly connected wetlands. However, wetland drainage and habitat fragmentation impact the species. These changes can lead to net habitat loss and place wandering individuals in harm's way during peak road use by vehicular traffic. Although invasive fire ants pose a threat to nests, their long-term impact upon the species is unknown. Chicken turtle populations in Florida have been recognized as two subspecies, essentially peninsular and panhandle, but conservation and management should simply address protection of the species and its habitat statewide.

Conservation Status. – FNAI Global - G5 (Demonstrably Secure), State - S4 (Apparently Secure); ESA Federal - Not Listed; State - Not Listed; CITES – Not Listed; IUCN Red List - Not Listed (LC-Least Concern).

Species Recognition. — The carapace of chicken turtles has a dark to light olive ground color with a strong net-like (or reticulated, thus *reticularia*) pattern of pale yellow lines (Fig. 17-1). These lines link more strongly across adjacent scutes than along the seams between them, a feature unique to this species. The plastron of individuals from Florida is immaculate pale yellow to yellow-orange. The bridge on each side often, though not always, has two dark blotches, which may coalesce into a single bar. Turtles from northern Florida (the subspecies *D. r. reticularia*) typically have a single dark spot on the underside of each marginal (Fig. 17-2). The submarginal spots and the blotches on the bridge are smaller or absent in turtles from central to southern peninsular Florida (*D. r. chrysea*) (Fig. 17-3). In all *Deirochelys*, the dorsal surface of the head and neck has several long yellow stripes against a dark background (Figs. 17-1, 17-4). The outer surfaces of the forelimbs usually feature a broad yellow stripe against a dark background. The posterior surfaces of the thighs have dark vertical stripes against a light background (Fig. 17-5).

This species grows to a moderate size for North American freshwater turtles: 250 mm straight carapace length (CL) for females, with males smaller (to at least 157 mm CL; Carr, 1952). The neck is unusually long, and the skull is elongate posteriorly. The carapace, as viewed from above, typically has the widest point well behind the middle of the shell. The overall shape suggests a broad wedge with the turtle's head beyond the apex. In combination with the very long neck, this shell shape can lead to a graceful appearance (Pope, 1939). Shells of adult females and large males appear highly domed because the sides of the carapace are broadly rounded. *Deirochelys* shares this prominent feature with other larger freshwater emydids (*Pseudemys*, *Trachemys*) of Florida. The plastron, however, is narrower than in these species.

The shell of hatchlings is sometimes wider than long, and always distinctly less elongate than the shells of adults. Hatchlings and very small juveniles have similar coloration to adults, but with more sharply contrasting markings (Fig. 17-6). Particularly in the subspecies *D. r. chrysea*, the carapace of hatchlings has a distinct yellow border as seen from above (see Ernst et al., 1994). This border stands out prominently as a yellow circumferential ring when the hatchling is swimming against a dark background.

Taxonomic History. — Latreille (1801) first recognized the chicken turtle as a new species, which he named *Testudo reticularia*. The genus *Deirochelys* was first proposed by Agassiz (1857). The binomial used in all modern treatments of the species is *Deirochelys reticularia*. Schwartz (1956) recognized three subspecies, of which *D. r. reticularia* and *D. r. chrysea* occur in Florida; *D. r. miaria* occurs only west of the Mississippi River. Analysis of mitochondrial DNA

Figure 17-1. Adult male chicken turtle, *Deirochelys reticularia,* from Glades Co., Florida. Photo by Barry Mansell.

among populations indicates that *D. r. miaria* is distinct from the two eastern subspecies, which do not differ in mtDNA (Walker and Avise, 1998).

The common name "chicken turtle" presumably refers to the palatability of the flesh, which, as in many freshwater emydids, can taste like chicken. When dressed for cooking, however, the disarticulated long neck can also look like that of a chicken. Either way, the name has questionable unique bearing on *D. reticularia* (see Carr, 1952). The adult females, which are large enough to be worth eating, are likely to have been encountered while active on land during much of the fall and winter, when most other turtles remain in water or become dormant. This availability during the "off season" may have fostered unique recognition of this species historically when several kinds of turtles were regularly sold for food in southern meat and fish markets.

DISTRIBUTION

Geographic Distribution. — *Deirochelys* is strictly North American in current distribution as well as in known fossil history (Jackson, 1978). It occurs at generally low elevations (< 200 m) from extreme southeastern Virginia southwestward along the Atlantic Coast states, and westward through the Gulf Coast states to central Texas.

Deirochelys occurs throughout most of Florida (Fig. 17-7). However, there are gaps in the distribution in the Everglades, in the Kissimmee River basin, and in the western third of the panhandle (the sandhill-dominated area south of Interstate Highway 10). These gaps may only represent inadequate surveys and not absence. *Deirochelys* is known from the Florida Keys but is most likely introduced there (Butterfield et al., 1994). The

Figure 17-2. Plastron of adult male chicken turtle, *Deirochelys reticularia,* from Hernando Co., Florida. Note dark blotches on bridge and marginals of this individual. Compare with 17-3. Photo by Ben Atkinson.

Figure 17-3. Plastron of adult male chicken turtle, *Deirochelys reticularia,* from Lee Co., Florida. Note absence of dark blotches on bridge and marginals of this individual. Compare with 17-2. Photo by Dick Bartlett.

Figure 17-4. Adult female chicken turtle, *Deirochelys reticularia chrysea,* from Alachua Co., Florida. Photo by John Iverson.

Figure 17-5. Posterior view of adult female chicken turtle, *Deirochelys reticularia,* from Miami-Dade Co., Florida. Photo by Brian Mealy.

subspecies *D. r. chrysea* is endemic to peninsular Florida, from south of a line extending roughly from the mouth of the Suwannee River to northern St. Johns County. A few individuals referable to *D. r. chrysea* have been observed just north of this line in central Dixie County. Other individuals from along this line are referable to *D. r. reticularia*, as are all specimens from northern and western Florida. Analysis of variation in mitochondrial DNA did not differentiate *D. r. reticularia* from *D. r. chrysea* and does not support continued recognition of these two subspecies, which are based on minor color differences (Walker and Avise, 1998).

Ecological Distribution. — *Deirochelys* prefers shallow lentic habitats with water depths less than 50 cm. Natural habitats include isolated wetlands in sandhill savanna and pine flatwoods, standing waters in wet prairies, and shallow bay heads with bald cypress (Dodd, 1992; this account). In southern Florida (e.g., the Everglades) where sawgrass marsh and less permanently flooded wet prairies with shorter grass are the main choices for habitat, wet prairies seem to be preferred (W. Meshaka, *pers. comm.*). Favored habitats tend to dry up regularly, although not necessarily every year. Association with deeper water is rare. At only one in a sample of 10 widely dispersed Florida study sites was a chicken turtle seen basking on a log in water deeper than 2 m (Ewert, unpubl. data).

Deirochelys in Florida appears to avoid big river floodplain swamps, such as along the Apalachicola and Ochlockonee rivers. *Deirochelys* also appears to avoid Florida's lakes, as well as spring-fed runs and other flowing water. In a detailed survey of Lake Conway, Orange Co. (Bancroft et al., 1983), the authors reported capturing only two *Deirochelys* among 688 emydid turtles, and these two were not in the main arms of the lake but in a channel that joins two arms. Sightings of *Deirochelys* in shallow spring-fed streams, such as Juniper and Rainbow runs in Marion Co. have occurred but are rare. During a 13-year study of turtles in Rainbow Run (Huestis and Meylan, 2004), there was a single *Deirochelys* among 2500 turtles captured. One actively feeding female was observed swimming in shallow flowing water 2 km north of the Florida line in Alabama (Cowarts Creek, Houston Co.), a site that has dried occasionally. Nonetheless, neither lentic permanent water nor flowing water appear to support significant populations and may support only transient individuals.

Deirochelys appears to avoid brackish water, and its natural occurrence in the Lower Keys is most unlikely. However, there are three records associated with freshwater ponds on St. Vincent Island (Franklin Co.), a Gulf barrier island surrounded by brackish to fully saline sea water (Peacock and Lewis, 2000). During most of the year there is strongly saline water between this island and the mainland, but flooding of the Apalachicola River briefly freshens the water.

Examples of altered environments that have become habitat in which chicken turtles are often observed include many roadside ditches and borrow pits from Franklin Co. (Apalachicola National Forest) to Collier Co. (Fakahatchee Strand) and southern Miami-Dade Co. (Florida City).

HABITAT RELATIONS

Aquatic Activity. — Direct observations on aquatic activities of *Deirochelys* have been made in Dixie Co. in clear, shallow-water borrow pits, often 20–70 cm deep. Individuals of both sexes have seemed most active in the morning and for a few hours after sundown. When spotlighted in the dark, many individuals have had their necks extended, and have been stationary or moving slowly across the bottoms of clear water areas with sparse vegetation.

Figure 17-6. Hatchling chicken turtle, *Deirochelys reticularia,* from Pinellas Co., Florida. Photo by George Heinrich.

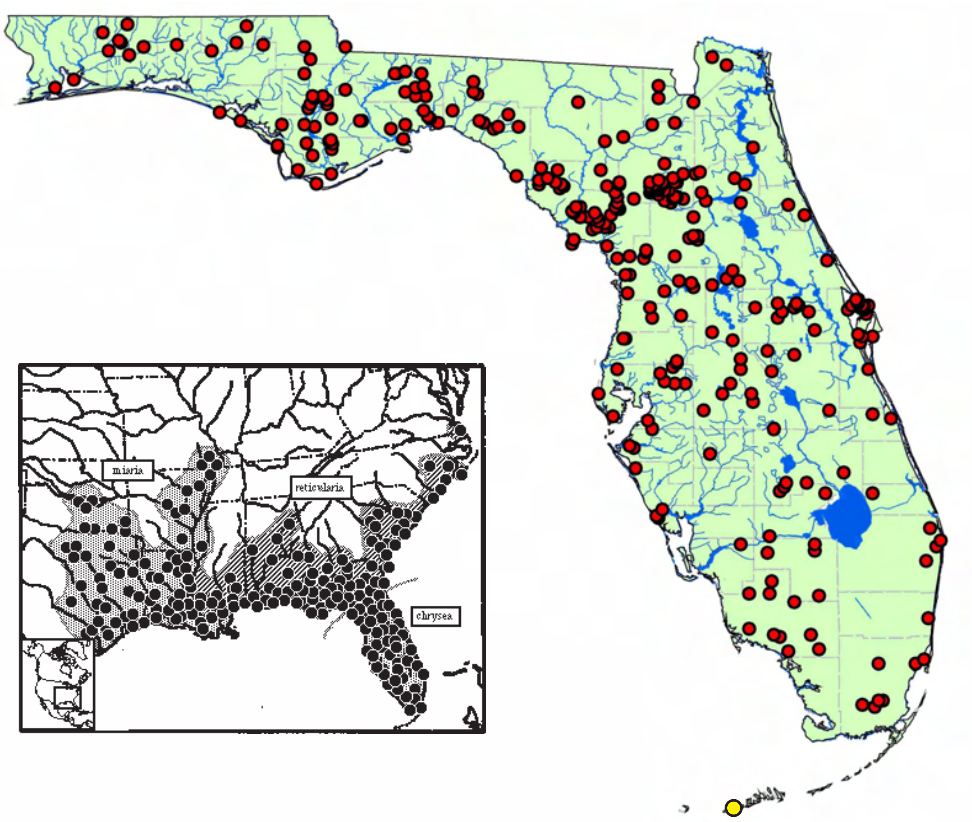

Figure 17-7. Distribution records for the chicken turtle, *Deirochelys reticularia,* from Florida. Inset: distribution records from entire range of *D. reticularia* (adapted from Iverson, 1992; distribution in inset map not current for Florida as presented here). The record for Key West (yellow dot) may represent an escaped individual.

Typically, inactive individuals have been in water under overhanging bushes or under floating mats of debris, floating emergent plants, or floating algae.

The shallow-water habitat at these sites has typically become completely dry every other year, most often during the fall. Even with water present, however, the ease of encountering turtles in borrow pits during the late winter and spring suggests that more individuals use these areas at this time than in the fall. Otherwise, turtles have been easiest to find when flooding appeared to have been recent, or at least, when the water appeared fresh and without excessive growths of epiphytic algae on the submerged vegetation. In such situations, tiny crayfish, an important prey of *Deirochelys*, have been extremely abundant during nocturnal observations. Both sexes of *Deirochelys* have been active in the water at this location as late in the year as 14 November (Ewert, unpubl. data). In Florida as in Virginia and South Carolina, some individuals may leave water for terrestrial refugia in the fall (Buhlmann, 1995, 1998).

Terrestrial Activity. — Captures on land indicate that many female *Deirochelys* are active throughout the winter in north-central as well as southern Florida. Most of these females have or appear to have been engaged in activities related to nesting (Jackson, 1988; W. Meshaka, *pers. comm.*). In a sample of 34 chance finds in northern and central Florida, 27 females were on land between October and May, with 22 of these in December, January, and February. Only seven finds (21%) came from May through September. In southern Florida, 16 of 17 females were encountered on land between September and February. Males, in contrast, appear to be more active on land during the late spring and summer than during the winter. Eight of 12 encounters (67%) of males on land in northern and central Florida came from May through September, with just one encounter, a severely burned individual, in December through February. All seven observations of males on land in southern Florida took place during wet periods from May to September. This seasonal pattern of movement on land, with males more active during the late spring and summer, and females more active at other times, has general support from drift fence records in South Carolina (Gibbons, 1969; Gibbons and Greene, 1978, 1990). These observers proposed that most male movements were responses to drought, whereas most female movements were related to nesting (Gibbons and Greene, 1978). Males in Virginia and South Carolina have been tracked from aquatic areas to terrestrial refugia (Buhlmann, 1995, 1998). When water has persisted in Dixie Co., Florida, males were approximately as common as females in these waters in October, November, March, and April (Ewert, unpubl. data).

Although some of the males as well as non-gravid females encountered on land have been moving away from wetlands that were drying, terrestrial movement may also be a normal response to waters that are only experiencing seasonal or hydroperiodic ebbs in food supply. There may be some terrestrial summer movement between adjacent wetlands that differ in the availability of food (Buhlmann, 1995). Turtles in South Carolina that move from water to upland situations burrow and become quiescent and do not feed (Buhlmann, 1998). Given that the specialized method of feeding (see below) used by *Deirochelys* is unknown among terrestrially feeding turtles, *Deirochelys* is probably unable to feed on land.

In South Carolina, a severe drought only slightly exaggerated terrestrial movement of *Deirochelys* away from a drying but normally aquatic habitat (Gibbons et al., 1983). A small increase such as this would be expected if we are correct in our assumption that most individuals normally leave water every year. In Florida, observations have also followed a severe drought-induced drying, that of Station Pond, a shallow but normally permanent marshy lake in Levy Co. Here, also, *Deirochelys* appeared to have sought upland refugia. The survey of this pond at the height of the drought yielded just 10 *Deirochelys* among 1007 carcasses of emydid turtles (mostly *Pseudemys floridana*, with some *P. nelsoni*). Whereas most of the carcasses were scattered about the dry lake bed, most *Deirochelys* carcasses were distributed above the normal shoreline (Jackson and Deitz, 1978, unpubl. data). Thus, *Deirochelys* was present near the lake and probably a normal resident, but it is unclear whether drought or some other factor, such as predation, caused the few deaths.

In Florida, there has not been any systematic effort to associate *Deirochelys* found on land with specific aquatic habitats. Radio-tracking in Virginia and South Carolina has shown that woodland areas adjacent to wetlands provide terrestrial refugia for *Deirochelys* (Buhlmann, 1995, 1998). Of 169 refugia located near a wetland in South Carolina, roughly half occurred > 50 m from the wetland, and some were located up to 165 m distant. Most refugia were in areas of mixed pine and deciduous forest, where the canopy was mostly closed in summer. Turtles that initially chose open pine woods tended to abandon these sites if they experienced high temperatures. Yearling juveniles, as well as adults, use terrestrial refugia (Buhlmann and Gibbons, 2001).

Turtles entering refugia have buried themselves in a few cm of soil below the leaf litter and humus. Sojourns to these refugia have usually exceeded six months (Buhlmann, 1998; Buhlmann and Gibbons, 2001). The longest recorded terrestrial sojourns, more than nine months by both sexes in South Carolina, and up to five months in Virginia, have been concomitant with overwintering (Buhlmann, 1995; Buhlmann and Gibbons, 2001). In Virginia, at least, overwintering occurs on land rather than in water (Buhlmann, 1995). In contrast, the presence of a terrestrial overwintering pattern in Florida seems unlikely for adults, at least, given the records of nesting and other winter activity mentioned above.

Home Range. — The sizes of home ranges for individuals in Florida are speculative at best. In one instance, turtles occasionally visited a very small, very temporary wetland located more than 300 m from a larger one (Dodd, 1992; Dodd and Cade, 1998). In an area of Virginia that is appreciably encroached upon by human activity, home ranges of adult turtles have measured roughly 500–900 m long by 300 m across and have included 1–9 small ponds (Buhlmann, 1995).

Temperature Relationships. — As some individuals in Florida are active during every month of the year, there is no clear evidence of any prolonged thermally-based quiescence. However, individuals have rarely if ever been seen moving on land during periods of cold winter weather, when temperatures have fallen below 10°C.

When heated experimentally, three individuals from Marion Co., Florida, became stressed at 38.5–39.5°C and evidenced critical stress at 40.8–42.2°C, the "critical thermal maximum." This tolerance to heating was typical among freshwater emydid turtles from central Georgia and Florida (Hutchison et al., 1966). Post-diapause embryos (see below) have been able to complete development and hatch across a constant temperature test range of 24–31°C.

In some localities, eggs or hatchlings in nests may require two extensive periods of cool temperatures before the hatchlings will emerge and seek water. Freshly laid eggs almost always fail to develop much beyond their freshly laid condition unless they have been chilled (Ewert, 1985; Jackson, 1988; see below also). In South Carolina, after the eggs have hatched, the hatchlings wait in the nest, through another period of cool temperatures, before they become motivated to seek water (Gibbons and Nelson, 1978). A hatchling-sized individual found on land in Hillsborough Co., Florida, on 2 February 1981 may have followed such a pattern of delayed emergence after hatching the previous summer. However, two fresh, road-killed hatchlings found close together in Wakulla Co. on 23 July 1990 could well have emerged from a nest just after completing incubation during the same summer.

GROWTH AND REPRODUCTION

Sexual Dimorphism. — Females become substantially larger (to 250 mm CL) than males (to 157 mm CL). Average sexual size dimorphism (SSD) of *Deirochelys* in Florida is pronounced: 1.47 for CL (in a sample of 50 females/19 males), and 3.66 for live mass (42 females/10 males). The smallest gravid female was larger than the largest male. At sexual maturity, however, the tail of the male is thicker and longer than that of any female. The sexual divergence in tail size is evident when young turtles have grown to 88 mm CL (62 mm PL). The claws of both sexes are similar in size, in contrast to most other aquatic emydids in Florida, in which the foreclaws are much longer in males than in females.

Growth and Sexual Maturity. — The smallest mature female (with ovarian corpora lutea from shed follicles) from northern Florida was 160 mm CL and 147 mm plastron length (PL) (Jackson, unpubl. data). Another mature female, from southern Florida, was 161 mm CL (W. Meshaka, *pers. comm.*). In South Carolina, one primiparous female of known age was 5 yrs old (151 mm PL, ca.165 mm CL; Buhlmann, 1998). Males in northern as well as southern Florida are mature at 112–116 mm CL (Jackson, 1988; W. Meshaka, *pers. comm.*). In South Carolina, males mature by

2–3 yrs in age (Gibbons, 1969), as confirmed by examination of gonads.

Male Reproductive Cycle. — Patterns of circulating reproductive hormones remain unknown in *Deirochelys* of either sex. Dissections of four males (from late May to mid-October) from northern and central Florida indicated that testes were largest in July and August and that epididymides contained sperm through the period (Jackson, unpubl. data). In a small sample from South Carolina, the testes were enlarged in several individuals captured during May, June, and July, and small in individuals collected from October through April (Gibbons, 1969). Peak spermiogenesis, therefore, occurs during a warm part of the year as in many other north temperate turtles (see Moll, 1979).

Female Reproductive Cycle. — Each adult female probably produces eggs almost every year, but in a fall-winter period rather than spring-summer cycle. In north-central Florida, most females have laid their last clutch of the season before March (Jackson, 1988), and this appears to be true in south Florida (Collier Co.) as well. Dissections of females collected from March to June have revealed only small ovarian follicles (usually < 12 mm) (Jackson, 1988; this account). One female (from Houston Co., Alabama, on the Florida border) dissected in late May had many moderately enlarged follicles (to 16–17 mm), which suggests that yolking of follicles for the next nesting season can commence before summer. In northern Florida (Leon Co.), ovarian follicles must occasionally achieve ovulatory size by mid-August, given the find of a gravid female with mature, shelled eggs on 1 September.

Severe drought appears to curtail the female reproductive cycle. In South Carolina, a drought greatly reduced the proportion of females that laid eggs in the subsequent year (Gibbons et al., 1983).

Courtship and Mating. — Knowledge of social interactions in *Deirochelys* has come only from observations in captivity (Ewert, unpubl. data). Courtship occurs under water. In several cases, the male swam obliquely, with a forelimb leading, as he approached the female from the front. During the approach, the male fluttered both forelimbs in a series of many (often > 10) short, rapid swimming strokes, with his head partly extended and with his gaze from one eye seemingly focused on the female's head. The duration of copulation is unknown.

Nesting. — Nesting in northern Florida may commence in late August in some years. It continues throughout the fall and winter in northern and central Florida, with brief pauses during cold weather, especially from late November to early December. Nesting typically ceases by March, although the collection of one female with enlarged ovarian follicles in early February suggested that a March nesting might be possible. Gravid females have been observed on land from 1 September (Leon Co.) to 22 February (Alachua Co.). One female observed on land with mature eggs on 1 October was already carrying her second clutch of the season (Jackson, 1988; unpubl. data). In southern Florida nesting begins in September and continues at least through February (W. Meshaka, *pers. comm.*).

Observations of gravid females wandering on land have spanned most daylight hours. However, observations of nest excavation have, so far, suggested that this activity occurs between 1100 and 1400 hrs, and takes place on sunny days, often following cool rainy days. The few known locations of nests have been open to the sky above, in short herbaceous vegetation (including lawns) or semi-barren places, such as in sandy roads and along the shoulders of paved roads (D. Jackson, K. Studenroth, and A. Carr, unpubl. data).

Clutch Size and Reproductive Potential. — The published clutch size for *Deirochelys* from Florida ranges from 2 to 19 oviductal eggs (both from Alachua Co), and averages 9.5 eggs for 29 clutches (Jackson, 1988). An additional sample of 16 clutches, mostly from Dixie and Taylor Cos., yielded 6–18 eggs, with an average of 10.9 eggs. In the southeastern Everglades (Miami-Dade Co.), clutches range from 2–16 eggs (W. Meshaka, unpubl. data). Generally, clutch size does not decrease across a season (Jackson, 1988), but an unusually small clutch (2 eggs) was a female's last clutch for the season. Relative clutch mass (RCM, clutch mass/spent female mass) averaged 11.5% in 13 females from near Gainesville (Jackson, 1988) and 10.5% for 11 females from Dixie and Franklin counties. The RCM for individual females has ranged from 2.4% for a 2-egg clutch to 14.5% for an 18-egg clutch (Ewert, unpubl. data).

Dissection of reproductively active females has revealed that an annual production of at least 2 normal-sized clutches per year occurs regularly in Florida. Nearly half of the females probably laid 3 (rarely 4) clutches per season, leading to a conservative estimate of seasonal productivity of 20 eggs per female per year and rarely more than 30 eggs (Jackson, 1988; unpubl. data). One to two clutches are reported for South Carolina females (Gibbons, 1969).

In South Carolina, a female that survives to maturity can be expected, on average, to survive for fewer than 10 breeding seasons (Buhlmann, 1998). In a sample of 24 marked individuals that had survived at least 10 yrs, only one survived beyond 20 yrs (Gibbons, 1987). Thus, *Deirochelys* appears, under natural conditions, to be rather short-lived relative to other aquatic turtles.

Eggs, Incubation, Development, and Hatching. — The eggs of this species are elongate, varying in northern Florida from 31.5 x 20.4 to 37.3 x 24.9 mm, and from 7.6 to 13.5 g in mass. In the southeastern Everglades, eggs may be up to 41.2 mm in length and 19.3 mm or greater in width (W. Meshaka, *pers. comm.*). As in other Florida emydids, the eggs have pliable eggshells and succumb rapidly to dehydration if exposed to air.

Although *Deirochelys* nests as early as late summer, it appears that the eggs of populations in Florida must remain in the nest throughout the winter before they commence any appreciable development (Jackson, 1988). These thermal requirements for embryonic development correspond to a classical view of diapause, in which current conditions are suitable for development, but in which development will not occur unless an additional environmental condition occurs first (Ewert,1985; Ewert and Wilson, 1996). For embryos of

Deirochelys, this condition appears to be a period of chilling at 15–22ºC. Such cool temperatures alone, without subsequent warming, have been too cool to sustain development. In two sets of observations, however, this chilling followed by warming promoted development in 65–75% of incubated eggs, whereas only 8–13% of unchilled eggs commenced development (Ewert, 1985; Jackson, 1988).

Experimental chilling of eggs for about 90 days has assured development in every egg produced during the fall. The duration of cool soil temperatures from fall to spring extends for four or more months throughout most of Florida, which agrees well with the requisite period for chilling (Jackson, 1988; Ewert, unpubl. data). *Deirochelys* is unusual among North American turtles in having this strong level of embryonic diapause. It shares this more typically subtropical to tropical attribute with only three other species north of Mexico, all kinosternids (*Kinosternon baurii*, *K. hirtipes*, and *K. sonoriense*; Ewert and Wilson, 1996, Ewert, unpubl. data). *Deirochelys* is the only known species among North American emydid turtles, as well as the only known turtle with pliable eggshells, that also has post-ovipositional embryonic diapause. Given a long evolutionary history within Florida (Jackson, 1978), it seems likely that the climate of Florida was mild enough to have allowed diapause to evolve here, too (Jackson, 1988).

Interestingly, some eggs of *Deirochelys* have been able to develop and hatch with little or no exposure to cold. These eggs have come mainly from females found gravid from late January and February. If incubated naturally, these late season eggs would have experienced a shorter duration of cool soil temperatures before spring. Perhaps, as in the striped mud turtle (*K. baurii*) in Florida, a seasonal dichotomy in the requirements for chilling is also manifest in the fall versus late winter eggs of *Deirochelys* (Ewert and Wilson, 1996). Eggs of *Deirochelys* collected during the spring in South Carolina had a prolonged incubation period but were able to develop through hatching without any chilling (Congdon et al., 1983). Regardless of date of laying, it appears that embryonic development in natural nests resumes from its arrested condition in the spring, and hatching occurs during the summer.

Because hatchling movement from land to water occurs mostly in March in South Carolina, it is assumed that hatchlings spend the fall and winter there on land, if not actually in the nest cavity (Gibbons and Nelson, 1978). It has been hypothesized (Ewert, 1985) and then demonstrated (Buhlmann, 1998) that residency in the nest in South Carolina by an arrested embryo, then a developing embryo, and then as a quiescent hatchling, is prolonged relative to most other turtles and can last up to 18 months (from late summer in one calendar year to early spring two calendar years later). The timing of hatchling emergence from nests and movement to water in Florida is unknown. In northwestern Florida, hatchlings may behave like those in South Carolina. In southern Florida, however, where fall can often be wet and conducive to hatchling activity, hatchlings of *Deirochelys* may behave like those of *K. baurii*, another species with diapause (Ewert and Wilson, 1996), which emerge and move from early fall into the spring (Mushinsky and Wilson, 1992; Wilson et al., 1999). Hatchlings of *Deirochelys* in South Carolina (Congdon et al., 1983; Congdon and Gibbons, 1990), like adults from throughout Florida (see below), have large fat reserves. These reserves presumably equip both age groups for long periods without feeding.

Female *Deirochelys* in South Carolina have retained eggs in their oviducts for several months during the winter (Buhlmann et al., 1995). Although the supporting data have been from drift fence captures and the turtles subjected to brief handling, egg retention appears to be a natural process. In Florida, evidence for normal egg retention is less clear. One gravid female, taken in mid-November and induced to lay in early December, contained a clutch of eggs. These eggs subsequently resumed development but died as early embryos, a typical outcome when eggs are overmature (held in the female for abnormally long periods of time). This female was missing her hind legs and apparently had been unable to oviposit because she could not dig a nest. A second gravid female found on land in September contained both thin and thicker shelled eggs when induced to lay in November. It appeared that this female had ovulated and shelled some new eggs and had partially reshelled (i.e., added additional calcium deposits to) some older eggs still present from the previous clutch, which is not a normal process (see Ewert et al., 1984). None of the thicker-shelled eggs were able to develop.

Laboratory incubation has shown that temperature determines sex in *Deirochelys*. Constant temperatures below 28ºC yield only males, whereas 30ºC yields mostly females. A temperature yielding nearly equal numbers of males and females from northern Florida was close to 29ºC (Ewert and Nelson, 1991; unpubl. data).

Hatchling Size. — Hatchling size in Florida ranges from 28.8–34 mm CL, 25.3–30.7 mm PL, 29.9–32.5 mm carapace width, and 6.1–10.2 g mass (Jackson, 1988).

POPULATION BIOLOGY

Density. — Dense populations of *Deirochelys* are unknown and may not occur. In shallow borrow pits in Dixie Co., Florida, a density approaching 10 *Deirochelys* (mostly juveniles) per ha was noted on one occasion, but normally, 3–5 turtles per ha has seemed abundant. By comparison, two other species, *Trachemys scripta* and *Sternotherus odoratus*, have been more abundant in *Deirochelys* habitat both in Dixie Co., Florida, and South Carolina. In South Carolina, a maximum population density of 17.7 *Deirochelys* per ha was one-half to one- fourth of the densities of each of two more common species in the same community (Congdon et al., 1986).

In two studies of small, isolated wetlands in Florida (Marion and Putnam counties), drift fence sampling indicated only small populations of *Deirochelys*. These studies demonstrated 7 visits by 6 individuals at one pond during a 6-year period, or 1.2 turtles per pond-year (Dodd, 1992), and 5 visits among 6 ponds during a 6-year period, or 0.14 turtles per pond-year (Greenberg, 2001; *pers. comm.*).

In 27 of 30 encounters of free ranging individuals in water, chicken turtles were found to be solitary. In two instances, two females were found together but not obviously interacting; in the third instance a male was near a female.

There is evidence that male *Deirochelys* are agonistic and impose spacing among adult males. Males in large indoor tanks have been aggressive toward each other, snapping and biting at their companions. Small as well as large males have caused their companions to cease feeding and to seek shelter until they have been separated. This social hierarchy of dominance may reflect artificially confining quarters, whereas wild individuals simply avoid contact. By contrast, *Trachemys scripta* and *Sternotherus odoratus* in the Dixie Co. habitat have often been clustered in distribution. Low densities of *Deirochelys* may reflect behavior evolved for ephemeral habitat and an ephemeral, invertebrate food supply (see below). Under these conditions, each individual may require a large area of habitat to meet its annual energy requirements.

INTERSPECIFIC INTERACTIONS

Community Structure. — The turtles most commonly encountered cohabiting shallow water areas with *Deirochelys* in Dixie Co. have been *Sternotherus odoratus* and *Trachemys scripta*, and both have appeared to be a little more common. *Kinosternon baurii* has been about as common as *Deirochelys*, and *K. subrubrum*, *Chelydra serpentina*, *Pseudemys floridana*, and *Apalone ferox* have been less to much less common (Ewert, unpubl. data). This species composition is similar to that found in a small wetland (“Carolina Bay”) in South Carolina (Buhlmann and Gibbons, 2001). Differences include the absence of *A. ferox* and near absence of *K. baurii* at the South Carolina site, and different relative frequencies of species. In the Apalachicola National Forest, *P. floridana* and *K. subrubrum* cohabit small water bodies with *Deirochelys*. In Putnam Co., a drift fence surrounding a very small (0.16 ha) wetland also captured several *P. floridana* and *K. subrubrum* along with a few *Deirochelys* and *A. ferox* (Dodd, 1992).

Diet and Feeding. — Digestive tract contents of *Deirochelys*, both in Florida and in South Carolina, indicate preference for a variety of mostly aquatic arthropods. Dragonfly and damselfly nymphs (Odonata), aquatic bugs (Hemiptera), aquatic diving beetles, and crayfish are common food items (Jackson, 1996; Demuth and Buhlmann, 1997). Depending on the phase of hydroperiod, these invertebrates can be abundant in temporary waters; they usually occur at lower densities, or perhaps in less accessible situations in permanent waters that contain predaceous fish (Demuth and Buhlmann, 1997).

The seasonally limited availability of its food supply may be reflected in the unusually large stores of body fat deposits often found in *Deirochelys*. Among Florida turtles, fat stores averaged 5.5% (to 12.4%) of body mass in six adult *Deirochelys*, as compared to 1.5% in 13 *P. floridana*, 1.4% in 10 *P. nelsoni*, 0.8% in 14 *Trachemys scripta*, and 4.3% in 13 *C. serpentina* (Ewert, unpubl. data). *Deirochelys* uses its long neck and large hyoid apparatus in specialized, aquatic, gape-and-suck feeding (Bramble, 1973; Jackson, 1996). This approach to feeding cannot occur on land and restricts this species to feeding in water. During droughts, *Deirochelys* must become quiescent and rely on its fat reserves while in terrestrial refugia.

Adaptation to a diet of small, seasonally available prey invites consideration of evolutionary changes in a suite of other morphological characters in *Deirochelys*. Fossil material referable to *Deirochelys* dates back to the Miocene in northern Florida (Gilchrist Co.). These oldest fossils (*Deirochelys* nr. *D. carri*) as well as subsequent *D. carri* represent individuals that were larger than any extant *D. reticularia*. They had thicker shells and, by indirect evidence, proportionately shorter necks than those of today’s *Deirochelys*. The Miocene and Pliocene forms thus had a more generalized emydid turtle morphology approaching that of extant *Trachemys* or *Pseudemys* in Florida (Jackson, 1978). Evidence from mitochondrial DNA supports the fossil evidence in suggesting that the lineage separating *Deirochelys* from Florida’s other emydid turtles is quite old (Walker and Avise, 1998).

The plastron of *Deirochelys* is narrow in comparison to other species in its subfamily, perhaps to facilitate crawling on pond bottoms. A specialization toward bottom-crawling is compatible with a bias toward use of small water bodies, where swimming through deep water is seldom necessary. The shell of extant *Deirochelys* is thin in comparison with its emydid relatives in Florida. For instance, the fresh shell weights of seven adult females averaged 30% of the base live weight, whereas similar determinations for other Florida species were 35% for 17 *P. floridana*, 38% for 10 *P. nelsoni*, and 44% for 18 *T. scripta* (Ewert, unpubl. data). Thinning of the shell in *Deirochelys* may reflect an adaptation and perhaps near restriction to small, seasonally flooded habitats. In these places large alligators, an apparent selective force favoring shell thickening in emydids (Jackson, 1984; unpubl. data), are rare.

THREATS

Documented Threats. — Perhaps the only directly observed threat in Florida has been loss due to road kills. Fully 38 of 58 (66%) of individuals that made up the data base for Jackson (1988), came from roadways. These included five road-kills. Several additional road-kills had to be omitted because they were too damaged. Although the proportion of road-kills may not seem large, three uninjured females in this group had placed themselves at risk by nesting in or along roadways, and several others appeared to be exploring for nest sites along roadways. Additionally, males as well as non-gravid females leave water and move about on land once or twice annually (e.g., in South Carolina; Buhlmann, 1998; Buhlmann and Gibbons, 2001). The risk for fatality thus seems significant. Two additional factors may aggravate this risk. First, the seasonally flooded ditches and borrow pits that have become artificial feeding habitat are often adjacent to roads and may lure turtles into roadside proximity. Second, females have their nesting season during the winter and make their nests during daylight hours. These are the months and hours when highway traffic in Florida is heaviest.

Loss of adults to indigenous animals (probably raccoons, *Procyon lotor*; and snapping turtles, *C. serpentina*) is known in Virginia (Buhlmann, 1995). Buhlmann and Gibbons (2001) suspected that raccoons were responsible for many turtles found eaten near their terrestrial refugia in South Carolina. River otters killed most adult females in a South Carolina wetland during one season (Buhlmann and Gibbons, 2001).

Historically, the sale of *Deirochelys* (as "chicken turtles") in meat and fish markets (Carr, 1952) may have been a threat. Because males are too small to be a practical source of meat, it is likely that mature females predominated in sales. In light of the apparent low natural population densities observed today, historical records of sales (if any exist) might cast light on former abundance, or otherwise provide a perspective on the former abundance of habitat available to *Deirochelys*.

Deirochelys is currently available in the internet pet trade at modest prices. However, we do not know of any simple method by which a commercial collector could systematically remove entire populations, as opposed to imposing light harvest over broad areas. As noted above, adults do poorly in high densities and thus are unsuitable for farming in large numbers. Other factors mitigating against widespread popularity of *Deirochelys* as pets include difficulty in stimulating wild-caught individuals from Florida into accepting immobile food (e.g., fish pellets, ground meat, or frozen fish), and the difficulty of hatching eggs.

Potential Threats. — Habitat loss is probably the leading factor in local population declines of this species. The often small size and slightly elevated aspect of individual wetlands renders them susceptible to ditching and draining. Other human-induced factors that cause declines in local water tables (such as over-pumping from aquifers) may have a negative effect on hydroperiod of these ephemeral wetlands. Various forms of land alteration (forestry, agriculture, surface mining, and urbanization) have obviously caused losses of a large proportion of original small wetlands in Florida. An estimated one-third of Florida's pre-settlement wetlands and freshwater areas had been drained by 1970, but with little change to tidal and riverine areas (Mossa, 1998). Thus, glades and isolated wetlands have suffered the greatest declines, and there is no evidence that the trend in decline has slowed.

Because fire is a necessary factor in sustaining many natural communities in Florida, its prevention by man has often resulted in a catastrophic type of burning with severe impacts on natural communities. Whereas in South Carolina the terrestrial refugia of *Deirochelys* tend to lie safely just below the flammable humus and fire appears not to be a threat, one occasionally observes fire-scarred individuals in Florida, perhaps victims of severe fires.

The impact of certain invasive alien species on nesting and nest success, while not extensively evaluated, probably is impacting many turtles including *Deirochelys*. That is, despite a well-known prevalence of nest depredation by vertebrate species, there are alternative concepts of nests as refugia (Gibbons and Nelson, 1978; Ewert, 1985; Jackson, 1988, 1994; Wilson et al., 1999). When both embryonic diapause and delayed emergence of hatchlings occur, the nest residence may be prolonged 2–4.5 fold beyond a liberal estimate of the time necessary just for the eggs to develop (e.g., 4 months of active embryogenesis for *Deirochelys* at a "cool" 24°C, this account). However, new, non-focused kinds of nest depredation may now render the greatly prolonged nest residence of *Deirochelys* especially vulnerable (Buhlmann, 1998; Buhlmann and Coffman, 2001). Fire ants (*Solenopsis invicta*) kill hatchlings, including those of *Deirochelys*, in or near their nests (Buhlmann and Coffman, 2001). While there is mixed evidence on whether fire ants are able to enter intact eggs (Buhlmann and Coffman, 2001; J. Brent Harrel, *pers. obs.*), toxins from fire ants may also kill eggs that have actually been laid within fire ant nests (Ewert and Jackson, 1994; unpubl. data on *Macrochelys temminckii*). In Florida's Big Bend area, the diggings of feral hogs have been so abundant locally that few turtle nests seem capable of escaping detection, if not random trampling. The very long nest residencies of *Deirochelys* are likely to increase risks of becoming sites for chance establishment of new fire ant colonies, as well as for chance encounters with hogs.

The presence of shells of dead *Deirochelys* around wetlands suggests that post-hatching predation occurs in Florida, as well as in Virginia (see above). We have also seen a few *Deirochelys* that have sustained injuries. One healthy female was functionally non-reproductive because she had lost both hind legs and was unable to dig a nest. In this regard, there is a consensus that the raccoon, a "subsidized" natural predator (Smith and Engeman, 2002), is now more abundant than in the past. Raccoons are quite capable at finding and depredating adult nesting turtles and turtle nests in low as well as high-density nesting environments.

STATUS

The Florida Committee on Rare and Endangered Plants and Animals has not listed *Deirochelys*, and the available evidence suggests that it does not warrant listing at this time. This status could change to a listing of "rare," however, if small wetlands, as well as their surrounding uplands throughout the state continue to be lost to development.

Because of its dependence on and the threat to ephemeral wetlands, this species was one of three turtles added to a list of "Species of greatest conservation need" during a Florida Comprehensive Wildlife Conservation Strategy Workshop held November 2004 (Meylan, this volume, Introduction).

CONSERVATION OPTIONS AND SOLUTIONS

Florida does not have any rule that applies specially to *Deirochelys*. However, Rule #68A-25.002(8) (effective in 1999 and thereafter) that limits collection of turtle eggs to an aggregate number of 50 eggs of common native species covers *Deirochelys*, as well as other unlisted turtles.

Although land use changes have not yet rendered *Deirochelys* endangered or threatened in Florida, humans have eliminated extensive areas of natural habitat. Further, the extent of inadvertent habitat compensation through construction of ephemerally flooded ditches and borrow pits is unclear but is probably inadequate to compensate for losses. Our present knowledge suggests that *Deirochelys* occurs only in low natural densities relative to many other kinds of turtles. Perhaps no natural habitat has high carrying capacity. Thus, preservation of large areas of ephemeral wetlands may be necessary to conserve this species. Certain large-scale ecosystem rehabilitation projects, either underway or planned, include many ephemerally ponded wetlands and may benefit *Deirochelys* as well as other wetland wildlife. For instance, rehabilitation of Tate's Hell Swamp, Franklin Co., from ditched and cutover pineland to wetland and mixed forest, is likely to benefit *Deirochelys*, which already occurs in nearby ditches and borrow pits and probably within the rehabilitation site. Rehabilitation of the Kissimmee River, however, offers a less certain prospect; the species is unknown from this project area, and the appropriate upland habitat elements may not be present. At either location an appropriate design for artificial enhancement would include a high degree of interspersion of temporary ponds and closed canopy, wooded uplands. Where large scale habitat protection seems unlikely, legal protection of individual small wetlands remains desirable to prevent population declines; however, political support for such protection seems to have weakened in recent years. A full design for the conservation of *Deirochelys* necessitates preserving not just ponds but also the surrounding upland including fully forested patches within this extended "core" habitat. That turtles in South Carolina often disperse 100 m and up to 165 m outward from their ponds into adjacent terrestrial habitat can serve as a guide to how much terrestrial habitat to preserve (Buhlmann and Gibbons, 2001).

Regarding non-native predators, hopefully, ongoing research on the biological control of fire ants will lead to effective solutions. Hunting regulations should be modified to result in a significant reduction of feral hog populations. The raccoon is an indigenous species but is subsidized to dangerously high abundance in many parts of Florida. It presents a more complicated situation. This is discussed in other species accounts that document raccoons as a major threat (see *Graptemys barbouri*, *Pseudemys concinna*, and *Caretta caretta*).

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LITERATURE CITED

AGASSIZ, L. 1857. Contributions to the Natural History of the United States of America, Vol. 1. Little, Brown and Co., Boston, 452 pp.

BANCROFT, G.T., GODLEY, J.S., GROSS, D.T., ROJAS, N.N., SUTPHAN, D.A., AND MCDIARMID, R.W. 1983. Large-scale operations management test of use of the white amur for control of problem aquatic plants; the herpetofauna of Lake Conway, Florida: species accounts. Misc. Paper A-83-5, U. S. Army Engineer Waterways Experiment Station, CE, Vicksburg, Mississippi.

BRAMBLE, D.M. 1973. Media dependent feeding in turtles. American Zoologist, 13: 1342.

BUHLMANN, K.A. 1995. Habitat use, terrestrial movements, and conservation of the turtle, *Deirochelys reticularia* in Virginia. Journal of Herpetology 29(2):173-181.

BUHLMANN, K.A. 1998. Ecology, terrestrial habitat use, and conservation of freshwater turtle assemblage inhabiting a seasonally fluctuating wetland with emphasis on the life history of *Deirochelys reticularia*. Ph.D. Dissertation. University of Georgia, Athens.

BUHLMANN, K.A., AND COFFMAN, G. 2001. Fire ant predation of turtle nests and implications for the strategy of delayed emergence. Journal of the Elisha Mitchell Scientific Society 117:94-100.

BUHLMANN, K.A., AND GIBBONS, J.W. 2001. Terrestrial habitat use by aquatic turtles from a seasonally fluctuating wetland: implications for wetland conservation boundaries. Chelonian Conservation and Biology 4:115-127.

BUHLMANN, K.A., LYNCH, T.K., GIBBONS J.W., AND GREENE, J.L. 1995. Prolonged egg retention in the turtle, *Deirochelys reticularia*. Herpetologica 51(4):457-462.

BUTTERFIELD, B.P., MESHAKA, W.E., JR., AND HAUGE, J.B. 1994. Two turtles new to the Florida Keys. Herpetological Review 25:81.

CARR, A.F. 1952. Handbook of Turtles: Turtles of the United States, Canada, and Baja California. Cornell University Press, Ithaca, New York, 542 pp.

CONGDON, J.D., AND GIBBONS, J.W. 1990. Turtle eggs: their ecology and evolution. In: Gibbons, J.W. (Ed.). Life History and Ecology of the Slider Turtle. Smithsonian Institution Press, Washington D.C., pp. 109-123.

CONGDON, J.D., GIBBONS, J.W., AND GREENE, J.L. 1983. Parental investment in the chicken turtle (*Deirochelys reticularia*). Ecology 64:419-425.

CONGDON, J.D., GIBBONS, J.W., AND GREENE, J.L. 1986. Biomass of freshwater turtles: a geographic comparison. American Midland Naturalist 115:165-173.

DEMUTH, J.P., AND BUHLMANN, K.A. 1997. Diet of the turtle, *Deirochelys reticularia* on the Savannah River Site, Aiken County, South Carolina. Journal of Herpetology 31(3):450-453.

DODD, C.K., JR. 1992. Biological diversity of a temporary pond herpetofauna in north Florida sandhills. Biodiversity and Conservation 1:125-142.

DODD, C.K., JR., AND CADE, B.S. 1998. Movement patterns and the conservation of amphibians breeding in small, temporary wetlands. Conservation Biology 12:331-339.

ERNST, C.H., LOVICH, J.E., AND BARBOUR, R.W. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington, D.C., 578 pp.

EWERT, M.A. 1985. Embryology of turtles. In: Gans, C., Billett, F., and Maderson, P.F.A. (Eds.). Biology of the Reptilia, Vol. 14. Wiley-Interscience, New York, pp. 73-267.

EWERT, M.A., AND JACKSON, D.R. 1994. Alligator snapping turtles, *Macroclemys temminckii*, and the lower Apalachicola River of western Florida. A Symposium on the Status and Conservation of Florida Turtles. Eckerd College, St. Petersburg, Florida, 2-3 April 1994.

Ewert, M.A., and Nelson, C.E. 1991. Sex determination in turtles: patterns and some possible adaptive values. Copeia 1991:50-69.

Ewert, M.A., and Wilson, D.S. 1996. Seasonal variation of embryonic diapause in the striped mud turtle (*Kinosternon baurii*) and general considerations for conservation planning. Chelonian Conservation and Biology 2:43-54.

Ewert, M.A., Firth, S.J., and Nelson, C.E. 1984. Normal and multiple eggshells in batagurine turtles and their implications for dinosaurs and other reptiles. Canadian Journal of Zoology 62:1834-1841.

Gibbons, J.W. 1969. Ecology and population dynamics of the chicken turtle *Deirochelys reticularia*. Copeia 1969:669-676.

Gibbons, J.W. 1970. Terrestrial activity and population dynamics of aquatic turtles. American Midland Naturalist 83:404-414.

Gibbons, J.W. 1987. Why do turtles live so long? Bioscience 37:262-269.

Gibbons, J.W. 1990. Turtle studies at SREL: a research perspective. In: Gibbons, J.W. (Ed.). Life History and Ecology of the Slider Turtle, pp. 19-44. Smithsonian Institution Press, Washington D.C.

Gibbons, J.W., and Greene, J.L. 1978. Selected aspects of the ecology of the chicken turtle *Deirochelys reticularia* (Latreille) (Reptilia, Testudines, Emydidae). Journal of Herpetology 12:237-241.

Gibbons, J.W., and Greene, J.L. 1990. Reproduction in the slider turtle and other species of turtles. In: Gibbons, J.W. (Ed.). Life History and Ecology of the Slider Turtle. Washington: Smithsonian Institution Press, pp. 124-134.

Gibbons, J.W., and Nelson, D.H., 1978. The evolutionary significance of delayed emergence from the nest by hatchling turtles. Evolution 32:297-303.

Gibbons, J.W., Greene, J.L., and Congdon, J.D. 1983. Drought-related responses of aquatic turtle populations. Journal of Herpetology 17:242-246.

Greenberg, C.H. 2001. Spatio-temporal dynamics of pond use and recruitment in Florida gopher frogs (*Rana capito aesopus*). Journal of Herpetology. 35:74-85.

Huestis, D.L., and Meylan, P.A. 2004. The turtles of Rainbow Run (Marion County, Florida): observations on the genus *Pseudemys*. Southeastern Naturalist 3:595-612.

Hutchison, V.H., Vinegar, A., and Kosh, R. 1966. Critical thermal maxima in turtles. Herpetologica 22:32-41.

Iverson, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately printed, 363 pp.

Jackson, D.R. 1978. Evolution and fossil record of the chicken turtle *Deirochelys*, with a re-evaluation of the genus. Tulane Studies in Zoology and Botany 20:35-55.

Jackson, D.R. 1985. Predation on turtles by the American alligator: ecological and morphological correlates. Proceedings of the Combined Annual Meetings of ASIH, HL, SSAR, University of Oklahoma, Norman, Oklahoma, 28 July-3 August 1985, 64/32/27:135.

Jackson, D.R. 1988. Reproductive strategies of sympatric freshwater emydid turtles in northern peninsular Florida. Bulletin Florida State Museum Biological Science 33:113-158.

Jackson, D.R. 1994. Overwintering of hatchling turtles in northern Florida. Journal of Herpetology 28:401-402.

Jackson, D.R. 1996. Meat on the move: diet of a predatory turtle, *Deirochelys reticularia* (Testudines: Emydidae). Chelonian Conservation and Biology 2:105-108.

Jackson, D.R., and Deitz, D.C. 1978. Effects of severe drought on the herpetofauna (and ichthyofauna) of a Florida marsh. Joint Annual Meetings of ASIH, HL, SSAR, Arizona State University, Tempe Arizona, 31 May-7 June 58/26/21 (unpaginated).

Latreille, P.A. 1801. In: Sonnini de Manoncourt, C.N.S. and P.A. Latreille. Histoire Naturelle des reptiles. Vol. 1. Deterville, Paris, 280 pp.

Moll, E.O. 1979. Reproductive cycles and adaptations. In: Harless, M., and Morlock, H. (Eds.). Turtles: Perspectives and Research. John Wiley & Sons, New York, pp. 305-331.

Mossa, J. 1998. Surface water. In: Fernald, E.A., and Perdum, E.D. (Eds.). Water Resources Atlas of Florida. Florida State University Institute of Science and Public Affairs, Tallahassee, pp. 64-81.

Mushinsky, H.R., and Wilson, D.S. 1992. Seasonal occurrence of *Kinosternon baurii* on a sandhill in central Florida. Journal of Herpetology 26:207-209.

Peacock, T., and Lewis, T.E. 2000. Geographic distribution: *Deirochelys reticularia* (chicken turtle). Herpetological Review 31:110-111.

Pope, C.H. 1939. Turtles of the United States and Canada. Alfred A. Knopf. Inc. New York, 343 pp.

Schwartz, A. 1956. Geographic variation in the chicken turtle *Deirochelys reticularia* Latreille. Fieldiana: Zoology 34(41):461-503.

Smith, H.T., and Engeman, R.M. 2002. An extraordinary raccoon, *Procyon lotor* density at an urban park. Canadian Field-Naturalist 116:636-639.

Walker, D., and Avise, J.C. 1998. Principles of phylogeography as illustrated by freshwater and terrestrial turtles in the southeastern United States. Annual Review of Ecology and Systematics 29:23-58.

Wilson, D.S., Mushinsky, H.R., and McCoy, E.D. 1999. Nesting behavior of the striped mud turtle, *Kinosternon baurii* (Testudines: Kinosternidae). Copeia 1999:958-968.

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Graptemys barbouri – Barbour's Map Turtle

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SUMMARY. — Barbour's map turtle, *Graptemys barbouri*, is one of two map turtles found in the panhandle of Florida. Adult females are larger than any other map turtles and have extremely broad heads; adult males are much smaller, with narrow heads. This species was first discovered in the Chipola River, at which time it was the first map turtle recorded from Florida. The distribution is now known to include parts of several river systems, including the Apalachicola and Chattahoochee at least as far north as Stewart County, Georgia, the Flint River north to Meriwether County, Georgia, and the Choctawhatchee and Pea River systems as far as Geneva County, Alabama. It appears to be introduced into the Ochlockonee River and possibly the Wacissa River. The Florida distribution is important to this species as a large portion of its range lies within the state. Favored habitat includes sections of free-flowing rivers with limestone outcrops; this environment supports good populations of gastropod mollusks, important in the diet of the adult females. However, use of silty channels is also widespread. Females appear to require many years to mature, perhaps as many as 14 years, and reach maximum size at around 24 years, whereas males mature in just 3–4 years. They have a prolonged nesting season (late April to early August) with relatively low clutch size (usually 7-10 elongate, soft-shelled eggs), but they may lay several clutches of eggs. Populations appear mostly to be fairly stable. In the Choctawhatchee River system there is suggestion of introgressive hybridization with *G. ernsti*, which could locally deplete *G. barbouri* as a pure form. Genetic evaluation of the Choctawhatchee map turtles is needed. Water flow in the Apalachicola River system is controlled or limited by dams, and this may have deleterious effects upon the habitat and populations of *G. barbouri* in this system.

CONSERVATION STATUS. – FNAI Global - G2 (Imperiled), State - S2 (Imperiled); ESA Federal - Not Listed; State - SSC (Species of Special Concern); CITES - Appendix III (USA); IUCN Red List - NT (Near Threatened).

Species Recognition. — *Graptemys barbouri*, the largest species of map turtle, reaches 330 mm in carapace length (CL) and 78 mm across the enormously broad head of adult females (Figs. 18-1, 18-2). Males are much smaller, reaching only 130 mm CL (Sanderson, 1974; Pritchard, 1980; Lovich and McCoy, 1992) (Fig. 18-3).

The carapace is oval, or slightly broader posteriorly as viewed from above, with its widest point near marginal 7 in most adults. In hatchlings, the carapace is nearly as wide as long. The marginal scutes are strongly serrated in hatchlings, and become less jagged in adults, with serrations persisting posteriorly but reduced to rounded bumps, or lost, anteriorly. The "sawback" morphology, consisting of a raised point at the rear of vertebral scutes 2 to 4, is prominent in hatchlings and persists in reduced form in all but the oldest adults. Old females have the appearance of an anteriorly "inflated" carapace. The highest tubercle is located at the rear of the second vertebral scute, but is less prominent than in *G. ernsti* or other species of the *G. pulchra* group. The plastron is broad, truncated anteriorly, and with a variable anal notch. The plastron is flat in males, slightly convex in females.

The head of the female is strikingly megacephalic in comparison with the "narrow-headed" map turtles (*G. caglei*, *G. ouachitensis*, etc.), as well as with *Pseudemys* species and most individuals of *Malaclemys*. In ventral aspect, the lower rhamphotheca tends to be more rounded than in other broad-headed map turtles, and the snout is blunter than in *G. ernsti* or *G. pulchra*. In large females, the mandibular rhamphotheca reaches as far forward as the maxillary rhamphotheca, and the tomial surfaces are very broad and unridged, with a narrow anterior extension of the fleshy palate almost completely separating the left and right sections of the maxillary rhamphotheca. The head of the male is not enlarged and the crushing surfaces within the mouth are narrow.

The tail of the male is proportionally larger than that of the female and is absolutely larger in large males, although these males may be less than 10% of the mass of adult females. The pre-cloacal part of the tail of the mature male is more than 20 mm longer than the pre-cloacal tail of a comparably-sized female (Sanderson, 1974).

The ground color of the carapace is some shade of greenish-brown, with a large, wandering, posteriorly-incomplete, dark-edged yellowish ocellus on each costal scute,

Figure 18-1. Adult female Barbour's map turtle, *Graptemys barbouri*, from Florida. Photo by David Dennis.

and a curved yellowish bar on each marginal scute. The plastron is very pale yellow to pale tannish yellow, with narrow dark edges to the transverse seams in hatchlings and juveniles. These dark edges degrade and essentially disappear in adults (Fig. 18-4). The head pattern includes a distinct tan to yellow, yellow-edged interorbital blotch that tapers between the orbits to a point near the external nares (Figs. 18-1, 18-2, 18-3, 18-5). There are also tan to yellow, yellow-edged postorbital blotches on a darker background; typically, these blotches are connected to the interorbital blotch. The chin bears a bold, light, transverse, slightly curved stripe against a dark background. This character distinguishes *G. barbouri* from *G. ernsti* and other members of the *G. pulchra* complex (Ernst et al., 1994; for additional characters see Carr, 1952).

Figure 18-2. Head of adult female *G. barbouri*, from Liberty Co., Florida, showing megacephaly. Photo by Robert T. Zappalorti.

The population of the lower Apalachicola River (i.e., below the confluence with the Chipola River) expresses a conspicuous dichromatism in hatchlings (Ewert, 1979). About 75% of turtles in a sample of 85 hatchlings from 11 clutches had dark, almost black points on the "saw tips" of the carapace, blackened seams along the plastron, and dark lines on the skin. The remaining 25% of the sample lacked very dark pigmentation, but retained pale yellowish markings on a pale olive green background (Fig. 18-6). Possibly the dichromatism results from different incubation temperatures, although one could speculate that it was controlled by a simple dominance-recessive relationship in a single gene for pigmentation and that the pallid condition is recessive, comprising half the alleles for the trait in pigmentation. Two pallid hatchlings became increasingly drab overall as they grew in captivity (Ewert, unpubl.). A similar dichromatism occurs in the Choctawhatchee River population (see Distribution, below; Godwin, 2002.).

Taxonomic History.—*Graptemys barbouri* (Barbour's map turtle) was described by Carr and Marchand (1942) on the basis of specimens collected in 1941 in the Chipola River north of Marianna (Jackson County). Except for McDowell's (1964) reclassification of all *Graptemys* as species of *Malaclemys*, an action followed by Sanderson (1974) but rejected by recent authors, this nomenclature has remained stable.

Carr (in Crenshaw and Rabb, 1949) suggested that *Graptemys pulchra* (then including *G. ernsti* and *G. gibbonsi*) might be a senior synonym of *G. barbouri*, but Cagle (1952) examined 393 *G. barbouri*, 5 *G. ernsti*, and 110 *G. gibbonsi* and demonstrated that *G. barbouri* was clearly distinct.

Analysis of mitochondrial DNA suggests that *G. barbouri* has closer affinities to *G. ernsti* and *G. pulchra* than to *G. gibbonsi* or any other *Graptemys* (Lamb et al., 1994;

Figure 18-3. Adult male *G. barbouri,* from Jackson Co., Florida. Photo by Michael Redmer.

Walker and Avise, 1998). This finding is consistent with the relative geographic proximity of these riverine turtles.

DISTRIBUTION

Geographic Distribution. — A large portion of the range of *G. barbouri* lies within Florida (Fig. 18-7). Until recently, the known range included only the Apalachicola River system, where it extended north of Florida in the Chattahoochee River to Stewart Co., Georgia, and in a long section of the Flint River north to central Meriwether Co., Georgia. Recent records have identified *G. barbouri* in the Choctawhatchee River and its tributary, the Pea River, well into Geneva Co., Alabama (Godwin, 2002).

Graptemys barbouri probably occurs throughout the main course of the Apalachicola, but records fail to cover large stretches of the river. Documented localities include Seminole Co., Georgia (Lake Seminole, Pritchard, unpubl.); ca. 2 km WNW of Sweetwater (Liberty Co., D.R. Jackson, *pers. comm.*); 2 km N and 2 km S of Florida Hwy 20 (Liberty Co.); Fort Gadsden Historical site (Franklin Co.); and downstream to the northern edge of Apalachicola Bay (Franklin Co.; Ruhl, 1991; Cox and Kautz, 2000). In the lower Apalachicola, records include waters on all sides of Forbes Island, the St. Marks/East River distributary, and the main channel of the Apalachicola extending 2 km into the Intracoastal Waterway (Ruhl, 1991). There are numerous records from the Chipola River (Carr and Marchand, 1942; Carr, 1952; Sanderson, 1974; Moler, 1986), including the lower reaches of Spring Creek, Jackson Co., Florida.

Recent observations identify *G. barbouri* in the Choctawhatchee River system (Wallace, 2000; Godwin, 2002). However, Godwin (2002) suspected that *G. ernsti* is also present in this drainage. Accordingly, the distribution in Alabama may be partitioned, with *G. barbouri* in the upper Choctawhatchee River, *G. ernsti* in the upper Pea River tributary, and hybrids of these species in the lower Pea River. Godwin (2002) provided diagnostic photos of *G. barbouri* from the upper Choctawhatchee. However, photos of *G. ernsti* and purported hybrids from this drainage are less convincing, and genetic analysis is recommended.

In Florida, captured turtles from the Choctawhatchee that appear to be *G. barbouri* include one juvenile from 1 km

Figure 18-4. Adult female *G. barbouri,* from Leon Co., Florida, in ventral view. Photo by Matt Aresco.

Figure 18-5. Head of hatchling *G. barbouri,* from Calhoun Co., Florida. Photo by Dick Bartlett.

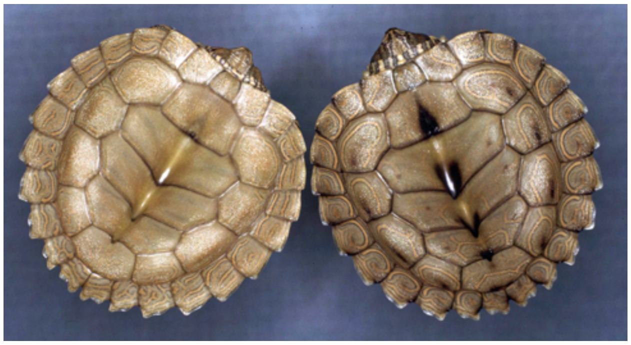

Figure 18-6. Hatchlings of light (left) and dark (right) color morphs of *G. barbouri* from Franklin Co., Florida. Photo by Mike Ewert.

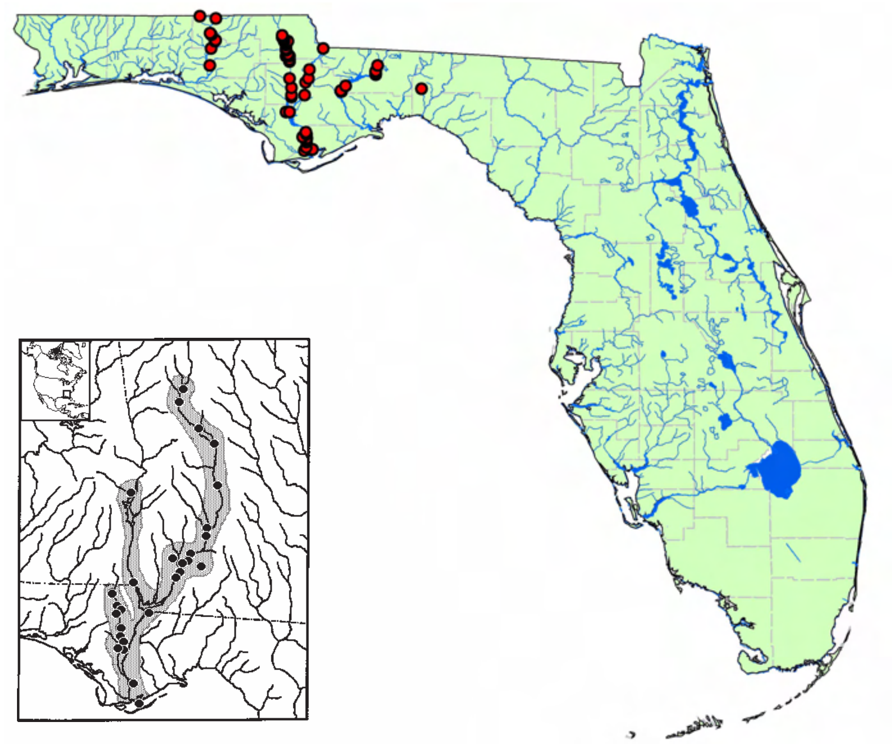

Figure 18-7. Available distribution records for Barbour's map turtle, *Graptemys barbouri*, in Florida. Inset: distribution records from entire range of *G. barbouri* (adapted from Iverson, 1992; distribution in inset map not current for Florida as presented here).

south of the Alabama state line, three from ESE of Cerrogordo and one from Caryville (all adjacent to Holmes Co., Florida). Sightings of basking map turtles, rather than captures, provide much additional documentation (Wallace, 2000), but the exact status of *G. barbouri* (vs. *G. ernsti* or hybrids) in the Florida drainage remains ambiguous in light of the claims for Alabama (Godwin, 2002). However, no map turtles examined from the Florida portions of the Choctawhatchee have shown *G. ernsti* influence. The sightings have occurred at numerous locations southward from the Alabama line and within the small dip that the Pea River makes from Alabama into Florida in northwestern Holmes Co. to northeast Walton Co. Despite additional surveys of the lower Choctawhatchee, this portion has not yielded sightings of map turtles from Camel Bluff (Walton Co.) south to Florida Hwy 20, nor in the lower sections of two tributaries (Holmes Creek in Washington Co.; Wrights Creek in Holmes Co.; Wallace, 2000).

In the Ochlockonee River, there are records of four sightings or captures of *G. barbouri* near Tallahassee. These span a straight line distance of 7.2 km. Three additional sightings, also from Leon Co. but below Lake Talquin, span 4.8 km (Enge et al., 1996; Wallace, unpubl.). Further search for basking individuals has extended from Leon Co. downstream along the Wakulla Co. border to tidewater without yielding sightings. It is rumored that *G. barbouri* was introduced into the Ochlockonee River during the early 1970s (D.B. Means, *pers. comm.*). However, the recently documented turtles were all juveniles whereas surviving turtles released during the 1970s would have been adults by the mid-1990s.

There is one additional record of *G. barbouri* from the Tallahassee area. This is from Jefferson Co., near the headwaters of the Wacissa River (33.34°N, 83.99°W). Jackson (2003) found a nesting female, which laid 12 fertile eggs. The occurrence of *G. barbouri* in drainages east of the Apalachicola River, while potentially of recent anthropogenic origin, is compatible with the paleontological record. Fossils identifiable as G. *barbouri* have been found in the Santa Fe River, part of the Suwannee River drainage (Jackson, 1975). Thus, four independent Gulf drainages currently contain *G. barbouri*, whereas in the past the range may have extended considerably further to the southeast.

Ecological Distribution. — The two sites that provided the most habitat information for this species both represent lotic, free-flowing sections of rivers, but also show striking contrast. The Chipola River site has high banks, submerged limestone outcroppings, and high water clarity much of the year (Carr, 1952; Sanderson, 1974). The lower Apalachicola site has low banks, a silty to sandy bottom that is naturally devoid of rocks, and low water clarity, except during times of extreme low water. *Graptemys barbouri* also occurs in the tidal distributaries of the Apalachicola (Ruhl, 1991), and there is one sighting in the East Bay arm of Apalachicola Bay (Pritchard, 1979). Generally, the species seems much more common in the main channel of the Apalachicola than in the typically slackwater floodplain channels associated with the main river. However, there are 18 recorded sightings in the Brothers River (Ruhl, 1991), which has turbid slackwater most of the time. The species does not appear to frequent blackwater tributaries of any of the rivers within its overall range. It does enter Spring Creek (Jackson Co.), a clear, spring-fed stream with a sand, gravel, and bedrock bottom. However, the free-flowing section of this stream deepens and backs up extensively when the Chipola River floods, and thus sporadically gives turtles broad access to a different habitat type.

Favored habitat in the Choctawhatchee River is much like that in the Chipola River, and features extensive limestone outcrops with their concomitant gastropod feeding resource. This habitat occurs from within Alabama downstream to 4–5 km south of the Highway I-10 crossing (Holmes Co., Florida). Downstream from the limestone outcrops, where the channel is narrow and sandy, *G. barbouri* declines from abundant to uncommon, judging by sighting frequency (Wallace, 2000, unpubl.).

Despite the preference for lotic habitat, individuals have been observed in the artificially lentic waters of Dead Lakes reservoir in the Chipola River (Sanderson, 1974), Lake Seminole in the Apalachicola River (Pritchard, unpubl.), and in Apalachicola Bay.

HABITAT RELATIONS

Activity. — As with many map turtles that seek emergent sections of fallen trees (“snags”) in rivers for aerial basking sites (Lindeman, 1999), *G. barbouri* uses these structures along the Chipola, Choctawhatchee, and lower Apalachicola rivers. In the lower Apalachicola, turtles frequent partially submerged willows (*Salix* sp.) that recline outward from the shoreline, despite much shading from full sunlight. It appears that most females favor the willows over exposed logs, although it may simply be a question of accessibility for the larger-bodied females. Post-hatchlings and juveniles bask upon small logs and plant debris in the Apalachicola River, adjacent to known nesting areas.

In the Chipola River, basking also occurs on exposed limestone ledges. In contrast to the apparent tolerance for shaded basking sites along the Apalachicola River, individual turtles in the Chipola River shifted sites during the day in order to stay in full sunlight. Basking activity, however, appeared to be most concentrated in the early afternoon (Sanderson, 1974; Moler, 1986).

When approached by observers in a small boat, adult females basking along the lower Apalachicola River often abandoned their perches at distances exceeding 100 m, whereas smaller turtles tolerated approaches of 10–25 m. In a similar pattern of response along the Choctawhatchee River, large individuals return to the water when the observer is at an appreciable distance, whereas small ones have tolerated approaches to within 3 m. Although the turtles apparently become inactive at night, they have been stimulated to swim to the surface (Sanderson, 1974) using the boat motor vibration “revving” technique of Chaney and Smith (1950).

During cool weather, females aggregate in deep pockets within submerged limestone outcrops. Divers have found that some of these turtles were coated with silt, as if they had been quiescent for some time (Carr, 1952). During low flow periods, females also use deep pockets in the limestone bottom as well as sandy holes adjacent to the limestone (Sanderson, 1974). However, the lower Apalachicola lacks these bottom features, and *G. barbouri* must brumate elsewhere.

Home Range. — Linear home ranges, as measured along the Chipola River, averaged 273 m for 18 females and 364 m for 38 males, with an extreme of 1750 m for one male (Sanderson, 1974). Multiple observations per individual turtle over about two years formed the basis for these estimates. However, the mean values include records of sedentary individuals recorded repeatedly at a single spot.

Terrestrial Activity. — Terrestrial activity is minimal. Females come on land to nest up to 100 m from water, and hatchlings must crawl from their nests to water, although summer floods may lessen this distance. Hatchlings may overwinter in the nest cavity (see below).

Temperature Relations. — Cloacal temperatures of turtles captured during or just after basking at the Chipola River ranged from 12 to 35.4°C in 87 readings, with 18 readings over 30°C and just six readings below 20°C. Temperatures of basking turtles were often 10°C warmer, and only seldom cooler, than concurrent water temperatures (Sanderson, 1974).

GROWTH AND REPRODUCTION

Growth. — Males and females grow at nearly the same linear rate until they are approximately four years old. Thereafter, growth in males almost ceases. Linear growth in females continues at about a third of the rate of growth in small juveniles (Sanderson, 1974). Intercostal fontanelles of bony shells are open in all small juveniles but close at a CL of about 80 mm in males, while remaining open to about 150 mm in females. When about 50 mm in plastron length (PL), the heads of females start to broaden relative to those of males of the same size (Sanderson, 1974), and this broadening appears to be genetically programmed rather than a response to a durophagous diet. The heads of two females reared in captivity on the same soft diet as males became proportionately broader and commensurate with the relative head width of wild female turtles of the same size (Columbus Zoo data base, compared with Sanderson, 1974). Phylogenetic evidence also suggests that while females of many *Graptemys* species eat mollusks, they become broad-headed in only a minority of these species (Ernst et al., 1994). Males of the species of which females have broad heads also have jaws with broad crushing surfaces, but their heads do not undergo overall broadening (Lindeman, 2000; Lindeman and Sharkey, 2001).

Sexual Size Dimorphism. — Females attain much larger sizes than males. The sexual size dimorphism index (SSDI; Lovich and Gibbons, 1992) in *G. barbouri* is remarkable, probably the most extreme of any turtle in the western hemisphere except for other members of its species group (see Gibbons and Lovich, 1990). In terms of CL the index is +2.3 to +2.6, as derived from the data of Cagle (1952), Sanderson (1974), and this account. In terms of mass, females along the lower Apalachicola River weigh 2500–

3300 g and large males weigh about 206 g, giving an SSDI of +12 to +16.

Size and Age at Maturity. — The smallest sexually mature wild female collected by Cagle (1952) from the Chipola River measured 176 mm PL (ca. 199 mm CL). Sanderson (1974) suggested that females attained maturity at 165 mm PL. The smallest captive female (reared in captivity at the Columbus Zoo) that has laid normal-sized eggs, measured about 165 mm PL (186 mm CL, 949 g). Another captive female, weighing 878 g, produced abnormally small eggs. Both of these females were older than 15 years when they began laying (Columbus Zoo data records). Sanderson (1974) estimated that females take close to 20 years to mature, which is distinctly longer than the 14-year estimate for sexual maturity in *G. ernsti* from a larger study (Shealy, 1976).

Males reach maturity at 69-70 mm PL (ca. 78–79 mm CL; Cagle, 1952; Sanderson, 1974). Given that post-hatching growth commences during the next growing season following hatching, males attain adult size after 3–4 years (Cagle, 1952; Shealy, 1976).

Reproductive Cycles. — Despite collection of many individuals for museum specimens and dissection of several of these, there has not been an attempt to describe the seasonal gonadal cycle of either sex. The major museum series, having been collected only from late November (about 80 individuals, Carr, 1952) and mid-July (393 individuals, Cagle, 1952), are too temporally constrained to suffice for such analyses.

Nesting Season, Nest Sites, Nesting Behavior. — A female found nesting on 29 April 1991 near Ft. Gadsden (Franklin Co.) represents the earliest known nesting date. Other specific dates for oviposition include 30 April (1986, 1991), and 12 dates during five different years between 2 and 17 May. Near Ft. Gadsden the latest known dates of nesting were 4–6 July 1972 for four fresh nests. One additional record, 7 July 1972, came from near the Florida Highway 20 bridge (Liberty Co.). Close examination of known nesting areas on 14–16 August 1990 and 1991 gave no evidence of recent nesting along the lower Apalachicola River.

Apparently, nesting along the upper Chipola River occurs later in the season, not starting until June, and then continuing into early August (Sanderson, 1974). About 50% of 25 females collected on 12–14 July 1950 were gravid, and about half of these contained incompletely shelled eggs, indicating that they would not have been ready for laying before the third week of July (Cagle, 1952). The only observed nest along the Choctawhatchee River was laid 2 km north of the Florida border on 29 May 1999 (Godwin, 2002). The single nest from the Wacissa River was laid on 30 May 2002 (Jackson, 2003).

Observations of nests and nesting along the lower Apalachicola River (Franklin Co.) include recently completed nests as well as sightings of gravid females on land, a few of which were actually nesting. In clear weather, nesting females were observed from soon after dawn until mid-morning. During stormy weather, nesting continued almost until noon. Two individuals were found nesting in heavy rain. Nests along the Choctawhatchee and Wacissa rivers were complete or nearly complete by mid-morning (Godwin, 2002; Jackson, 2003).

Most of the nests of *G. barbouri* observed along the lower Apalachicola River in recent years were in anthropogenic mounds of dredged sand, roughly 25–40 years old (see below). Woody vegetation has partially reclaimed these mounds and has resulted in a patchwork of shady and open areas. Nesting typically occurs in the open areas, although often close to shrubs or trees. Neither the nest sites nor the evidence of gaps in the local floodplain forest appear obvious from the water and at least one site was over 100 m inland. The mounds were far more conspicuous 20 years ago (Ewert, unpubl.) and some turtles may have become imprinted to them at that time.

The natural nesting habitat appears to be the original river berm, which is wooded except for a few small tree-fall gaps. One nest in this habitat was in very fine sand from a recent flood. Sand of the dredged spoil mounds is coarser and contains many small shells of an Asiatic clam (*Corbicula alumina*). Four nests in the spoil mounds were 9–12 cm in depth to the top of the egg chamber and 16–19 cm deep overall. Disturbed females may flee during the oviposition phase of nesting. One fleeing female had laid three eggs in the nest and retained four eggs in her oviducts. In another case, an uncovered nest was discovered containing three intact eggs, and an additional egg laid on the surface closer to the river. Only fresh turtle tracks led from the nest to the river; no predator tracks were apparent.

Although alluvial, sandy areas appear to be ideal for nesting, such features appear to be absent along the middle and upper Chipola River. Turtles in those areas must nest in other microhabitats, although Sanderson (1974), who worked extensively on the Chipola populations, provided no details.

Clutch Size, Reproductive Potential, Relative Clutch Mass. — Clutch size from along the lower Apalachicola River ranged from 4–14 eggs (usually 7–10), and averaged 8.8 (*n* = 20); total mass of clutches ranged from 100–184 g (*n* = 16; Ewert and Jackson, 1994, and unpubl.). Clutches ranged from 3–11 eggs along the Chipola River (Cagle, 1952). One clutch of 15 eggs was observed on the Choctawhatchee River in Alabama just north of the Florida state line (Godwin, 2002).

Cagle (1952) provided strong evidence that individual females produce more than one clutch per season. Available data on duration of the nesting season, although a bit problematic, allows an estimate of seasonal fecundity. Whereas the nesting season appears to commence earlier along the lower Apalachicola River than along the Chipola River, it may end earlier there as well. We do not know exactly when the nesting season ends along either river. The aggregate of nesting seasons at the two locations, however, appears to exceed three months. As with Florida's other large emydid turtles, *G. barbouri* shows low proportional investment in each clutch (clutch mass/spent body mass or relative clutch mass (RCM): 3.8–6.4% in 8 documented cases from 3 rivers, Ewert, unpubl.). Therefore, an RCM of 12.8% (Iverson et al., 1993), probably based upon mismatched clutch and body masses, appears to be too high. An RCM and nesting pattern similar to that of *Pseudemys concinna* (Jackson and Walker, 1997) and Florida's other large emydids (Jackson, 1988) seems more likely. Thus, an average adult female *G. barbouri* is estimated to lay a total of 25–40 eggs in 3–5 clutches per season. This estimate is somewhat conservative relative to the six or more clutches regarded as possible for ecologically similar *G. ernsti* in southern Alabama (Shealy, 1976).

Eggs, Incubation, Development, Hatching. — A sample of 141 freshly laid eggs from 20 clutches from along the lower Apalachicola River averaged 15.16 ± 1.59 SD g. They ranged in mass and dimensions from 11.9 g (35.0 x 24.4 mm) to 18.5 g (42.3 x 27.2 mm). Data from the Chipola River sample (Cagle, 1952) suggest that small or recently matured females may lay slightly smaller eggs. As in other Florida emydids, the eggs have pliable eggshells and succumb rapidly to dehydration in open air.

In the laboratory, thermal requirements and incubation times for eggs of *G. barbouri* (from Franklin Co.) to complete incubation are about average for emydid turtles from the southeastern U.S. (Ewert, 1979). Eggs from one Franklin Co. nest, discovered on 16 August 1991 and candled shortly thereafter, contained mid-stage embryos. These eggs, subsequently incubated at 30°C, hatched 18–21 September. According to projections from the cooler nest temperatures, these eggs would have hatched naturally during early October.

Incubation temperature determines sex in *G. barbouri* (Ewert et al., 1994). A constant incubation temperature of 25°C produces only males, whereas 29–30°C yields only females. The pivotal temperature (i.e., yielding nearly equal numbers of males and females) for the lower Apalachicola population is close to 28.2°C (Ewert et al., 1994 and subsequent unpublished observations).

Along the Chipola River, an absence of late summer or fall sightings of hatchlings suggests that they overwinter on land, perhaps in the nest (Sanderson, 1974). Similarly, hatchlings have not been reported along the Apalachicola River during the fall. At both locations hatchlings have been seen in the spring, in March in the Chipola River (Sanderson, 1974). They are often seen basking on floating debris adjacent to known nesting areas. According to observations in Georgia (Mitchell Co.), some hatchlings enter the water by mid-August but others not until the latter part of September (Wahlquist and Folkerts, 1973).

Hatchling Size. — Hatchling size from five laboratory incubated clutches from along the lower Apalachicola River ranged from 32.4–38.0 mm CL (30.3–33.5 mm PL; 7.9–11.6 g mass). By estimation, hatchlings from the largest eggs (>18 g) probably exceed 13 g in mass. The smallest hatchling collected from the Chipola River measured 30.2 mm PL (Sanderson, 1974).

POPULATION BIOLOGY

Much of the available population data are from the Chipola River. Carr (1952) reported collecting about 80 individuals from about half of the Florida section of the Chipola River. Cagle (1952) collected 393 individuals from an unspecified length of this river. Sanderson (1974) captured 386 individuals in repeated sampling of a 5.65 km reach (68.3 turtle/km) in southern Jackson Co., and four individuals from the Dead Lakes before the dam was breached. More recent basking surveys have yielded far lower densities. One survey (Moler, 1986) yielded 221 sightings in a section that nearly overlapped the one mentioned by Carr (1952). Sightings of basking *G. barbouri* averaged 2.64 turtles/km, with some stretches having 5.66 turtles/km. The highest numbers were seen basking during the early afternoon (Moler, 1986), which concurs with the observations of Sanderson (1974). Moler (1986) concluded from his survey that the population trend during the 45 years since the observations by Carr (1952) was as compatible with a stable population as with a decline.

Observations on abundance along the lower Apalachicola River include only one formal basking survey (Ruhl, 1991), conducted during August, that recorded 79 *G. barbouri* downstream from the upper end of Forbes Island (Franklin Co., Florida). There were 32 sightings along the eastern side of Forbes Island, or 1.43 turtles/km. However, the river level was too high for easy observation during this survey. Also, a higher proportion of turtles are likely to engage in basking, and thus be counted, during the spring when the river water is cooler. A more casual, but still conservative estimate allows that a minimum of 100 *G. barbouri*, or 4.46 turtles/km, occupied the same reach during the springs of 1990 and 1991. Independent springtime observations during the same period have estimated 350-500 *G. barbouri* along the lower Apalachicola River (R. Zappalorti, *in litt.*).

A basking survey along the Choctawhatchee River recorded 256 map turtles (putative *G. barbouri*) within Florida. About 97% of these sightings, or 5.93 turtles/km, were between Caryville (Holmes Co.) and the Alabama line. The highest density, 7.05 turtles/km, occurred along a 12.2 km stretch south of Florida Highway 2 (Wallace, 2000). This survey was conducted during the late summer and early fall when, as noted above, many turtles may not engage in basking because the water is warmer. Records along the Ochlockonee River are limited to just 7 juveniles (3 seen and collected during 1993–94 and 4 seen during 2000) along two separate reaches totaling about 14 km (Enge et al., 1996; Wallace, unpubl.).

Adult sex ratios have shown a strong male bias. Cagle (1952) reported 67% males and Sanderson (1974) reported 78%. In these samples, the proportions of juveniles were 32 and 55%, respectively, and the juvenile groups were female-biased. Observed adult sex ratios are thus compatible with the difference in maturation times (because females require 5–6 times as long as males to mature, see above) as reviewed by Gibbons (1990). However, few collecting methods are likely to be free of bias when the adult males and females are of such different sizes. Thus, the ratio between natural (or anthropogenic) mortality rates of adult males and females is likely to remain unclear for the foreseeable future. The small males may be more subject to aquatic predation, but only nesting females are exposed to terrestrial predators, including raccoons (*Procyon lotor*). The presence of headless carcasses of adult females on the Apalachicola nesting grounds suggests that this loss may be severe.

INTERSPECIFIC INTERACTIONS

Community Structure. — In the Chipola River, both Carr (1952) and Sanderson (1974) mentioned co-occurrence of *G. barbouri* with *Pseudemys concinna*, and Moler (1986) observed *Trachemys scripta* as well as *P. concinna* basking with *G. barbouri*. *Sternotherus minor* is also common in the river (J.F. Berry, *pers. comm.*). In Spring Creek (Jackson Co.), a tributary of the Chipola, small *G. barbouri* have been rarely present and *S. minor*, *T. scripta*, and juvenile *P. concinna* are more common. In the lower Apalachicola River, *T. scripta* and *P. concinna* have often been seen basking adjacent to *G. barbouri*. *Macrochelys temminckii* and *S. minor* also frequent the main channel of the Apalachicola. In the Choctawhatchee River, 509 basking turtles seen in addition to (putative) *G. barbouri* included *P. concinna*, *P. floridana*, *T. scripta*, and *Apalone spinifera* (Wallace, 2000).

Diet and Feeding. — Digestive tract samples from turtles from the Chipola River have indicated that *G. barbouri* is essentially carnivorous (Sanderson, 1974; Lee et al., 1975). Males and small juvenile females preyed on generally similar foods, whereas large females became predominantly molluscivorous. Males and small juveniles favored aquatic insects, especially larvae of caddisfly (Trichoptera) and an aquatic moth (Pyralididae) that frequent the more rapidly moving water, but also beetles (Coleoptera) and other groups. Male and juvenile turtles also consumed small gastropods (snails). Large females consumed few insects, favoring snails and bivalves instead (Sanderson, 1974). In a separate sample from the Chipola River, fecal material from large females was composed predominantly of snails, with a few bivalves (Cagle, 1952). Casual inspection of fecal remains from large females from the lower Apalachicola River also suggested more snails than bivalves. Here, this proportion was not expected because the firm substrates typically used by snails are a minor component of the habitat, whereas shifting sands and silts are rich with bivalves (especially the exotic Asiatic clam, *Corbicula fluminea*). This invasive clam was the bivalve in the Apalachicola River fecal samples; it is also common in the Choctawhatchee River (Blalock et al., 2000)

Predation. — Along the lower Apalachicola River, nests of *G. barbouri* are regularly depredated. Most tracks at depredated nests have been those of raccoons, although some tracks belong to fish crows (*Corvus ossifragus*). Another potential predator of turtle nests, the nine-banded armadillo (*Dasypus novemcinctus*), became established along the lower Apalachicola between 1973 and 1981. Despite their abundant tracks and diggings, there is no evidence that armadillos disturb turtle nests in this area. First-generation feral hogs have been present in this region on a sporadic basis but have not shown evidence of depredating turtle nests. Canid species left no evidence of being a problem, and their tracks have consistently been rare in the area.

There is one well-documented instance of bald eagles (*Haliaeetus leucocephalus*), based in Torreya State Park (Liberty Co.), preying on mid-sized *G. barbouri*. Over five nesting seasons, 38 carcasses, all in a narrow range of 93–131 mm PL, were found under two trees used by a pair of eagles. Turtles of this size include very large adult males and mid-sized subadult females (Means and Harvey, 1999).

Dead adult females have been found in nesting areas, suggesting they had been killed while attempting to nest. The cuts and tears on a freshly dead individual were consistent with an attack by a raccoon. We expand on the threat posed by predation below.

THREATS

Documented Threats. — Local harvest of *G. barbouri* along the Chipola River probably continues. Moler (1986) observed basking turtle traps in several places in 1985–86, but did not give actual trap counts. Usually, these traps temporarily capture turtles as they flee basking logs and retain the turtles at least several minutes, long enough for a person in a boat to reach the traps and remove the turtles. The traps favor capture of emydids, such as sliders, cooters, and *G. barbouri*. Additional evidence of harvest is the observation of scattered refuse of dead turtle shells and fragments (though not identified to species) at river access points (Moler, 1986). Researchers and others can fairly easily capture *G. barbouri* in numbers by diving for them when the Chipola is low and clear (Sanderson, 1974, 1992).

We have no evidence for use of basking traps along the main channel of the Apalachicola River south of Florida Highway 20. This absence may be a consequence of sparse human settlement along the shoreline as well as the presence of hazardous currents that in many places limit boat access to basking sites. As the waters of the Apalachicola are almost always turbid, diving for turtles is ineffective. In 1992 a refuse deposit of turtle shells near Eastpoint (Franklin Co.) contained many *Pseudemys* but no *G. barbouri*. During the early 1970s “plinking” wildlife (including turtles) along the shoreline with firearms seemed a frequent pastime. Since the early 1990s this activity has seemed a lot less common although it has not ceased entirely.

Adult female turtles clearly have non-human, natural predators. Casual observation along the lower Apalachicola River yielded one shell in 1973, three in 1986, one in 1990, and one freshly dead turtle in 1993. Carcasses of dead females were on land in open nesting areas rather than along the berm between nesting areas or in deposits of water-born debris, which have contained turtle carcasses of other species. The freshly dead female, still containing four viable eggs, was partially eviscerated through an inguinal pocket, as if by a raccoon. It is probable that this turtle had been killed when she had come ashore to nest (Ewert, unpubl.). A brief search of nesting habitat along the middle Apalachicola

River in 2000 (near Sweetwater) yielded four additional dead females, including a freshly killed one with scattered eggshells nearby (D.R. Jackson and R. Franz, *pers. comm.*). Raccoons are now well documented as a serious predator of adult emydid turtles (Shealy, 1976; Seigel, 1979; Tucker et al., 1999). The listing of mankind as the only serious predator on adult turtles (e.g., Ernst and Barbour, 1972) may be overemphasized and distract attention from other significant predators.

Nest depredation is an obvious factor in reducing the annual recruitment of hatchlings into populations. For *G. barbouri*, there are no estimates of the proportion of nests destroyed. However, searches following turtle tracks in open sandy areas have found that nearly all tracks older than a day lead to depredated nests. Along the lower Apalachicola River, both raccoons and fish crows are serious nest predators. Raccoon tracks are abundant at depredated nests and ubiquitous throughout the area. Fish crows are also common in the area and have left tracks at depredated turtle nests. Fish crows were observed on the ground next to one nesting female on 6 May 1991, and are known to be serious predators on eggs of other southern emydid and trionychid turtles (LaClaire, 1995; Jackson and Walker, 1997).

Potential Threats. — Probably the most important component of the habitat of *G. barbouri* is the Apalachicola River, the downstream continuation of the Chattahoochee and Flint rivers in Georgia. This river is subject to ongoing major human demands and stresses and to political tension over future demands. Alabama, Georgia, and Florida all demand use of the river water in large quantities for numerous purposes (B. Ritchie, *Tallahassee Democrat*, 3–11 November 2001). Georgia, with several million people and significant industrial development in the Apalachicola drainage, may pose the greatest threat, in that a single major industrial disaster or spillage could inflict long-term damage upon aquatic life, including turtles. However, *G. barbouri* as a species does seem moderately safe from potential threats because four rivers (Choctawhatchee, Chipola, Chattahoochee, Flint) and possibly five (Ochlockonee) would all have to experience major disasters to cause extinction of the species. At the level of distinguishable genotypes, however, the status of the Choctawhatchee map turtles requires genetic analysis. A determination of uniqueness or of introgressive hybridization (with *G. ernsti*) will mean that habitat quality and risks for both of these main drainages with *G. barbouri* will warrant more monitoring than would otherwise be the case.

At present, Lake Blackshear, an impoundment on the Flint River in Georgia, is the only seriously polluted (highly eutrophic) section within the distribution of *G. barbouri* (see Garner et al., 1997). The Florida portion of the Apalachicola River drainage is not quite free of EPA Superfund Sites (6 of ca. 1050 Florida sites) but has included only two National Priority List Sites (among 70 Florida sites). One site, Sapp Battery Salvage, is on the Dry Creek drainage of the Chipola River, Jackson Co., and still requires attention (EPA Superfund Website).

The Apalachicola River has a long history of utilization as an inland waterway. For the last 40 years, the U.S. Army Corps of Engineers has maintained a 3 m deep channel for barge traffic. As part of the initial construction as well as early maintenance, river bottom substrates were dredged and transported as pumped slurry onto the formerly natural riverbanks and into the adjacent floodplain forest. These artificial areas, which initially were low, barren sandy mounds, date back to 1957–76, when such riverbank deposition of dredged spoil was legally permitted (see review in Ewert and Jackson, 1994).

Adult female *G. barbouri* have for years selected the sandy spoil mounds for nest sites. The mounds themselves are undergoing change; since the early 1970s they have become increasingly overgrown with brush, hardwoods, and occasionally cabbage palms (*Sabal palmetto*). As nesting turtles seem to prefer partially open situations, turtle nesting has become ever more clumped in such areas. This situation may facilitate predation but also may favor warm nests that produce females through temperature-dependent sex determination. The latter process could favor buildup of populations in some parts of the river formerly populated through colonization from more distant female-producing areas. How turtles will adapt when the mounds become completely overgrown remains unknown.

Subsequent to 1976, dredged spoil slurry was placed back into the river water on either side of the navigation channel. The process almost certainly buries some live mussels and could also bury a few turtles, but is probably too localized to have significant effects. Sand mining has removed sand from a few small areas (B. Bergstrom, *Tallahassee Democrat*, 3 January 1995). In recent years, the U.S. Army Corps of Engineers has begun to return some locally high-piled sand into the river (K. Begos, *News Herald* [Panama City], 7 July 1999; P. Hasty, *The Apalachicola Times*, 19 November 2000). Renewed plans call for local mining of more sand (B. Ritchie, *Tallahassee Democrat*, 3 November 2001). In extreme cases, sand mining may extirpate turtle nesting habitat (review in Moll and Moll, 2000).

Another component of waterway maintenance has been the regular removal of floating dead trees, or “snags.” This practice at some level dates back to 1875 (Leitman et al., 1990), whereas our knowledge of *G. barbouri* is appreciably more recent. Thus, we lack a solid basis for evaluating snag management along the main channel of the Apalachicola. Presumably, the natural prominence and abundance of these features was greater before snag removal started. Snag control has occurred on a regular basis and could be regarded as significant habitat alteration, depending on the average size of the relocated dead trees. For example, during 1990, 272 snags, or 2.3 snags per km, were relocated (U.S. Army Corps of Engineers, 1990). Typically, the snags are not removed from the water, but rather they are pushed against the shoreline. Given that map turtles in general favor habitat with abundant emergent deadwood (Lindeman, 1999), the practice of snag relocation probably has been detrimental to

G. barbouri. Large map turtles use large snags as basking sites, which become more shaded when pushed up under the shoreline vegetation. It is noteworthy that naturally-occurring snags are a significant feature of the Choctawhatchee River and offer the basking surfaces most utilized by map turtles.

During the heavy hurricane season of 2004, forest ecosystems lost thousands of trees throughout northern and central Florida, and abundant new snags have been observed in the rivers inhabited by *G. barbouri*. Possibly these will prove to be beneficial to the species.

Given that *G. barbouri* is a lotic species, impoundments displacing the former flowing environment would seem to be detrimental. However, *G. barbouri* does occur in Lake Seminole (created from the Apalachicola River in 1955–57; Hubbell et al., 1956; Livingston, 1984). After Dead Lakes (on the lower Chipola River) was artificially impounded by a dam from 1960 to 1987 (Machlin and Sicchio, 1999), *G. barbouri* occurred in the lake at least into the early 1970s (Sanderson, 1974). The species also occurred there in the 1990s, following removal of the dam (R. Zappalorti, *pers. comm.*).

STATUS

Graptemys barbouri was listed by the Florida Committee for Rare and Endangered Plants and Animals (FCREPA) as Rare in 1978, and again in 1992 (Sanderson, 1978, 1992). The current FNAI status is Global - G2 (Imperiled) / State - S2 (Imperiled). It is not listed by the US ESA, but the State of Florida lists it as LS (Species of Special Concern). The IUCN Red List categorizes the species as NT (Near Threatened). All *Graptemys* spp. were recently listed on CITES Appendix III by the United States.

CONSERVATION OPTIONS AND SOLUTIONS

Graptemys barbouri is legally protected from most commercial use in Florida, according to Rule 68A-25.002(9), “No person shall buy, sell, or possess [the species] for sale...” The Game and Fresh Water Fish Commission first prohibited commercial take in 1972, and then imposed a bag limit of two individuals for personal use in 1974. Alabama and Georgia prohibit any take without special permits (Levell, 1997).

As summarized briefly above, populations of *G. barbouri* have been surveyed recently along the lower Apalachicola, the middle Chipola, the Choctawhatchee, and the middle Ochlockonee rivers. However, much of the Apalachicola River remains essentially unsurveyed.

Despite lingering ignorance regarding distribution and abundance, some easing of the concerns regarding endangerment already may be falling into place within the current framework of legal protection and economic trends. The outlawing of both buying and selling the species in Florida has curtailed former high volume trade in hatchlings, juveniles, and subadults, as exemplified during the 1960s at the Ross Allen Reptile Institute, Silver Springs (Pritchard, pers. obs.). However, legislation has not ended trade. Recently, small numbers of *G. barbouri* have been offered for sale in the internet pet trade, and there has been one announcement of intentions to captive breed *G. barbouri* for commercial purposes. Data originating with the U.S. Fish and Wildlife Service indicate a documented export of 747 *G. barbouri* individuals in 1997 (Telecky, 2001). Although such trade engenders many negatives, to put it within the perspective of population management, if even 10% of the eggs currently lost to nest depredation were to be incubated for the pet trade, the domestic market would be saturated at current asking prices. The export market may be more threatening, but export listings do not include the sources or life stages of the exported animals. Taking and hatching eggs for export is least likely to stress populations whereas taking adult females is far more damaging (Congdon et al., 1993).

Egg production through captive breeding has been achieved at the Columbus Zoo over several years (Goode, 1997). However, clutch size has been lower than in the wild and hatching success of the eggs has been poor, much poorer than with other species of *Graptemys* housed at that institution. Furthermore, growth to adulthood in females is much more protracted than in related species (M. Goode, unpubl. data).

It appears to us that most of the ongoing collection of adult *G. barbouri* occurs in the Chipola River. This take could be modified and probably reduced by local wildlife regulation to prohibit use of basking traps along the river. At that point, diving, which is limited by the weather and personal physical ability, and chance finds of nesting females would comprise nearly the entire human take of this sensitive component of map turtle populations. It is unclear how much recreational shooting at turtles affects *G. barbouri*, but shooting turtles is currently illegal in Florida. Casual “plinking” may diminish with additional public education toward respect for the law and respect for rare species belonging to the natural heritage of the South.

A reduction in the depredation on nests and adults by raccoons may not come about easily. Although the raccoon is a native predator, it has become “subsidized” (Smith and Engeman, 2002) in that it has achieved abnormally high abundance where humans have eliminated natural enemies and provided alternative food sources, such as certain row crops, garden produce, and refuse. Although recent census data on raccoon populations in most states are lacking, available data suggest recent surges in population growth (Gehert et al., 2002). In the face of increasing raccoon populations, there is conflicting evidence as to how much reduction in raccoon populations is necessary to benefit turtles. Modest raccoon removal may fail to bestow benefit (Ratnaswamy et al., 1997; Ratnaswamy and Warren, 1998). Alternatively, focused removals can yield benefit for one or two nesting seasons before resurgence in raccoon numbers (Christiansen and Gallaway, 1984). Raccoon removal under contract may be the best procedure to protect sea turtle nests (Engeman et al., 2002). Protecting nests in place from raccoons or transplanting the eggs as proposed for sea turtles (Ratnaswamy et al., 1997) is an unrealistic option for *G. barbouri* because the nests are difficult to locate in advance of depredation. Improvement in the market for hides as an incentive for private take of raccoons remains as the simplest option for reducing their populations. Perhaps remaining impediments to profitability of cheap hides can be reduced in recognition of nuisance level abundance. Whatever the approach to this problem, simply to ignore it and to legislate further blanket restriction on human take of *G. barbouri* diverts attention from the real needs of the species.

Proposed decommissioning of the Apalachicola River waterway for commercial barge traffic, while just a proposal (e.g., T. Croft, *News Herald* [Panama City], 13 May 2001; B. Ritchie, *Tallahassee Democrat*, 13 May 2001), could have some distinct benefits. Floating deadwood might once again accumulate in natural configurations. It is unclear, however, that the U.S. Army Corps of Engineers would reduce river management to this extent, given the concerns of pleasure boaters. Regardless, the complex demand for water use is bound to result in appreciable distortion of flows away from natural ones (e.g., U.S. Army Corps of Engineers, 1998; for general overview, R. Ritchie, *Tallahassee Democrat* 3–11 November 2001). With retention of dams, especially the Jim Woodruff Dam on Lake Seminole, entrenchment of the main channel of the Apalachicola (Light et al., 1998) will continue. This probably will be aggravated if river management continues removing dredged sand from the river and its vicinity. Abandonment of the commercial waterway, however, may allow return of somewhat more natural dispersal of remaining sand and somewhat more natural variation in water level. Then, wet year / dry year variation in flows might expand availability of natural sandbar habitat for nesting.

Most of the banks of the lower Apalachicola River are protected from shoreline housing development through public ownership. Much of this protection has arisen to sustain the health of Apalachicola Bay. While the current level of development along the rest of the Apalachicola shoreline is slight, additional protection should be beneficial. With human population growth, some of the unprotected Apalachicola shoreline is certain to become attractive waterfront real estate. Development often brings local point-source pollution, trampling, and other disturbance to nesting areas, and more high-impact river management, including snag removal. The uppermost limestone reaches of the Chipola River, upstream from Mariana (Jackson Co.), have protected shoreline as part of the NW Florida Water Management District. The Choctawhatchee River habitat is minimally developed and has nearly complete protection as managed watershed downstream from northern Holmes Co. (Jue et al., 2001). As the small remaining unprotected portion in Holmes Co. includes some of the favored limestone habitat, this section, too, deserves protection (see Cox and Kautz, 2000).

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LITERATURE CITED

Blalock, H.N., Herod, J.J., and Williams, J.D. 2000. Freshwater mussels of the Choctawhatchee River drainage in Alabama and Florida. American Fisheries Society 130th Annual Meeting, St. Louis, Missouri, p. 53.

Cagle, F.R. 1952. The status of the turtles *Graptemys pulchra* Baur and *Graptemys barbouri* Carr and Marchand, with notes on their natural history. Copeia 1952:223-234.

Carr, A.F. 1952. Handbook of Turtles. The Turtles of the United States, Canada, and Baja California. Ithaca, NY: Cornell University Press, 542 pp.

Carr, A.F., Jr. and Marchand, L.J. 1942. A new turtle from the Chipola River, Florida. Proceedings of the New England Zoology Club 20:95-100.

Chaney, A., and Smith, C.L. 1950. Methods for collecting map turtles. Copeia 1950:323-324.

Christiansen, J.L., and Gallaway, B.J. 1984. Raccoon removal, nesting success, and hatchling emergence in Iowa turtles with special reference to *Kinosternon flavescens* (Kinosternidae). Southwestern Naturalist 29:343-348.

Congdon, J.D., Dunham, A.E., and Van Loben Sels, R.C. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. Conservation Biology 7:826-833.

Cox, J.A., and Kautz, R.S. 2000. Habitat conservation needs of rare and imperiled wildlife in Florida. Report, Florida Game and Freshwater Fish Commission, Office of Environmental Services, Tallahassee, 156 pp.

Crenshaw, J.W., and Rabb, G.B. 1949. Occurrence of the turtle *Graptemys barbouri* in Georgia. Copeia 1949:26.

Enge, K.M., Cailteux, R.L., and Nordhaus, J.J. 1996. Geographic distribution: *Graptemys barbouri*. Herpetological Review 27:150-151.

Engeman, R.M., Shwiff, S.A., Constantin, B., Stahl, M., and Smith, H.T. 2002. An economic analysis of predator removal approaches for protecting marine turtle nests at Hobe Sound National Wildlife Refuge. Ecological Economics 42:469-478.

Ernst, C.H., and Barbour, R.W. 1972. Turtles of the United States. Lexington: University Press of Kentucky, 347 pp.

Ernst, C.H., Lovich, J.E., and Barbour, R.W. 1994. Turtles of the

United States and Canada. Smithsonian Institution Press, Washington, D.C., 578 pp.

Ewert, M. A. 1979. The embryo and its egg: development and natural history. In: Harless, M., and Morlock, H. (Eds.). Turtles: Perspectives and Research. John Wiley & Sons, New York, pp. 333-413.

Ewert, M.A., and Jackson, D.R. 1994. Nesting ecology of the alligator snapping turtle (*Macroclemys temminckii*) along the lower Apalachicola River, Florida. Florida Game and Freshwater Fish Commission, Nongame Wildlife Program Report NC89-020, Tallahassee, Florida, 45 pp.

Ewert, M.A., Jackson, D.R., and Nelson, C.E. 1994. Patterns of temperature-dependent sex determination in turtles. Journal of Experimental Zoology 270:3-15.

Garner, M.M., Herrington, R., Howerth, E.W., Homer, B.L., Nettles, V.F., Isaza, R., Shotts, E.B, and Jacobson, E.R. 1997. Shell disease in river cooters (*Pseudemys concinna*) and yellow-bellied turtles (*Trachemys scripta*) in a Georgia (USA) lake. Journal of Wildlife Diseases 33:78-86.

Gehrt, S.D., Hubert, G.F., and Ellis, J.A. 2002. Long-term populations trends of raccoon populations in Illinois. Wildlife Society Bulletin 30:457-463.

Gibbons, J.W. 1990. Sex ratios and their significance among turtle populations. In: Gibbons, J.W. (Ed.). Life History and Ecology of the Slider Turtle. Smithsonian Press, Washington, D.C., pp. 171-182.

Gibbons, J.W., and Lovich, J.E. 1990. Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). Herpetological Monographs 4:1-29.

Godwin, J.C. 2002. Distribution and status of Barbour's map turtle (*Graptemys barbouri*) in the Choctawhatchee River system, Alabama. Alabama Natural Heritage Program: Report to the Alabama Department of Conservation and Natural Resources, 21 pp.

Goode, J.M. 1997. Eggs and clutch production of captive *Graptemys*. In: Van Abbema, J. (Ed.). Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles – An International Conference. N.Y. Turtle and Tortoise Society, p. 478.

Hubbell, T.H., Laessel, A.M., and Dickinson, J.C. 1956. The Flint-Chattahoochee-Apalachicola Region and its environments. Bulletin of the Florida State Museum, Biological Sciences 1:1-68.

Iverson, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately printed, 363 pp.

Iverson, J.B., Balgooyen, C.P., Byrd, K.K., and Lyddan, K.K. 1993. Latitudinal variation in egg and clutch size in turtles. Canadian Journal of Zoology 71:2448-2461.

Jackson, D.R. 1975. A Pleistocene *Graptemys* (Reptilia: Testudines) from the Santa Fe River of Florida. Herpetologica 31:213-219.

Jackson, D.R. 1988. Reproductive strategies of sympatric freshwater emydid turtles in northern peninsular Florida. Bulletin Florida State Museum, Biological Sciences 33:113-158.

Jackson, D.R. 2003. Geographic distribution. *Graptemys barbouri*. Herpetological Review 34:164.

Jackson, D.R., and Walker, R.N. 1997. Reproduction in the Suwannee cooter, *Pseudemys concinna suwanniensis*. Bulletin Florida Museum of Natural History 41:69-167.

Jue, S., Kindell, C., and Wojcik, J. 2001. Florida conservation lands 2001. Florida Natural Areas Inventory, Tallahassee, Florida, 316 pp.

LaClaire, L. 1995. New clues in map turtle decline. Endangered Species Bulletin 20:15.

Lamb, T., Lydeard, C., Walker, R.B., and Gibbons, J.W. 1994. Molecular systematics of map turtle (*Graptemys*): a comparison of mitochondrial restriction site versus sequence data. Systematic Biology 43:543-559.

Lee, D.S., Franz, R., and Sanderson, R.A. 1975. A note on the feeding habits of male map turtles. Florida Field Naturalist 3:45-46.

Leitman, S.F., Ager, L., and Mesing, C. 1990. The Apalachicola experience: environmental effects of physical modifications for navigation purposes. In: Livingston, R.L. (Ed.). The Rivers of Florida. Springer-Verlag, New York, NY and Berlin, Germany, pp. 223.

Levell, J.P. 1997. A Field Guide to Reptiles and the Law, 2nd Ed. Serpent's Tail Natural History Book Distributors, Lanesboro, Minnesota, 270 pp.

Light, H.M., Darst, M.R., and Grubbs, J.W. 1998. Aquatic habitats in relation to river flow in the Apalachicola River floodplain, Florida. U.S. Geological Survey Professional Paper No. 1594, 78 pp.

Lindeman, P.V. 1999. Surveys of basking map turtles *Graptemys* spp. in three river drainages and the importance of deadwood abundance. Biological Conservation 88:33-42.

Lindeman, P.V. 2000. Evolution of the relative width of the head and alveolar surfaces in map turtles (Testudines: Emydidae: *Graptemys*). Biological Journal of the Linnaean Society 69:549-576.

Lindeman, P.V., and Sharkey, M.J. 2001. Comparative analyses of functional relationships in the evolution of trophic morphology in the map turtles (Emydidae, *Graptemys*). Herpetologica 57:313-318.

Livingston, R.J. 1984. The ecology of the Apalachicola Bay system: an estuarine profile. U.S. Fish and Wildlife Service OBS-82/05, 165 pp.

Lovich, J.E., and Gibbons, J.W. 1992. A review of techniques for quantifying sexual size dimorphism. Growth, Development and Aging 56:269-281.

Lovich, J.E., and McCoy, C.J. 1992. Review of the *Graptemys pulchra* group (Reptilia: Testudines: Emydidae), with descriptions of two new species. Annals of the Carnegie Museum 61:293-315.

Machlin, E., and Sicchio, M. (Eds.). 1999. Dam Removal Success Stories. American Rivers, Friends of the Earth, and Trout Unlimited, 114 pp.

McDowell, S.B. 1964. Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae. Proceedings of the Zoological Society of London 43:239-279.

Means, D.B., and Harvey, A. 1999. Barbour's map turtle in the diet of nesting bald eagles. Florida Field Naturalist 27:14-16.

Moler, P.E. 1986. Barbour's map turtle census and habitat. Florida Game and Freshwater Fish Commission, Bureau of Wildlife Research Final Report Study #E-1-10-III-A, 11 pp.

Moll, E.O., and Moll, D. 2000. Conservation of river turtles. In: Klemens, M.W. (Ed.). Turtle Conservation. Smithsonian Press, Washington, D.C., pp. 126-155.

Pritchard, P.C.H. 1979. Taxonomy, evolution, and zoogeography. In: Harless, M., and Morlock, H. (Eds.). Turtles: Perspectives and Research. John Wiley & Sons, New York, pp. 333-413.

Pritchard, P.C.H. 1980. Record size turtles from Florida and South America. Chelonologica 1:113-123.

Ratnaswamy, M.J., and Warren, R.J. 1998. Removing raccoons to protect sea turtle nests: are there implications for ecosystem management? Wildlife Society Bulletin 26:846-850.

Ratnaswamy, M.J., Warren, R.J., Kramer, M.T., and Adam, M.D. 1997. Comparisons of lethal and non-lethal techniques to reduce raccoon depredation on sea turtle nests. Journal of Wildlife Management 61:368-376.

Ruhl, J.D. 1991. Barbour's map turtle survey, Apalachicola River wildlife and environmental area. Report, Florida Game and Freshwater Fish Commission, 7 pp.

Sanderson, R.A. 1974. Sexual dimorphism in the Barbour's map turtle, *Malaclemys barbouri* (Carr and Marchand). Masters Thesis, University of South Florida.

Sanderson, R.A. 1978. Rare: Barbour's map turtle, *Graptemys barbouri* (Carr & Marchand). In: McDiarmid, R.W. (Ed.). Rare and Endangered Biota of Florida, Vol. III: Amphibians and Reptiles. University Press of Florida, pp. 49-50.

Sanderson, R.A. 1992. Barbour's map turtle, *Graptemys barbouri* Carr & Marchand. In: Moler, P.E. (Ed.). 1992. Rare and Endangered Biota of Florida. University Press of Florida, pp. 196-199.

Seigel, R.A. 1979. Predation by raccoons on diamondback terrapins, *Malaclemys terrapin tequesta*. Journal of Herpetology 14:87-89.

Shealy, R.M. 1976. The natural history of the Alabama map turtle, *Graptemys pulchra* Baur in Alabama. Bulletin of the Florida State Museum, Biological Sciences 21:47-111.

Smith, H.T., and Engeman, R.M. 2002. An extraordinary raccoon, *Procyon lotor* density at an urban park. Canadian Field-Naturalist 116:636-639.

Telecky, T.M. 2001. United States import and export of live turtles and tortoises. Turtle and Tortoise Newsletter 4:8-14.

Tucker, J.K., Filoramo, N.I., and Janzen, F.J. 1999. Size-based mortality due to predation in a nesting freshwater turtle, *Trachemys scripta*. American Midland Naturalist 141:198-203.

U.S. Army Corps of Engineers. 1990. Apalachicola River 1990 maintenance report. Report, Mobile District, Corps of Engineers, Mobile, AL, 7 pp.

U.S. Army Corps of Engineers. 1998. Water allocation for the Apalachicola-Chattahoochee-Flint (ACF) River Basin. EPA 980396D, 583 pp.

Wahlquist, H. and Folkerts, G.W. 1973. Eggs and hatchlings of Barbour's map turtle *Graptemys barbouri* Carr and Marchand. Herpetologica 29:236-237.

Walker, D., and Avise, J.C. 1998. Principles of phylogeography as illustrated by freshwater and terrestrial turtles in the southeastern United States. Annual Review of Ecology and Systematics 29:23-58.

Wallace, G.E. 2000. Distribution and relative abundance of *Graptemys* c.f. *barbouri* on the Choctawhatchee River, Florida. Florida Scientist 63:41.

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Graptemys ernsti – Escambia Map Turtle

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Summary. – The Escambia map turtle, *Graptemys ernsti*, has the most restricted range of any turtle species found in Florida. The species, described in 1992, was formerly considered a geographic variant of the Alabama map turtle, *G. pulchra*. *Graptemys ernsti* is restricted to parts of the Escambia, Yellow, and Shoal rivers and their tributaries in the western Florida panhandle and adjacent Alabama. This map turtle, like its close relatives, is a riverine species with remarkable sexual dimorphism. Adult females attain lengths over twice those of adult males and have broad heads with greatly expanded alveolar surfaces of the jaws. Small juveniles of both sexes and adult males are primarily insectivorous, whereas females feed almost exclusively on freshwater mussels and snails. The introduced Asiatic clam, *Corbicula fluminea*, is the primary prey of female *G. ernsti*. *Graptemys ernsti* is strongly aquatic and is found exclusively in the main channels of rivers and large to medium-sized creeks and is not typically found in river floodplain swamps. The scarcity of molluscs in blackwater streams originating in the lower Coastal Plain may account for the absence of *G. ernsti* in the Blackwater and Perdido rivers and their tributaries. Although it is currently the most abundant turtle in certain portions of the rivers in which it occurs, it may be sensitive to habitat degradation and other threats. The primary threats include the use of all-terrain vehicles (ATVs) on sandy riverbanks used as preferred nesting sites, indiscriminant shooting of basking adults, water pollution, dam construction, river channelization, and removal of snags used as basking sites. Because *G. ernsti* occurs in such a small area, all threats to this species should be minimized and it should be closely monitored for any future changes in population status and demographic structure.

Conservation Status. – FNAI Global - G2 (Imperiled), State - S2 (Imperiled); ESA Federal - Not Listed; State - Not Listed; CITES - Appendix III (USA); IUCN Red List - NT (Near Threatened).

Species Recognition. — *Graptemys ernsti* is a moderate-sized map turtle (up to 28.5 cm carapace length [CL]) with a relatively high-domed shell. The ground color of the carapace is olive to dull green with each costal scute having a wide yellow ring at the lower edge (Figs. 19-1, 19-2). The upper surface of each marginal scute has a single yellow vertical bar; posteriorly, the marginals are serrate. The carapace has a distinct dorsal keel composed of a laterally compressed knob on the posterior part of each vertebral scute. The medial keel is most prominent in juveniles and males and becomes less conspicuous with increasing size, especially in females. A longitudinal black stripe or series of black blotches follows the dorsal keel. Ground color of the plastron is pale yellow with dark markings that follow the seams of the plastral scutes (Fig. 19-3). The head pattern is yellow or orange and consists of a three-pronged nasal trident connected to a large interorbital blotch that is separate from a pair of large postorbital blotches (Fig. 19-4). The back of the head has a pair of small, yellow, oval spots or bulbous expansions of the dorsal, paramedian neck stripes. The neck, legs, and tail are black with yellow or orange stripes. Hatchlings and juveniles are more brightly colored than adults (Fig. 19-5).

Graptemys ernsti exhibits pronounced sexual dimorphism with adult females attaining lengths over twice those of adult males. Adult females have broad heads with greatly expanded alveolar surfaces of the jaws, whereas males have small heads, narrower jaws, and longer tails. Large adult females appear humped-backed due to a dramatic incline of the anterior part of the carapace. This species is restricted to the Conecuh, Escambia, and Yellow rivers and their tributaries. It is not sympatric with any other species of *Graptemys*.

Taxonomic History. — Until 1992, *G. ernsti* was considered a geographic variant of the Alabama map turtle, *G. pulchra* (Baur, 1893; Cagle, 1952; Mount, 1975; Shealy, 1976). However, Lovich and McCoy (1992) demonstrated that *G. pulchra* (*sensu lato*) is actually a complex of three allopatric species (*G. ernsti*, *G. gibbonsi*, and *G. pulchra*) that are distinct in morphology and color pattern. *Graptemys gibbonsi* occurs in the Pascagoula and Pearl River systems in Mississippi and Louisiana, *G. pulchra* (*sensu stricto*) is found throughout the Mobile Bay drainage system in Alabama, eastern Mississippi, and northwestern Georgia (Lovich and McCoy, 1992), and *G. ernsti* is restricted to the Conecuh, Escambia, and Yellow River systems in southern Alabama and western Florida. These three species are also distinguished from each other by unique mitochondrial DNA genotypes and together with *G. barbouri* form a monophyletic clade, the *G. pulchra* group (Lamb et al., 1994; Stephens and Wiens, 2003). Lamb et al. (1994) proposed that the pronounced ende-

Figure 19-1. Juvenile Escambia map turtle, *Graptemys ernsti*, from Escambia Co., Florida. Photo by David Dennis.

mism of Gulf Coast *Graptemys* in adjacent drainages is associated with several isolation-dispersal events linked to Plio-Pleistocene changes in sea level.

DISTRIBUTION

Geographic Distribution. — *Graptemys ernsti* is restricted to the Pensacola Bay drainage system in southern Alabama and western Florida, including the Conecuh, Escambia, Yellow, and Shoal rivers (Lovich and McCoy, 1994). In Alabama, the species occurs in tributaries of the Conecuh River at least as far north as Persimmon Creek in Butler County, the Sepulga River and Murder Creek in Conecuh County, and Gantt Lake in Covington and southern Crenshaw counties (Godwin, 2000; Aresco, *pers. obs*.). In Florida, the species occurs in the Escambia River from the Alabama–Florida line to several miles south of FL Hwy 184 (Aresco, *pers. obs*.) and in the Yellow River at least as far south as Harold, Santa Rosa Co., FL (AUM 21980) (Fig. 19-6). This species apparently does not occur in either the Perdido River to the west of the Escambia River or the Blackwater River that enters Pensacola Bay between the Escambia and Yellow rivers. *Graptemys ernsti* has the most limited distribution of any map turtle and has one of the most restricted ranges of any turtle occurring in Florida.

Ecological Distribution. — *Graptemys ernsti* is strongly aquatic and within its range is found exclusively in the main channels of large and medium-sized rivers and creeks. The species is not typically found in backwater areas or river floodplain swamps and has not been observed in estuarine habitats in the extreme lower portions of the Escambia and Yellow rivers or in Escambia Bay, Blackwater Bay, or East Bay. The primary biotic factor influencing the distribution and abundance of *G. ernsti* is an adequate supply of aquatic molluscs, particularly freshwater mussels, the principal food item of adult and large juvenile females (Shealy, 1976). The

Figure 19-2. Adult female Escambia map turtle, *Graptemys ernsti*, from Escambia Co., Florida. Photo by Barry Mansell.

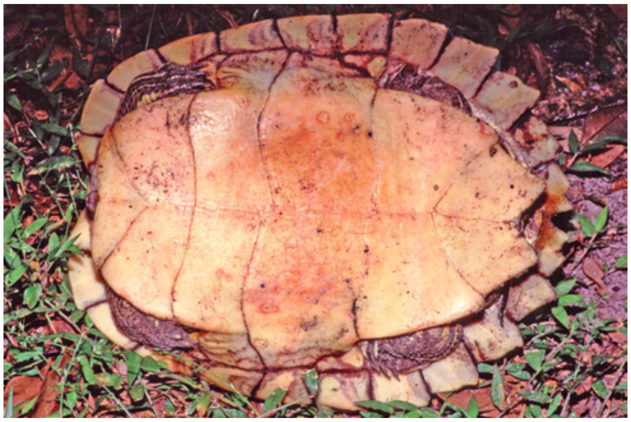

Figure 19-3. Plastral view of adult female Escambia map turtle, *Graptemys ernsti* from Escambia Co., Florida. Photo by Dick Bartlett.

Figure 19-4. Anterior view of adult female Escambia map turtle, *Graptemys ernsti*, from Escambia Co., Florida. Photo by Dick Bartlett.

scarcity of molluscs in blackwater streams originating in the lower Coastal Plain may account for the absence of map turtles in the Blackwater and Perdido rivers and their tributaries (Mount, 1975; National Biological Service, 1995). Suitable riverine habitat also requires an abundance of logs, stumps, and snags that provide basking sites and underwater hiding and resting sites (Godwin, 2000). Populations of *G. ernsti* are furthermore dependent on appropriate physical conditions for nesting—primarily large sandbars associated with sharp river bends. Females prefer nesting sites with a relatively open canopy, fine-grained sand, and an elevation of 2–3 m above water (Shealy, 1976). However, along straight sections of river channels, females nest in narrow zones of more stabilized sand deposits under moderate undergrowth and a closed canopy (Shealy, 1976). In Florida, large exposed sandbars and well-defined river banks are typical of the upper portions of the Escambia and Yellow rivers, but these are replaced by smaller and more vegetated sand banks and floodplain swamps along the lower river channels. These habitat differences may affect the local abundance of *G. ernsti* and population densities may be greater along meandering stretches of rivers with alternating series of large exposed sandbars opposite deep pools and undercut banks (Shealy, 1976; Aresco, *pers. obs.*). These sections of rivers also support high densities of mussels and are generally characterized by swift and turbulent water with sand-gravel sediments.

Figure 19-5. Hatchling Escambia map turtle, *Graptemys ernsti*, from Escambia Co., Florida. Photo by Dick Bartlett.

GROWTH AND REPRODUCTION

Growth. — Information on growth and age at maturity of *G. ernsti* is derived from Shealy's (1976) study at the Conecuh River in southern Alabama. Male growth rates are greatest among juveniles and decline sharply at about 100 mm CL. Growth in females is constant between 45 and 160 mm CL, followed by a slight increase during the subadult stage (160–220 mm CL), and then it rapidly approaches zero in large adults (Shealy, 1976; Lindeman, 1999a). Males mature at ≥ 80 mm CL, a size attained in 3–4 yrs. Females reach maturity at a much larger size, ≥ 212 mm CL, which requires at least 14 yrs of growth in the Conecuh River population (Shealy, 1976; Lindeman 1999a). Mature males range in size from 80–131 mm CL, and mature females range from 212–285 mm CL. Females attain close to maximum size in ca. 23 yrs and males in ca. 8 yrs (Shealy, 1976).

Nesting Season / Nest Sites / Nesting Behavior. — In a Conecuh River population in Alabama, *G. ernsti* nests mostly from May through July and nests are usually located 1–20 m from the water's edge on large, exposed sandbars (Shealy, 1976). Nest sites are most often associated with fine-grained sand that allows easy excavation without settling. The nest is a flask-shaped chamber about 15 cm deep consisting of a lower spherical chamber about 10 cm in diameter and a neck 4 cm in diameter. Clutch size ranges from 6–13 eggs (mean 7.2, *n* = 25) with an average of 4 (range 1–6) clutches per season per female (Shealy, 1976). Eggs are elliptical with flexible shells. Although sperm is present in male reproductive tracts throughout the year, mating activity has been observed only from September to November, suggesting that females store sperm over winter until ovulation begins in late April (Shealy, 1976).

POPULATION BIOLOGY

Density and Biomass. — *Graptemys ernsti* is apparently the most abundant turtle of the Escambia and Yellow rivers, outnumbering *Pseudemys concinna* at least 12:1 (Shealy, 1976; Godwin, 2000; Aresco, *pers. obs.*). Softshell turtles (*Apalone spinifera* and *A. mutica*) may be nearly as abundant as *G. ernsti* in some areas. Using a combination of basking and underwater collecting surveys in a 500 m section of the Conecuh River in southern Alabama, Shealy (1976) estimated a population density of one *G. ernsti* per 3–4 m of river length. Godwin (2000) observed an overall average basking density of 17.5 individuals per river km in a survey of *G. ernsti* in southern Alabama (including stretches of the Conecuh River, Yellow River, Sepulga River, and Patsaliga Creek). In late August 1999, we observed 97 basking *G. ernsti* in 19.3 river km of the Escambia River in Florida, between Molino Crossing and FL Hwy 184 (approximately 5 per km). Both sexes and various size classes were seen,

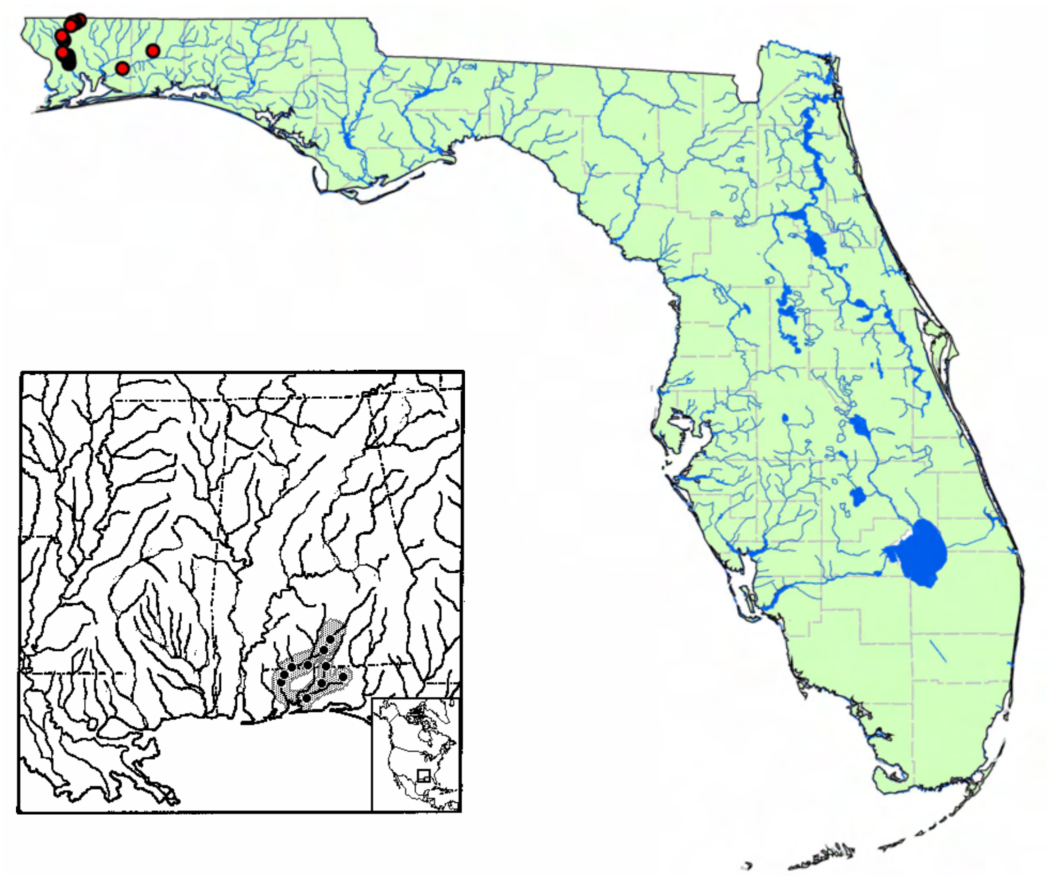

Figure 19-6. Available distribution records for the Escambia map turtle, *Graptemys ernsti*, in Florida. Inset: distribution records from entire range of *G. ernsti* (adapted from Iverson, 1992; distribution in inset map not current for Florida as presented here).

including several very small individuals, many adult males and subadult females, and 10 large adult females. Shealy (1976) reported that large adults were more abundant than juveniles in his study population. Godwin (2000) observed more adult females than males and juveniles.

INTERSPECIFIC INTERACTIONS

Diet and Feeding. — Small juveniles of both sexes and adult males are primarily insectivorous, whereas adult and subadult females feed almost exclusively on freshwater mussels and snails (Shealy, 1976). Adult females have enlarged heads with broad jaws and broad alveolar surfaces, obvious adaptations for crushing freshwater mussels. The most common mollusc in both the Escambia and Yellow rivers is the Asiatic clam, *Corbicula fluminea*, which was introduced to the area in the mid-1960s (McMahon, 1982). *Corbicula* is the primary prey of female *G. ernsti* (Shealy, 1976). The originally diverse native mussel fauna in the Escambia and Yellow rivers has declined greatly during the last several decades, probably due to changes in water quality (Fuller, 1974; National Biological Service, 1995; W. Heard, *pers. comm.*). The introduction of the Asiatic clam may have benefited *G. ernsti* by providing a replacement food source for native mussels.

Predation. — Nest mortality rates vary among reproductive seasons and locations but may exceed 95%, primarily due to predation by fish crows (*Corvus ossifragus*) and raccoons (*Procyon lotor*). Predation of hatchlings has not been directly observed but potential predators may include gar (*Lepisosteus* spp.), great blue herons (*Ardea herodias*), and alligator snapping turtles (*Macrochelys temminckii*). Although large adults probably have few natural predators, Shealy (1976) suggested that alligator snapping turtles may attack map turtles and observed many individuals that were missing portions of rear legs, tail, and/or carapace. Adult females are probably most vulnerable to predation while nesting and may occasionally be killed by raccoons or bobcats (*Lynx rufus*) (Shealy, 1976).

THREATS

Documented Threats. — *Graptemys ernsti* faces several documented and potential threats to its survival and population viability. Shealy (1976) reported that some residents along the Conecuh River in Alabama shot basking turtles for "sport" and he observed injuries caused by bullet wounds in several *G. ernsti*. The extent of this practice in Florida and the potential effect on *G. ernsti* populations is unknown. An additional documented problem is the unregulated use of recreational all-terrain vehicles (ATVs) on some large sandy riverbanks used as preferred nesting sites by *G. ernsti* (Aresco, *pers. obs*.). This practice may directly destroy eggs and kill hatchlings and also creates deep tire ruts that usually run parallel to the shoreline making it difficult for hatchlings to reach the water.

Potential Threats. — An important potential threat is the contamination of water and sediments by several pollution sources on the Conecuh and Escambia rivers in Alabama and Florida. These sources include a paper mill near Brewton, Alabama, approximately 80 km north of Escambia Bay, the Chumuckla (Florida) Waste Water Treatment facility, and a manufacturing facility approximately 11 km north of Escambia Bay. Water quality is also impacted by organic and chemical contaminants from agricultural runoff (M. Lewis, EPA, *pers. comm*.). Toxins produced by these sources, (such as polynuclear aromatic hydrocarbons [PAHs], polycyclic biphenyls [PCBs], metals [e.g., copper, aluminum, mercury], organochlorine pesticides, organic wastes and nutrients) might indirectly affect *G. ernsti* by reducing populations of freshwater mussels (Lewis et al., 1998). In addition, dioxins are documented to affect sex steroid hormone levels in *Graptemys*, reducing female fecundity and male viability in *G. flavimaculata* (Mendonça et al., 1996). Although the EPA regulates industrial sources, the potential for harmful toxic spills exists. For example, a severe dioxin release from a paper mill on the Pascagoula River in Mississippi caused the disappearance of a *G. flavimaculata* population within ca. 20 river km downstream of the spill (Jones, 1992). An accidental spill of 5 barrels of crude oil from an oil field occurred in 1997 along a tributary of the Conecuh River between Brewton and Flomaton, Alabama, and covered an area of ca. 13 km on the Little Escambia River. The effects of this spill on *G. ernsti* populations are unknown. Although *G. ernsti* appears to be abundant within its restricted range, a single catastrophic event could decimate a significant portion of the population. In addition, toxins that persist in the environment may cause diseases that result in tumors, shell lesions, lethargy, and emaciation that could lead to death in severe cases (Dodd, 1988; Lovich et al., 1996).

All species of map turtles are highly sought after by collectors, especially in Europe (Federal Register, 2000). The number of *G. ernsti* (if any) taken for the pet trade is unknown. However, the removal of just a few dozen adults could affect population stability.

Although the Escambia and Yellow rivers are not currently used for barge traffic, any future snag removal and stream channelization projects for large vessels would be detrimental to *G. ernsti* populations by reducing important basking sites and submerged overwintering shelters (Lindeman, 1999b). For the same reasons, the removal of old sunken logs by salvage loggers, which has occurred in other areas in Florida, should not be allowed in these rivers.

River impoundment projects would undoubtedly be detrimental to populations of *G. ernsti*. Dodd (1990) reported that dams in the Warrior River basin in Alabama have contributed to habitat fragmentation and decline of the flattened musk turtle (*Sternotherus depressus*). There is a current proposal by the County Water Conservation Committee in Okaloosa County to build a hydroelectric dam on the Yellow River and create a large reservoir. This project would severely alter natural water depth and velocity both above and below the proposed dam. Artificial fluctuations in water level downstream from an impoundment could affect the nesting ecology of riverine turtles (e.g., *Pseudemys*, *Graptemys*, *Apalone*). Nest inundation may significantly decrease nest success by drowning embryos or by physical destruction of the nest. In species with temperature-dependent sex determination, a reduction of potential nest sites (e.g. loss of unshaded sand bars) could create an unnatural male- or female-biased hatchling sex ratio. Bank erosion may prevent access to potential nest sites and force females to select sites that have a poor probability for nest success. In addition, reduced flow and increased siltation associated with dams could severely reduce the abundance of molluscs, the primary dietary source of *G. ernsti*. Dams also fragment populations of riverine species and may result in a loss of genetic viability and heterozygosity in small fragmented populations (Dodd, 1990).

STATUS

Escambia map turtles are restricted to a single drainage system and are therefore classified as "Rare" by the FCREPA (Shealy, 1992). Because there is no evidence at present that *G. ernsti* is in decline, we consider this to be the correct status for this species at this time. However, this species should be closely monitored for any future changes in population status and/or demographic structure. All *Graptemys* spp. were recently listed on CITES Appendix III by the United States.

CONSERVATION OPTIONS AND SOLUTIONS

The Florida Fish and Wildlife Conservation Commission (FFWCC) currently allows a possession limit of two *G. ernsti* per individual for personal use and requires no license or permit to take these turtles. Commercial use, including collection for the pet trade, buying, or selling of Escambia map turtles is prohibited. We believe that current regulations do not adequately take into account the population dynamics and demographic structure of this species (i.e., low recruitment, 14 yrs for females to mature) and will fail to protect populations of *G. ernsti* if many collectors remove legal limits. At a minimum, harvest of large subadult and adult females should be forbidden under any circumstances and a FFWCC permit should be required for collection of all other individuals. Outlawing the use of basking traps to capture turtles would provide additional protection for *G. ernsti*. Baseline data are needed for both the Escambia and Yellow River populations in support of long-term monitoring which can document changes in these populations and thus properly manage them.

Discharge of firearms over waterways and the shooting of basking turtles should be treated as a criminal wildlife violation and individuals should be prosecuted. The use of ATVs in nesting areas should be restricted during the nesting and hatching seasons (May–September).

Water quality, especially in the Escambia River, should be closely monitored and USEPA and Florida DEP regulation of pollution sources should be strictly enforced. Greater restrictions on both industrial discharge and agricultural runoff should be promulgated and supported. In addition, contingency plans for the rapid and effective cleanup of toxic spills should be in place to safeguard the Escambia River ecosystem. Possible future projects for river navigation or hydroelectric power, such as impoundments, dredging, snag removal, and channelization, would undoubtedly have negative effects on *G. ernsti* and riverine diversity in general, and should be carefully planned or denied permits.

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LITERATURE CITED

Baur, G. 1893. Two new species of North American Testudinata. Amer. Nat. 27:675-677.

Cagle, F. R. 1952. The status of the turtles *Graptemys pulchra* Baur and *Graptemys barbouri* Carr and Marchand, with notes on their natural history. Copeia 1952:223-234.

Dodd, C. K. 1988. Disease and population declines in the flattened musk turtle *Sternotherus depressus*. American Midland Naturalist 119:394-401.

Dodd, C. K. 1990. Effects of habitat fragmentation on a stream-dwelling species, the flattened musk turtle *Sternotherus depressus*. Biological Conservation 54:33-45.

Federal Register. 2000. Proposed rule: Notice of intent to include several native U.S. species in Appendix III to the Convention on International Trade in Endangered Species of Wild Fauna and Flora. 50 CFR Part 23, 65(17):4217-4221.

Fuller, S. L. H. 1974. Clams and mussels (Mollusca: Bivalvia). In: Hart, C.W. Jr., and Fuller, S.L.H. (Eds.). Pollution ecology of freshwater invertebrates. Academic Press, New York, pp. 215-273.

Godwin, J. 2000. Escambia map turtle (*Graptemys ernsti*) status survey. Report to the Alabama Natural Heritage Program, Montgomery, Alabama.

Iverson, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately printed, 363 pp.

Jones, R. L. 1992. Technical draft: yellow-blotched map turtle (*Graptemys flavimaculata*) recovery plan. U.S. Fish and Wildlife Service, Jackson, Mississippi.

Lamb, T., Lydeard, C., Walker, R.B., and Gibbons, J. W. 1994. Molecular systematics of map turtles (*Graptemys*): a comparison of mitochondrial restriction site versus sequence data. Systematic Biology 43:543-559.

Lewis, M. A., Weber, D. E., and Stanley, R. S. 1998. Comparative animal and plant toxicities of 10 treated effluents discharged to near-coastal areas of the Gulf of Mexico. Water Environmental Research 70:1108-1117.

Lindeman, P. V. 1999a. Growth curves for *Graptemys*, with a comparison to other emydid turtles. American Midland Naturalist 142:141-151.

Lindeman, P. V. 1999b. Surveys of basking map turtles *Graptemys* spp. in three river drainages and the importance of deadwood abundance. Biological Conservation 88:33-42.

Lovich, J. E., and McCoy, C. J. 1992. Review of the *Graptemys pulchra* group (Reptilia, Testudines, Emydidae), with descriptions of two new species. Annals of the Carnegie Museum 61:293-315.

Lovich, J. E., and McCoy, C. J. 1994. *Graptemys ernsti*. Catalogue of American Amphibians and Reptiles 585:1-2.

Lovich, J. E., Gotte, S. W., Ernst, C. H., Harshbarger, J.C., Laemmerzahl, A. F., and Gibbons, J. W. 1996. Prevalance and histopathology of shell disease in turtles from Lake Blackshear, Georgia. Journal of Wildlife Diseases 32:259-265.

McMahon, R. F. 1982. The occurrence and spread of the introduced Asiatic freshwater clam, *Corbicula fluminea* (Müller), in North America: 1924-1982. The Nautilus 96:134-141.

Mendonça, M., Shelby, J., Horne, B., and Seigel, R. 1996. Plasma sex steriods in yellow-blotched map turtles, *Graptemys flavimaculata*, from a dioxin-impacted river. American Zoologist 36:127A.

Mount, R. H. 1975. The reptiles and amphibians of Alabama. Auburn University Agricultural Experiment Station, Auburn, Alabama.

National Biological Service. 1995. Freshwater mussel museum records for the Escambia, Blackwater, Yellow, and Choctawhatchee Rivers in Alabama and Florida. Progress Report. National Biological Survey, Southeastern Biological Sciences Center, Gainesville, Florida.

Shealy, R. M. 1976. The natural history of the Alabama map turtle, *Graptemys pulchra* Baur, in Alabama. Bulletin of the Florida State Museum Biological Sciences 21:47-111.

Shealy, R. M. 1992. Alabama map turtle. In: Moler, P. E. (Ed.). Rare and endangered biota of Florida. Vol. III, amphibians and reptiles. University Press of Florida, Gainesville, pp. 200-203.

Stephens, P. R., and Wiens, J. J. 2003. Ecological diversification and phylogeny of freshwater turtles. Biological Journal of the Linnean Society 79:577-610.

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Malaclemys terrapin – Diamondback Terrapin

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Summary. – **The diamondback terrapin, *Malaclemys terrapin*, is found in brackish, salt marsh, and mangrove habitats along the coast of Florida. Seven subspecies have historically been recognized range-wide; five occur within Florida, and three of these are considered to be endemic. Although terrapins occur in 16 states along the Atlantic and Gulf coasts, the coastline of Florida represents approximately 20% of their entire range. Therefore, Florida terrapin populations and habitats are critical to the conservation of the entire species. Despite the importance of Florida to diamondback terrapin biology, little is known concerning this species over long stretches of Florida coastline. Severely depleted by commercial harvest for food a century ago, terrapins are currently threatened by drowning in crab pots, development of shoreline habitats and nesting beaches, predation of nests and adults, boat strikes, and road mortality.**

Conservation Status. – **FNAI Global - G4 (Apparently Secure), State - S4 (Apparently Secure); ESA Federal - Not Listed; State - Not Listed; CITES - Not Listed; IUCN Red List - NT (Near Threatened).**

Species Recognition. — The diamondback terrapin, *Malaclemys terrapin*, is distinguished from all other turtles by its distinctive coloration and shell and soft tissue markings. Seven subspecies have historically been recognized range-wide; five occur within Florida, and three of these are considered to be endemic. Even within each of the subspecies there is considerable variation in coloration and markings. Generally the carapace is oblong with a mid-dorsal keel, and dorsal scutes that exhibit very obvious concentric growth rings in young individuals. Size of females range-wide may be up to about 238 mm carapace length (CL) and males up to about 140 mm CL (Ernst et al., 1994). Carapace color ranges from light gray to a rich brown to black (Figs. 20-1, 20-2, 20-3). Lighter individuals often have dark concentric rings on dorsal and marginal scutes. Plastron color varies from cream to yellow/orange to black with some having a wood-grain appearance (Fig. 20-4). Plastral scutes may also show growth rings. Scute seams are sometimes outlined in black or speckled. Skin is usually light gray to bluish, and has dark spots. The light-colored upper jaw often has a dark “mustache,” and frequently a light or dark blaze occurs dorsally on the head between the eyes (Ernst et al., 1994). Hatchlings are lighter in color than adults. They frequently have exaggerated tubercles in the vertebral scutes (Fig. 20-5).

Sexual dimorphism exists; males are considerably smaller than females (Fig. 20-6), they have proportionally smaller heads than females, and their tails are wider and longer than those of females with the vent posterior to the edge of the carapace when the tail is fully extended (Ernst et al., 1994). The five terrapin subspecies that occur in Florida are described below.

Malaclemys terrapin centrata – Carolina Diamondback Terrapin. — This subspecies occurs from the Georgia border south to Volusia Co.. All physical and color varieties described above are present within this subspecies. The carapace edges are nearly parallel (Fig. 20-4), and the vertebral keel is often pronounced, but never knobbed. The posterior marginals flare upward. Most males have a black carapace, dark skin, and heavily marked plastron (Butler, unpubl. data). Mean carapace length (CL) for females is 177.3 mm (*n* = 378), and for males 117.6 mm (*n* = 42) (Butler, 2002). The head of a typical adult female is shown in Fig. 20-7.

Malaclemys terrapin tequesta – Florida East Coast Terrapin. — This subspecies was first described by Schwartz (1955) and occurs from Volusia Co. south to Miami (Miami-Dade Co.) and perhaps the upper Keys (Monroe Co.). It is likely the plainest of all recognized subspecies. The carapace is dark, with little trace of concentric light circles (Fig. 20-8). The head is silver to gray, with various patterns of dots and short stripes. The carapace has a median keel, with knobs most pronounced in males. The plastron is yellowish, often smudged with dark blotches. Specimens of this subspecies are difficult to distinguish from those of *M. t. centrata* from north Florida (Seigel, unpubl. data). Mean CL for females is 173.2 mm (*n* = 238), and for males 123.5 mm (*n* = 35) (Seigel, unpubl. data).

Malaclemys terrapin rhizophorarum – Mangrove Diamondback Terrapin. — This subspecies was described by Fowler (1906) from a single specimen collected in the southern Keys. Wood (1992) stated that this subspecies is found only in the lower Florida Keys, south of Vaca Key (Monroe Co.). Pritchard (1979) described their range as south of Fort Myers through the Florida Keys and Marquesas, suggesting a wider distribution, and Hart (2005) captured specimens meeting this subspecies’ description, along with others more similar to *M. t. tequesta* and *M. t. macrospilota* in Big Sable Creek in the western Everglades. Johnson (1952) reported finding *M. t. rhizophorarum* on an island

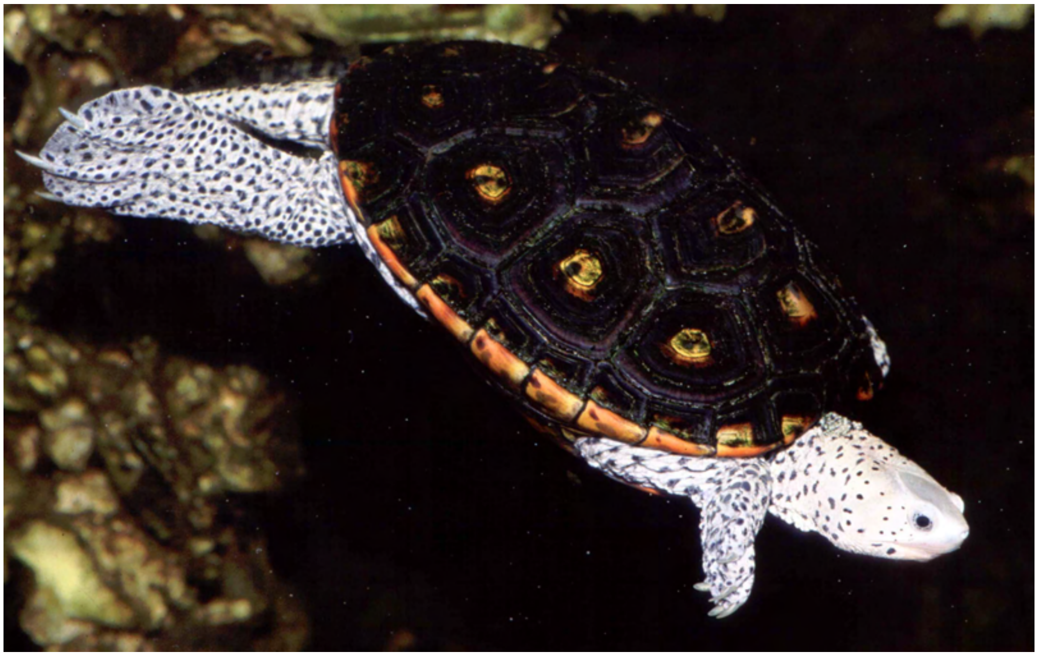

Figure 20-1. Adult male ornate diamondback terrapin, *Malaclemys terrapin macrospilota,* from Hillsborough Co., Florida. Photo by Dick Bartlett.

just south of Naples. The sides of the carapace are sometimes parallel, and this may be age and/or gender related. The carapace may be keeled, knobbed, flat or smooth, and with all the variable forms described above. Deeply ridged growth rings may be present. The carapace varies from a dark gray, to brown, to black, with individual dorsal scutes exhibiting various shades of a yellow diamond-shaped pattern (Fig. 20-3). The posterior marginals flare slightly. The plastron is orange to yellow, and black bands of varying widths border all scute seams. Skin is typically light gray, and the head has black speckles and a light dorsal blaze (Fig. 20-9) (Wood, 1981, 1992). The presence of "striped pants" noted by Wood (1981) is true for the Key West population and for Big Sable Creek in the western Everglades (K. Hart, unpubl. data) but is variable in other areas. Mean CL for females is 168.1 mm (*n* = 403), and for males 118.8 mm (*n* = 63) (Mealey, unpubl. data).

Malaclemys terrapin macrospilota – Ornate Diamondback Terrapin. — This terrapin occurs from Florida Bay (Monroe Co.) to the western part of the Florida panhandle (Walton Co.). The adult carapace is medium to dark gray, and scutes sometimes have an orange center, it may or may not have parallel sides, and the presence of a keel and knobs is variable (Figs. 20-1, 20-2, 20-5). The posterior marginals flare slightly. The plastron may be completely orange or marbled with black. Skin color varies from light to dark gray with black speckles or bars. The head blaze varies from light to dark, and therefore is not a dependable characteristic for identification. Mean CL of females is 180.6 mm (*n* = 535) and males 124.9 mm (*n* = 61) (Mealey, unpubl. data).

Malaclemys terrapin pileata – Mississippi Diamondback Terrapin. — In Florida, the Mississippi diamondback terrapin occurs only in the western-most panhandle. Florida sightings are rare, but this subspecies probably ranges from

Figure 20-2. Adult female ornate diamondback terrapin, *Malaclemys terrapin macrospilota,* from Monroe Co., Florida. Photo by Brian Mealey.

Figure 20-3. Adult female mangrove diamondback terrapin, *Malaclemys terrapin rhizophorarum,* from Monroe Co., Florida. Photo by Brian Mealey.

Figure 20-4. Plastral view of adult Carolina diamondback terrapin, *Malaclemys terrapin centrata,* from Duval County, Florida. Photo by Dick Bartlett.

Figure 20-5. Hatchling ornate diamondback terrapin, *Malaclemys terrapin macrospilota,* from Lee Co., Florida. Photo by Dick Bartlett.

the western Choctawhatchee Bay (Okaloosa Co.) on west through Louisiana. The sides of the carapace are usually parallel, but sometimes there is a modest posterior flare (T. Mann, *pers. comm*.). Marginals are always strongly upturned around the entire rim of the carapace. The knob on the fourth vertebral scute is enlarged, although this may be worn down in older females. Often one or more vertebral scutes are split along the midline. Female carapace color varies from black to yellowish brown, and even yellow carapaces occur. The upturned marginals may be yellow, orange, red, or even black. Occasionally females exhibit a light spot in the center of each costal scute, a characteristic not seen in males. Typical male carapace color is black with orange upturned marginals.

Plastron colors described above are present, although often scutes have a dark base color with lighter, colorful edges. Dots on the skin are sometimes elongated giving a barred or striped appearance. Most members of this subspecies exhibit both the "mustache" and dark blaze on top the head. In Mississippi, the mean CL for females is 168.0 mm (*n* = 34), and for males 121.4 mm (*n* = 49) (T. Mann, unpubl. data).

Taxonomic History. — The genus *Malaclemys* has a complex taxonomic history (see reviews in Dobie, 1981; Bickham et al., 1996; Lamb and Osentoski, 1997). The main issue has been the relationship of *Malaclemys* to the map turtles (*Graptemys*). Although these two genera are closely related (Dobie, 1981), their status has been hotly debated with several authors considering them congeneric (see reviews by Wood, 1977; Dobie, 1981). The most recent morphological and molecular data have established that *Malaclemys* and *Graptemys* are distinct, monophyletic clades (Dobie, 1981; Lamb and Osentoski, 1997; Stephens and Wiens, 2003).

Although the generic relationships of *Malaclemys* appear to be settled, taxonomic treatment of the single highly variable species within it remains problematic. Seven subspecies of *Malaclemys* are currently recognized. The only other North American turtle with such a high number of

Figure 20-6. Adult male (above) and adult female (below) ornate diamondback terrapin, *Malaclemys terrapin macrospilota*, from Monroe Co., Florida, showing sexual size dimorphism typical of the species. Photo by Brian Mealey.

Figure 20-7. Adult female Carolina diamondback terrapin, *Malaclemys terrapin centrata*, from nesting beach in Duval Co., Florida. Photo by Carla Van Ness.

Figure 20-8. Adult female Florida east coast diamondback terrapin, *Malaclemys terrapin tequesta,* from Martin Co., Florida. Photo by Dick Bartlett.

subspecies is *Apalone spinifera*. However, the validity of the seven subspecies of *Malaclemys* is questionable. In addition to the inherent problems with defining subspecies in a phylogenetic context (see review by Frost and Hillis, 1990), many of the morphological characters defining subspecies of diamondback terrapins are either poorly defined or clinal (Ernst et al., 1994; Seigel, unpubl. data). Molecular studies (Lamb and Avise, 1992; Lamb and Osentoski 1997; Hart, 2005) do not corroborate the existence of these subspecies.

Clearly, the molecular genetics of *Malaclemys* offer an invaluable source of additional data for this and other problems. The underlying genetic structure of animal populations is extremely valuable, if not critical, to the development of sound management plans (Avise, 1994, 1995, 1996; Moritz, 1994). Two recent studies of *Malaclemys* population genetics illustrate the potential of molecular ecology to elucidate biological parameters of interest to conservation biology. Hauswaldt and Glenn (2005) and Hart (2005) have both used nuclear microsatellite markers to study population structure in this species. Both studies attempted to detect genetic structure (differentiation) on a local, regional, and range-wide scale. Hauswaldt and Glenn (2003) used eight microsatellite loci to study variation among 320 individuals collected from nine sites in seven states from New York to Texas (one Florida site), whereas Hart (2005) used 12 different microsatellite loci to study variation among 1409 individuals collected from 31 sites in 10 states from Massachusetts to Texas (four Florida sites). Both studies detected a high degree of variation on a range-wide scale and moderate variation on a regional scale. Only the Hart (2005) study was able to detect a small amount of local variation, but the two studies agree that there was less differentiation on a local scale than that suggested by the site fidelity observed in mark and recapture studies. The Hart (2005) study was able to detect a male bias in gene flow, suggesting that it is the movement of males that is largely responsible for gene flow. This is disconcerting because males appear to be impacted more severely than females by crab traps (see below). Neither study supported the existence of the seven currently recognized subspecies, but Hart (2005) advocated recognition of at least six genetically distinct metapopulations or “management units” that do not coincide with subspecies boundaries. Additional molecular genetic data are being compiled currently from populations of *M. t. rhizophorarum* (lower Florida Keys) and *M. t. macrospilota* (Florida Bay) within Everglades National Park (M. Forstner, *pers. comm.*).

Figure 20-9. Adult female mangrove diamondback terrapin, *Malaclemys terrapin rhizophorarum,* from Monroe Co., Florida. Photo by Dick Bartlett.

DISTRIBUTION

Geographic Distribution. — Diamondback terrapins occur in coastal brackish waters from Massachusetts, south along the Atlantic Coast, around the Florida peninsula, and west across the Gulf of Mexico to the vicinity of Corpus Christi, Texas (Ernst et al., 1994). Only two of the seven named subspecies have ranges entirely outside Florida. The northern diamondback terrapin, *M. t. terrapin*, ranges from Cape Cod south to Cape Hatteras, North Carolina. The Texas diamondback terrapin, *M. t. littoralis,* is found from western Louisiana to Corpus Christi Bay. Five subspecies of diamondback terrapins are known from the coast of Florida (Fig. 20-10); their distributions are presented above.

Despite the importance of Florida to diamondback terrapin distribution and biology, little is known concerning this species over long stretches of Florida coastline. Several earlier biologists noted anatomic differences in terrapins from various Florida locales (Fowler, 1906; Carr, 1946; Johnson, 1952; Schwartz, 1955); but the first long-term ecological studies of terrapins in the state did not begin until the 1970s. On Merritt Island on the central Atlantic coast, terrapin courtship and mating were described along with nesting behavior, nest and adult predation, population estimates for two rivers, and barnacle fouling (Seigel, 1980a, b, c, 1983, 1984). Unfortunately these populations have experienced major declines since the original work was performed (Seigel, 1993). In the early 1980s in the Florida Keys and Florida Bay, Wood (1981, 1992) captured and marked

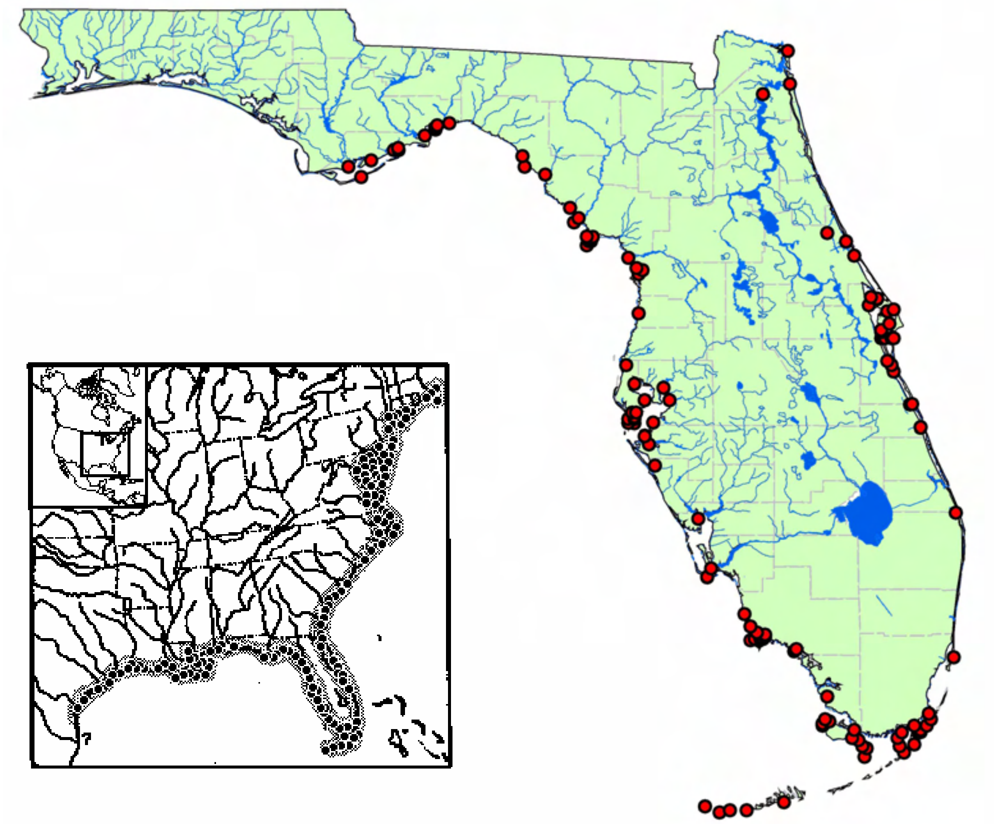

Figure 20-10. Available distribution records for the diamondback terrapin, *Malaclemys terrapin,* from Florida. Inset: distribution records from entire range of *M. terrapin* (adapted from Iverson, 1992; distribution not current for Florida as presented here).

over 300 terrapins and has revisited these populations periodically since then (R. Wood, *pers. comm.*). Baldwin et al. (2005) expanded the studies of those populations and added other sites in that area. They compiled some demographics, analyzed terrapin movements with radio telemetry, examined population genetic structure, and assessed the effects of hurricanes on terrapin dispersal. On the northeastern coastline of Florida, a variety of capture techniques were tested, nesting biology was assessed, seasonal movements were evaluated with radiotelemetry, and dietary preferences were recorded (Butler, 2000, 2002; Butler et al., 2004). Most recently, Hart (2005) studied terrapins in Big Sable Creek in Everglades National Park and estimated adult survivorship, capture probability, and local abundance. Other than Hart's work and some recent marking studies (C.S. Boykin, *pers. comm.*), information concerning terrapins along the entire Gulf Coast of Florida is limited to anecdotal accounts and several museum specimens. This is also true of the long expanses of Atlantic coastline lying between the study sites mentioned above.

Ecological Distribution. — Terrapins rarely stray from brackish water habitats. They are found in tidal creeks, coastal salt marshes, estuaries, lagoons, and mangrove islands. In northeastern Florida and along the northern Gulf Coast terrapins are most frequently sighted in tidal creeks and *Spartina* marshes, but they are known to travel up to nearly 10 km within estuarine river systems to reach their dry nesting areas (Butler, 2002). In eastern Florida, terrapins seem to prefer sheltered sites away from wave action and winds, although observations in more open waters are not rare (Seigel, unpubl. data). In southern Florida, terrapins often use mangrove root systems for cover (Wood, 1981; Mealey, unpubl. data) and shallow lagoons within small islands, where they often bury in the mud (Dunson and Mazzotti, 1989). On the southern Gulf Coast of Florida, within Everglades National Park, Hart (2005) captured most terrapins near submerged algal-covered logs at the upper reaches of tidal creeks during low tide.

Tides have a strong effect on habitat utilization; Tucker et al. (1995) found that female terrapins enter salt marshes on the rising tide for foraging then concentrate in tidal creeks during ebb tide. Roosenburg et al. (1999) showed that adult female terrapins remain in deeper water and farther from shore than adult males or juveniles of either sex.

HABITAT RELATIONS

Activity. — Hibernation and aestivation in terrapins is poorly known. The only detailed study was done by Yearicks et al. (1981) in New Jersey. Terrapins there hibernated in small tidal creeks, usually alone or in small groups, and remained dormant all winter. Lawler and Musick (1972) found a single juvenile hibernating in moist sand in Virginia.

In east central Florida, Seigel (1980b, 1984) was unable to locate active terrapins during December to mid-February, but observed large mating aggregations in March and early April. Specific hibernation sites were not identified. Telemetry studies of *M. t. centrata* in northeastern Florida suggest that they are relatively inactive from late November through February (Butler, 2002). One turtle followed during that time period remained buried in 3–5 cm of mud, but moved slightly. In the southwestern Everglades, Hart (2005) found terrapins active during winter months.

Terrapins on the east side of Florida Bay display some remarkable adaptations to the south Florida dry season. As water recedes from flooded islands, the terrapins dig headfirst vertically into the mud. Once submerged at 8–20 cm, they reorient their bodies so that they are parallel with the surface and then create a surface-breathing hole. As the water continues to recede and the mud hardens, the terrapins lie motionless until the inner parts of the islands flood once again (G. Parks, *pers. comm*.).

Osmotic Regulation. — The terrapin is the only North American turtle that lives exclusively in brackish water, and they have behavioral and physiological adaptations for osmoregulation in fluctuating salinities (Dunson, 1970; Dunson and Mazzotti, 1989). Terrapins can control salt intake by varying their drinking patterns as salinity changes. Under experimental conditions, they did not drink at all in high salinity medium, but drank large amounts when salinity was closer to 0% (Robinson and Dunson, 1976). After confinement to seawater for seven days terrapins given fresh water drank freely from surface film (from simulated rainfall) and even from puddles formed on their own body surfaces (Davenport and Macedo, 1990).

A physiological mechanism for maintaining osmotic balance in terrapins is the alteration of tissue and blood ion concentrations in response to varying salinity (Gilles-Baillien, 1973a, b). Terrapins in seawater increase their blood ion concentrations of sodium, chloride, and particularly urea. This hypertonicity helps prevent water loss to the saltier environment (Cowan, 1981a). A lacrimal gland secretes sodium in response to increasing environmental salinities at rates dependent on acclimation (Dunson, 1970; Cowan, 1981b). The importance of the osmotic contribution of the lacrimal gland has been questioned. Although the lacrimal secretes sodium at higher concentrations than seawater, its output volume is low (Cowan, 1990). Hatchlings reared in 50% seawater exhibit impaired growth when compared to those raised in 25% seawater. Also, there is an inverse relation between body size and water loss in hatchling terrapins raised in 100% seawater. Both of these factors are likely to influence habitat preferences of hatchlings (Dunson, 1985).

GROWTH AND REPRODUCTION

Size at Maturity. — Female Florida east coast terrapins reach sexual maturity at a PL of 135 mm or 4–5 yrs of age (Seigel, 1984). This is similar to sizes reported for female northern terrapins (132 mm, Montevecchi and Burger, 1975) and Carolina terrapins (138 mm, Lovich and Gibbons, 1990; Gibbons et al., 2001). Females in the Carolinas take 7 yrs to reach maturity (Hildebrand, 1932; Lovich and Gibbons, 1990), presumably due to the shorter growing season. In Maryland females take from 8–13 yrs to mature at a PL of 175 mm (Roosenburg, 1991a). The Mississippi diamondback terrapin may also require more time and mature at a larger size (Cagle, 1952; Mann, 1995).

Males mature at PL's from 90–100 mm at ages from 2 to 7 yrs throughout their range (Cagle, 1952; Lovich and Gibbons, 1990; Roosenburg, 1991a; Gibbons et al., 2001). The Florida east coast terrapin does so at 95 mm at age 2–3 yrs (Seigel, 1984).

Longevity. — Hildebrand (1932) referred to individuals and groups of terrapins that survived in captivity up to 22 yrs (still living at the time he was writing), and suggested a captive life span of over 40 yrs. Seigel (1984) estimated that the largest female he studied in the wild to be about 15 yrs old and suggested a longevity of 20 yrs in his study population (Brevard Co., Florida). Mangrove terrapins marked as adults in the early 1980s were recaptured in 1999 suggesting a life span in excess of 20 yrs (R. Wood and B. Mealey, unpubl. data).

Courtship and Mating. — In central Florida terrapins aggregate in groups of up to 75 individuals in canals and lagoons from late March through April, and courtship and mating occur during daylight hours (Seigel, 1980c). As the female floats on the surface the male approaches from the rear and nudges her cloacal region with his snout. If she is receptive the male mounts her in the water, and copulation lasts several minutes (Seigel, 1980c).

Nesting Season. — In northeastern Florida *M. t. centrata* nests from late April through the end of July (Butler et al., 2004). Seigel (1980b) found gravid Florida east coast terrapins from 28 April through 1 July in Brevard Co.. In south Florida nesting by *M. t. macrospilota* and *M. t. rhizophorarum* begins by mid-May (Mealey, unpubl. data). Nesting seasons in the extreme northern range are restricted to June and July (Burger and Montevecchi, 1975; Lazell and Auger, 1981; Goodwin, 1994).

Nest Sites. — Palmer and Cordes (1988) reviewed nesting requirements of terrapins. Terrapins nest on dunes, beaches, sandy edges of marshes, islands, and dike roads (Burger and Montevecchi, 1975; Seigel, 1980b; Dunson, 1985; Roosenburg, 1994). The common denominator of all these habitats is sandy soil which does not clog eggshell pores, thus allowing sufficient gas exchange between the developing embryo and the environment (Roosenburg, 1994). Nest sites are usually flat with a mean slope < 7º, a characteristic that facilitates postures assumed by turtles during digging and egg deposition (Burger and Montevecchi, 1975; Goodwin, 1994). Areas with < 25% shrub canopy cover are optimum for nesting, as more wooded areas provide better habitat for nest predators (Burger and Montevecchi, 1975; Seigel, 1980b; Goodwin, 1994). Generally, terrapins tend to nest in areas where grass cover is 5–25%. This choice may represent a balance between the effects of two types of predation. Avian predation on nests in New Jersey was highest in open, less grassy areas (Montevecchi and Burger, 1975; Burger, 1977). Conversely, some eggs laid in more vegetated areas risk destruction by plant roots (Lazell and

Auger, 1981; Roosenburg, 1992; Butler et al., 2004). Also, nest construction in dense grass can be difficult because plants and roots hinder digging (Goodwin, 1994).

Nesting Behavior. — Terrapins sometimes travel relatively long distances from feeding areas to reach preferred nesting beaches. Using radiotelemetry, Butler (2002) found that Carolina terrapins in northeastern Florida moved between 6.28 and 10.4 km from the nesting beach where they were captured, moving to marshes where they spent the rest of the year. In Delaware a terrapin was found nesting 8 km from where she was first captured (Hurd et al., 1979).

Aggregations of two or more females were recorded offshore of nesting beaches throughout the nesting season in Maryland (Roosenburg, 1993). The author suggested that such groups may be instrumental in locating appropriate beaches, specific habitats on those beaches, or at pinpointing terrestrial predators.

In a northeastern Florida study, 66% of all diurnal captures of Carolina diamondback terrapins on the nesting beach occurred within two hours before and one hour after high tide (J. Butler and G. Heinrich, unpubl. data). Similar findings have been reported for northern populations (Burger and Montevecchi, 1975; Auger and Gioviannone, 1979; Goodwin, 1994). A lack of synchrony between nesting and tidal fluctuations in Maryland was credited to meager tidal changes in the area (Roosenburg, 1992). Nesting at high tide reduces the distance traveled by females from the water to the actual nesting sites (Burger and Montevecchi, 1975). This conserves energy, reduces exposure to terrestrial predators, and facilitates nest placement above the high tide line.

Diurnal nesting is the rule for most terrapin populations (Burger and Montevecchi, 1975; Seigel, 1980b; Goodwin, 1994). Roosenburg (1992) found nocturnal nesting to be rare in Maryland, but on Cape Cod 45% of nesting occurred at night (Auger and Giovannone, 1979). During a seven-day period in May 1997, with equal effort during day and night, 20% of Carolina terrapins captured on a nesting beach in northeastern Florida were found at night (J. Butler and G. Heinrich, unpubl. data).

Florida east coast terrapins nested at ambient temperatures from 28–36ºC, and they preferred sunny to overcast days (Seigel, 1980b). Terrapins have not been found to nest on rainy days, but on sunny days following rains the number nesting may be higher than on days not preceded by rain (Burger and Montevecchi, 1975; Goodwin, 1994).

Searching for nest sites by terrapins includes sand sniffing and/or facial probing of sand (Burger, 1977; Lazell and Auger, 1981; Goodwin, 1994; Roosenburg, 1994). When a suitable site is located the female begins nest excavation with her forelimbs until she has cleared an area about 105 mm wide, 175 mm long, and 50 mm deep. She then positions herself over the area and finishes digging with her hind limbs while propped up by her forelimbs (Burger, 1977). The result is a flask-shaped hole about 150 mm deep and 73 mm wide at the bottom (Montevecchi and Burger, 1975). Nesting females are extremely wary and, if disturbed before all of the eggs are deposited, will abandon the nesting process. If the procedure is successful, she deposits her clutch of oblong pinkish eggs into the nest and uses the excavated sand to refill the hole leaving an inconspicuous "cover up" pattern at the site (Burger, 1977). The entire nesting process can occur in less than 20 min (Burger, 1977; Roosenburg, 1991b; Goodwin, 1994). The mean depth to the top of the first egg ranges from 94.1–106.5 mm, and mean depth to the bottom of the egg chamber ranges from 139.9–165.0 mm (Montevecchi and Burger, 1975; Roosenburg, 1992; Butler, 2000).

Estimated nest densities have been reported as 0.52/ha in Cape Cod (Auger and Giovannone, 1979), 11.9/ha in Rhode Island (Goodwin, 1994), and 157.1/ha in New Jersey (Burger and Montevecchi, 1975). The wide disparity likely reflects variations in population sizes and nesting area sizes. The proximity of nests to one another may be a factor in nest success as both Burger (1977) and Roosenburg (1992) found increased nest predation with higher nest densities.

Clutch Size. — Clutch size ranges from 4–22 eggs. Larger terrapins produce larger clutches (Montevecchi and Burger, 1975; Seigel, 1980b; Goodwin, 1994). The northern subspecies has the highest mean clutch sizes of 12.9 in Maryland (Roosenburg and Dunham, 1997) and 15.8 in Rhode Island (Goodwin, 1994), while those of the Florida east coast terrapin and the Carolina terrapin in northeastern Florida are both 6.7 (Seigel, 1980b; Butler, 2000). Four gravid ornate terrapins captured and x-rayed on 23 June had a mean clutch size of 5.75 eggs, and one mangrove terrapin nest discovered in late May 1998 had 4 eggs (Mealey, unpubl. data). Several turtle species exhibit decreasing clutch sizes in southern parts of their ranges (Tinkle, 1961; Powell, 1967; Christiansen and Moll, 1973; Moll, 1973), and terrapins may be another example (Seigel, 1980b; Goodwin, 1994). However, a clear trend in this direction is obscured, because clutch size in New Jersey (9.2) (Burger, 1977) is lower than that for Maryland (12.9) (Roosenburg and Dunham, 1997).

Eggs. — Eggs are somewhat elongated and symmetrical with fairly blunt ends. When first deposited they are translucent and pink, but within 24–48 hrs formation of embryonic membranes changes them to opaque white (Butler, unpubl. data). Within a population of northern terrapins it was found that mean egg lengths and widths vary more between clutches than within them. Also, while clutch size correlates positively with clutch mass, it does not relate to any measure of egg size. Consequently, when clutch sizes of individuals increase, egg size does not decrease, and vice versa (Montevecchi and Burger, 1975). Similarly, Roosenburg and Dunham (1997) found that average clutch size varied more than average egg mass in Maryland terrapin populations, and when individual females produced multiple clutches there was no consistent trade-off between clutch size and egg mass. Montevecchi and Burger (1975) found that all egg measurements decreased as the season progressed.

Mean egg dimensions fall within the following ranges: length = 31.1–39.0 mm; width = 19.7–23.9 mm; mass = 7.7–12.4 g. Northern subspecies exhibit smaller egg sizes (McCauley, 1945; Montevecchi and Burger, 1975; Goodwin, 1994) than those in the south (Burns and Williams, 1972;

Seigel, 1980b; Butler, 2000). Data for *M. t. littoralis* are lacking, but the combined trends for terrapins are that an apparent decreasing clutch size is accompanied by increasing egg size as latitude decreases. Moll (1979) described two nesting strategies exhibited by turtles. In Type I females lay large clutches of small eggs in a well-defined area and season; Type II females lay smaller clutches of large eggs at various times and areas. Temperate species usually fall into Type I and tropical species conform to Type II. Seigel (1980b) suggested that terrapins in central Florida were intermediate between the types, as they lay small clutches of large eggs, but the season and nesting areas are well defined. Terrapins in northeastern Florida are similar (Butler, 2000). Goodwin (1994) characterized terrapins in Rhode Island as Type I.

Captive terrapins in North Carolina laid up to five clutches in a season (Hildebrand, 1932). Multiple clutching has been reported from most natural terrapin populations, although the number is limited to two or three. Internesting intervals of 15 and 16 days have been observed (Roosenburg and Dunham, 1997; Goodwin, 1994), and shorter northern nesting seasons limit the number of clutches possible. Three clutches have been suggested for terrapins in central Florida and Maryland (Seigel, 1980b; Roosenburg and Dunham, 1997).

Incubation and Hatching. — Hatching occurs from early to mid-August and continues through mid-October in northern populations (Burger, 1977; Roosenburg, 1991b). In northeastern Florida *M. t. centrata* nests begin hatching in early July, continuing through early October (Butler et al., 2004). Incubation period is the time it takes for eggs to develop and hatch, while emergence period includes whatever time hatchlings spend within the nest before actually leaving it. In New Jersey the mean incubation period was 76.2 days. Once hatching commenced within a nest it took from 1 to 4 days for all eggs to hatch, and hatchlings took up to 9 days to emerge (Burger, 1977). In northeastern Florida the mean emergence period was 68.9 days with a range of 55–97 days (Butler et al., 2004). Hatchling terrapins have been reported to over-winter within the nest in some areas (Lazell, 1979; Marion, 1986).

Incubation temperature influences development time, and terrapins have been successfully hatched artificially at temperatures between 18 and 34ºC. Eggs incubated at higher temperatures within this range hatched earlier than those at lower temperatures (Dimond, 1987; Roosenburg and Kelly, 1996). Eggs incubated at constant temperatures of 35ºC or higher failed to hatch (Cunningham, 1939). In Florida, eggs of *M. t. tequesta* hatched in 60–73 days after incubation at temperatures that fluctuated between 20 and 34ºC (Seigel, 1980c). Burger (1976b) reported that nests on north-facing slopes in New Jersey registered slightly lower mean daily temperatures than those on south-facing slopes and took an average of eight days longer to hatch.

Terrapins exhibit temperature-dependent sex determination (TSD – also known as environmental sex determination [ESD]), and eggs artificially incubated at constant temperatures between 24–27ºC produced males while those at 30–32ºC produced all females (Sachsse, 1984; Ewert and Nelson, 1991; Jeyasuria et al., 1994; Roosenburg and Kelly, 1996). Although natural nests are not subject to constant incubation temperatures the fact that TSD occurs may influence nest choices by females. Roosenburg (1996) found that females most frequently chose nest sites away from shade and vegetation. He further suggested that females are able to differentiate and choose nests sites that will produce the different sexes (Roosenburg, 1996). Roosenburg and Niewiarowski (1998) reviewed these and other maternal effects on TSD. An important consideration is that growth of vegetation during the incubation period may influence nest temperature, and the effects of habitat management practices such as removal or addition of vegetation on nesting beaches need to be studied to determine if terrapin development is affected (Goodwin, 1994; Roosenburg and Place, 1994). Also, TSD may be a factor in biased sex ratios reported in some populations (Sachsse, 1984; Auger, 1989, Lovich and Gibbons, 1990; Ewert and Nelson, 1991; Morreale, 1992).

Hatchling Size. — Roosenburg and Kelly (1996) showed that terrapin egg mass is the primary factor affecting hatchling mass. Northern terrapin hatchlings have a mean carapace length (CL) near 27.5 mm and a mean mass of 6.8 g (Reid, 1955; Burger, 1977). Hatchling sizes of the southern subspecies are a bit larger: *M. t. pileata* from Louisiana has a mean CL of 29.9 mm and mean mass of 8.1 g (Burns and Williams, 1972), in Florida *M. t. tequesta* has a mean CL of 31.9 mm and mass of 8.8 g (Seigel, 1980c), and *M. t. centrata* has a mean CL of 33.9 mm and mean mass of 9.5 g (Butler et al., 2004). Larger hatchling size in southern populations is consistent with larger egg and smaller clutch sizes discussed above, and it has been suggested that larger hatchlings may be less vulnerable to some predators (Moll and Legler, 1971). It is perplexing to envision how these hatchling size differences could confer advantage against most terrapin predators, unless they somehow facilitate refuge seeking.

Hatchling Behavior. — In New Jersey 92 of 98 hatchlings emerged from their nests during the day despite the threats of diurnal predators such as gulls and crows, and all sought refuge in the closest vegetation. When tested artificially on an incline hatchlings also moved toward the closest vegetation even if that meant traveling uphill. When on an incline with no vegetation hatchlings moved downhill (Burger, 1976a). Lovich et al. (1991) showed that when artificially incubated hatchlings were released offshore from their nesting beach they all swam back to shore, proceeded up the beach, and sought refuge under tidal debris. Twelve hatchling or juvenile terrapins were discovered over a three-year period on a tidal mudflat under debris such as *Spartina* mats, rocks, and boards (Pitler, 1985). Roosenburg (1991b) reported observing numerous hatchlings seeking refuge in salt marshes adjacent to nesting beaches rather than venturing to open water. In northeastern Florida 160 of 172 (93%) hatchling crawls from nests headed in the direction of the vegetation and adjacent salt marsh rather than open water (Butler et al., 2004). This propensity to avoid open water and seek refuge in vegetation and/or marshes may account for the lack of hatchlings and juveniles when techniques designed to capture adults are used (i.e., Hurd et al., 1979; Lovich and Gibbons, 1990).

Nest Success. — Nest success can be measured by the percent of nests that hatch and/or the number of eggs that hatch from each nest (Burger, 1977). The reported percent of wild nests that hatch ranges from 3.3% in Maryland (Roosenburg, 1992) through 12.8% in Rhode Island (Goodwin, 1994), and 84% and 25% in successive years in New Jersey (Burger, 1977). In northeastern Florida 23% of 114 nests hatched in 1997, and 38% of 112 nests hatched in 2000 (Butler et al., 2004). For the same studies, the percent of eggs that hatched from successful nests was 47.7%, 85.5%, and 39% and 18% (these data not available for Florida). The most important factor in low hatching success in both categories was nest predation (Burger, 1977; Goodwin, 1994).

The greatest source of mortality for diamondback terrapins is predation at the egg stage (Roosenburg, 1990). Nest predation of the northern diamondback terrapin ranges from 24–88% (Burger, 1977; Auger and Giovannone, 1979; Roosenburg, 1992; Goodwin, 1994). Predation claimed from 82–87% of Carolina terrapin nests in northeastern Florida (Butler et al, 2004). Nests are most vulnerable to predation during the first 24–48 hrs, presumably when nesting scents are strongest (Roosenburg, 1991b; Goodwin, 1994). However, nest (and hatchling) predation increases again at the time of hatching (Burger, 1977; Auger and Giovannone, 1979; Roosenburg, 1992). The primary nest predator in all studies is the raccoon. Others of significance are foxes, otters, skunks, crows, and laughing gulls. The black rat, *Rattus rattus*, is a suspected nest predator in Florida Bay (Mealey, unpubl. data), and Norway rats (*R. norvegicus*) are confirmed predators of hatchling and juvenile terrapins in New York (Draud et al., 2005). In some areas, rhizomes from dune and marsh grasses have infiltrated nests penetrating and destroying eggs (Lazell and Auger, 1981; Stegmann et al., 1988; Roosenburg, 1992; Butler et al., 2004). Ants were responsible for some mortality as they mined calcium from terrapin eggshells in Maryland (Roosenburg, 1992). Fire ants (*Solenopsis invicta* and *Conomyrma* sp.) have been found feeding on hatchling terrapin carcasses from nests depredated by raccoons in northeastern Florida, and it is likely the ants were scavenging rather than the initial predators (Butler et al., 2004). Nematode worms and fly maggots have been found in damaged eggs or embryos, but it is likely these entered after depredation occurred (Auger and Giovannone, 1979; Roosenburg, 1992; Goodwin, 1994). Roosenburg (1992) noted that some northern terrapin nest mortality resulted from tidal inundation due to storms, and in one season 22% of Carolina terrapin nests in Florida were destroyed in this way (Butler et al., 2004). Hatchlings are sometimes preyed upon by ghost crabs (Arndt, 1991, 1994; Butler et al., 2004).

POPULATION BIOLOGY

Population Structure. — Reports of variation in sex ratios in terrapin populations have been contradictory. Seigel (1984) found a strongly female-biased sex ratio in east central Florida, even during the mating season when males should have been most concentrated. Roosenburg et al. (1997) also found a female-biased sex ratio in Maryland, but Lovich and Gibbons (1990) reported a male-biased sex ratio in South Carolina. In northeastern Florida males were trapped more frequently than females (Butler, 2002), and in Big Sable Creek the sex ratio was 1:1 (Hart, 2005). The differing ratios among these studies may be due to the variety of capture methods employed, geographic variation in population biology, and/or to incidental drowning in crab traps, which kills more males than females (Roosenburg et al., 1997).

Density and Biomass. — Estimates of population size and density for terrapins are uncommon in the literature, but some evidence suggests that terrapins (when undisturbed) may be locally abundant. For example, Roosenburg et al. (1997) estimated terrapin populations at 2778–3730 individuals at a single site in Maryland. Seigel (1984) estimated populations at 213 and 404 at two sites in east central Florida, and Hurd et al. (1979) calculated a maximum of 1655 terrapins at a Delaware site. Butler (2002) suggested a population of 3147 terrapins associated with a northeastern Florida nesting beach, and Hart (2005) estimated the Big Sable Creek population to be 1545 individuals. Density estimates ranged from 1.8 terrapins/linear meter of marsh in Delaware (Hurd et al., 1979; Ernst et al., 1994) to 53–72 terrapins/ha in central Florida (Seigel, 1984).

INTERSPECIFIC INTERACTIONS

Diet and Feeding. — Wild terrapins have been reported to feed on snails, clams, mussels, crabs, insects, fish, annelid worms, and vegetation (Coker, 1906; Cagle, 1952; Carr, 1952; Spagnoli and Marganoff, 1975; Cochran, 1978; Hurd et al., 1979; Middaugh, 1981; Bishop, 1983; Marion, 1986; Roosenburg, 1994; Tucker et al., 1995). Coker (1906) examined stomach contents of 14 freshly captured terrapins from North Carolina and found the marsh periwinkle (*Littorina irrorata*) to be the most abundant food item, followed by annelid worms, small crabs, and other snails. Cagle (1952) reported fragments of small snails and clams in intestinal contents and feces of terrapins from Louisiana, and Hurd et al. (1979) found shell fragments of the mussel, *Mytilus edulis*, in terrapin feces from Delaware. Feces of seven female ornate diamondbacks contained shell fragments of the Florida marsh clam, *Pseudocyrena floridana* (G. Parks, *pers. comm.*).

Tucker et al. (1995) did an exhaustive dietary study of Carolina terrapins near Kiawah Island, South Carolina. Analysis of nearly 2000 fecal samples revealed that 76–79% of total prey mass was periwinkles (*L. irrorata*), with several crab species, a clam, and barnacle accounting for the rest. They further suggested that terrapin dimorphism in head size could result in resource or habitat partitioning between the sexes (Tucker et al., 1995). By contrast, the Carolina terrapin in northeastern Florida over a two-year period preferred the dwarf surf clam, *Mulinia lateralis* (J. Butler and G. Heinrich, unpubl. data). This was true for small, medium and large head sizes and both sexes in both years. Adult females collected at a nesting beach had slightly more diverse diets than those collected elsewhere, and the larger head size may allow them to exploit alternative food sources when forced to travel to nesting areas where favored prey may not be available (J. Butler and G. Heinrich, unpubl. data).

Captive terrapins have been successfully reared with a variety of gastropods, bivalves, crustaceans, insects, fish, and even beef (Coker, 1906; Hildebrand, 1929; Carr, 1952; Allen and Littleford, 1955; Dunson, 1985; Roosenburg and Kelly, 1996). Allen and Littleford (1955) found that captive food preferences may change over time as tuna, salmon, and liver were taken initially, but after several weeks were refused most or all of the time. In their study shellfish and snails were preferred foods. In a feeding study using only male terrapins, Davenport et al. (1992) found that they consistently chose the smallest sizes of both snails and mussels. Further, they reported that adult males could take whole fiddler crabs, and with medium-sized blue crabs they described a behavior they called “cropping” whereby terrapins approached from the side or rear and took legs off without necessarily killing the crabs. Larger crabs (carapace width of 30–40 mm) were generally avoided by terrapins (Davenport et al., 1992).

Predation. — Most mortality and predation of this species occurs at the egg stage (Roosenburg, 1990). Survivorship of adult terrapins and turtles in general is high (Seigel, 1980a; Iverson, 1991). A raccoon attack on an adult female *M. t. tequesta* broke the turtle’s neck, severed a hindlimb, and tore the flesh in the groin region so that evisceration could be accomplished (Seigel, 1980a). The same study found numerous other freshly killed females and concluded that females are most susceptible to raccoon predation during the nesting season when they come ashore. We recorded similar predation of Carolina terrapins in northeastern Florida (Butler, unpubl. data), and this was the case for ornate terrapins on Tarpon Key in Tampa Bay (C.S. Boykin, *pers. comm.*).

Lovich and Gibbons (1990) reported missing feet on 12% of female and 8% of male terrapins in South Carolina and suggested encounters with terrestrial mammals to be the cause. About 6% of both sexes were missing feet or limbs in northeastern Florida, and others had tail, jaw, and shell damage (Butler, unpubl. data). Hart (2005) recorded an injury rate of 16% in the Big Sable Creek terrapin population. Terrapins are also prey for nesting bald eagles in Maryland (Clark, 1982) and in Florida Bay (Baldwin et al., 2005). Mann (1995) noted that the presence of alligators might account for the absence of terrapins at some potentially good Mississippi sites.

Parasites and Disease. — Little is known of diseases of terrapins in the wild. Terrapins in both the Atlantic and Gulf coasts of Florida are known to host large numbers of barnacles that may interfere with nesting and sometimes cause death (Jackson and Ross, 1971; Ross and Jackson, 1972; Jackson et al., 1973; Seigel, 1983).

The utility of routine bacteriological culture in captive management of turtles has become increasingly clear in recent years, however, the monitoring of wild populations is still in its infancy. In northeastern Florida numerous coliform bacteria including *Eschericia coli*, *Klebsiella pneumoniae*, and *Salmonella* sp. were isolated from cloacal swabs of terrapins (Harwood et al., 1999). In 45 cultures from south Florida terrapins the most prevalent bacteria were *Aeromonas hydrophila*, *Pseudomonas* sp., and *E. coli* (Mealey, unpubl. data).

THREATS

In the late 1800s and early 1900s terrapins were a gourmet food item used in turtle soup in many restaurants. Increasing demand for terrapin meat led to their artificial propagation on farms on the eastern coast of the United States (Coker, 1920). Studies of these confined terrapins produced propagation methods and increased growth rates under captive conditions (Coker, 1906; Hay, 1917; Barney, 1922; Hildebrand, 1929, 1932). Even with the farms, the popularity of this delicacy continued to decimate natural populations for decades. In Maryland in 1891 over 89,000 pounds of terrapin were sold, but by 1920, despite continued high demand, that figure dropped to 829 pounds (Carr, 1952). By the late 1920s harvest laws were generated in some states. With supply low and demand high, the price of terrapin meat soared beyond the reach of most consumers. With the advent of prohibition (sherry was part of the recipe) and the economic depression of the 1930s, the craving for terrapin meat all but ended (Roosenburg, 1990). Since then some decimated populations have gradually recovered (Finneran, 1948; Coker, 1951). Although terrapins are still collected and sold for food, they are not usually targeted by fishermen, but rather captured as bycatch (Marion, 1986; Roosenburg, 1990; Morreale, 1992).

Two surveys of terrapin biologists taken in 1994 and 2004 both ranked drowning in crab pots as the primary threat to terrapin survival (Seigel and Gibbons, 1995; Butler et al., in press). Crabs can survive in the pots for days or longer, while terrapins drown in them in a matter of hours (Fig. 20-11). That terrapins enter and drown in crab pots was noted decades ago (Davis, 1942). It has been reported from New Jersey (Burger, 1989; Wood and Herlands, 1996; Wood, 1997), Maryland (Roosenburg et al., 1997; Roosenburg and Green, 2000), North Carolina (Hart, 2005), South Carolina (Bishop, 1983; Hoyle and Gibbons, 2000), Florida (Butler, 2000, 2002), Alabama (Marion, 1986), and Mississippi (Mann, 1995). Roosenburg (2004) reviewed published studies on the impact of crab pots on terrapins. Catch rates are difficult to compare due to variation in methods, equipment, terrapin population density, habitats, and study goals. However, rates of 0.15–0.49 terrapins/pot/day have been reported (Bishop, 1983; Mann, 1995; Roosenburg et al., 1997;

Figure 20-11. A crab trap containing a carcass of an adult Carolina diamondback terrapin, *Malaclemys terrapin centrata*, recovered from coastal wetlands in Duval Co., Florida. Photo by Joe Butler.

Wood, 1997). Estimates of mortality due to crab pots are also difficult to compare, but they vary from 1759 per year (occurring in April and May) in South Carolina (Bishop, 1983), to 17,748–88,740 per year in New Jersey (Wood and Herlands, 1996), and between 15% and 78% of the yearly population in the Chesapeake Bay (Roosenburg et al., 1997). Clearly, with such high capture rates local terrapin populations can be quickly extirpated.

Bishop (1983) found that when crab pots were deployed from April to November in South Carolina, 87% of terrapin captures occurred in April and May. This seasonal trend was attributed to post-hibernation feeding which takes place at that time. Comparable results were noted in North Carolina (Hart, 2005) and northeastern Florida (Butler, 2002). Pot openings are small enough to exclude most large, sexually mature females, and in most studies where these openings were not altered there was a distinctly male-biased sex ratio in the pots (Bishop, 1983; Roosenburg et al., 1997). Differential survivorship of one sex or size group likely contributes to biased sex ratios, and the consequences of this are not yet understood (Roosenburg et al., 1997).

When a terrapin enters a crab pot this often attracts others to follow, and Bishop (1983) found multiple terrapins in pots nearly half the time. Traps lost or abandoned by fishermen, so- called “ghost pots,” are insidious in that they often continue to capture terrapins as long as they are in place. Bishop (1983) found 28 decomposing terrapins in one ghost pot, and Roosenburg (1991a) found 49 in another.

In some areas recreational crab potting by residents may be more damaging to terrapins than commercial potting (Roosenburg et al., 1997; Hoyle and Gibbons, 2000). Commercial potting is usually restricted to the deeper water, which most terrapins of vulnerable size do not frequent. In Maryland local residents are allowed to fish two crab pots from their docks to catch crabs for their personal consumption, and it is these shoreline habitats that are inhabited by smaller terrapins. This problem is compounded when pots are left in the water for long periods, which often happens with weekend visitors (Hoyle and Gibbons, 2000).

While predation on nesting females and their nests undoubtedly has natural origins, several authors have noted that human activities can make natural nesting areas more accessible to some predators (Seigel, 1980a; Morreale, 1992). A specific example of how humans may inadvertently facilitate terrapin predators can be given for an island nesting beach in northeastern Florida. Nest predation may be enhanced because the island is connected to larger landmasses on two sides by bridges which provide raccoons easy access to the beach (Butler, unpubl. data). Roosenburg (1991a) suggested that because raccoons have no remaining natural predators and interface well with human suburban life, this could lead to increases in their populations that could adversely affect their prey populations.

Real estate development of beaches and marshes clearly deprives terrapins of appropriate habitat. Site development that includes dredging may alter channel depths and water flow, undercut banks and shorelines causing erosion, and may use prime nesting habitat for spoil deposition (Marion, 1986; Roosenburg, 1991a; Morreale, 1992; Wood and Herlands, 1996). These changes also can alter siltation rates to the detriment of habitats (Seigel, 1993). Bulkheading or addition of seawalls or rip rap to prevent erosion may block terrapins from accessing their nesting areas. Also, planted vegetation for erosion control may overtake beaches rendering them inappropriate for nesting (Roosenburg, 1991a).

Several roads that traverse the salt marshes in Cape May Co., New Jersey, are notorious for their road-killed terrapins. Between 1989 and 1995 Wood and Herlands (1997) counted 4020 road-kills on 11.5 km of those roads. The roads provide access to the barrier island resort communities and are heavily traveled in the warmer months when terrapins are nesting. A similar situation occurs in the Jacques Cousteau National Estuarine Research Reserve, New Jersey, where numerous terrapins are killed by automobiles as they cross Great Bay Boulevard (Hoden and Able, 2003; Szerlag and McRobert, 2006). The causeway to Jekyll Island, Georgia, is also a noted terrapin road kill area (Mann, 1995).

Nearly 20% of adult females from the Patuxent River, Maryland, bore propeller scars from encounters with motor boats, and this was the primary identifiable cause of death for these mature females (Roosenburg, 1991a). By contrast only about 2% of males had scars, and it was suggested that large females may be less able to avoid the boats. Also, the propensity for females to aggregate offshore of nesting beaches at certain times may be a factor, as some of the beaches are adjacent to popular boating channels (Roosenburg, 1991a).

Other survival threats include pollution of terrapin habitat, which has been corrected in New Jersey (Wood and Herlands, 1996). Terrapins are sometimes captured as bycatch in shrimp trawls, but no quantifiable data are available (Butler, 2000). Finally, the collection of terrapins for the pet trade may affect local populations (Marion, 1986), but little is known of its impact. Over a two-year period, Enge (1993) reported 176 terrapins taken from the wild in Florida and sold in the pet trade. Most of those originated in the Florida panhandle region.

STATUS

The only terrapin subspecies listed in the most recent FCREPA account is *M. t. rhizophorarum*, which was considered“rare” (Wood, 1992). The Carolina, ornate, and Mississippi diamondback terrapins are all listed as candidates for monitoring and research efforts by the Florida Fish and Wildlife Conservation Commission (FFWCC) (Millsap et al., 1990). All Florida subspecies of *Malaclemys* are considered to have among the greatest conservation needs by the Florida Wildlife Legacy Initiative (FFWCC, 2005). The IUCN Red List (IUCN, 2004) categorizes this species as Near Threatened.

CONSERVATION OPTIONS AND SOLUTIONS

Population Assessment. — Population monitoring is an important conservation tool, and in order to accomplish this one needs to capture turtles without harming them. Large numbers of captures are necessary for mark-recapture studies, assessment of population size, density, structure, movements, and other studies. Terrapins can be extremely challenging to catch, and numerous methods have been employed to capture them for scientific study, including various kinds of nets (gill, trammel, dip, and fyke nets), crab traps, hoop traps, road collecting, seining, and hand capture. Netting is probably the most commonly used technique. However, the effectiveness of any method in a particular region depends on the habitat use of terrapins in that area. For example, Seigel (1984) used gill nets to capture terrapins at one site at the Kennedy Space Center in Florida, but found that hand capture (by walking in shallow waters near spoil islands) was more effective at a nearby site. Similarly, hand capture has been used effectively in south Florida (Mealey, unpubl. data). Morreale (1992) captured most of his terrapins simply by snorkeling after them. Although this technique has also been successful in south Florida (Mealey, unpubl. data), waters in northeastern Florida were too murky for this method (Butler, 2000). At a tidal marsh in South Carolina, Lovich and Gibbons (1990) used a combination of gill or trammel nets and seines in tidal creeks at low tide as complimentary collecting techniques. Cast netting is useful at certain times of the season when terrapins aggregate at the surface (Butler, 2002). Roosenburg et al. (1997) used fyke nets, gill nets, bank traps, and crab traps to mark over 5000 terrapins in Chesapeake Bay in Maryland. Hart (2005) had much success capturing terrapins with a dip net in Big Sable Creek. Because terrapins are known to enter crab traps, several workers have used modified crab traps successfully to capture terrapins. Roosenburg et al. (1997) provided a diagram of such a modified trap.

Patrolling areas near nesting beaches to collect nesting females is very effective but sexually biased (e.g., Montevecchi and Burger, 1975; Seigel, 1980b; Goodwin, 1994; Roosenburg and Dunham, 1997; Butler et al., 2004). When done near roadsides, this reduces the high terrapin mortality caused by automobiles (Wood, 1997). Otter trawls were productive in tidal creeks in Delaware (Hurd et al., 1979), but in habitats with channel obstructions (i.e., oyster mounds, mangroves) this will not work. Trawling at low rather than high tide yields better results (Hurd et al., 1979; Butler, 2000). Yearicks et al. (1981) probed muddy bottoms and banks with poles to locate hibernating terrapins. In some cases terrapins buried in soft mud near the surface can be located simply by stepping on them or raking through the mud (Butler, 2002; C.S. Boykin, *pers. comm.*).

Crab Potting. — Terrapins drowning in crab pots is the most acute survival threat to this species (Seigel and Gibbons, 1995; Butler et al., in press). Several legal restrictions and trapping gear modifications have been tested and are either in use or are being recommended to regulating authorities in parts of the range. Roosenburg et al. (1997) tested a modified version of the traditional crab pot that was tall enough to allow captured terrapins to surface for air until they were released. The pots did not affect crab capture rate, and the only times terrapins drowned were when pots were knocked over by storms. The pots are too big and unwieldy for commercial use, but it has been recommended that they be mandated for recreational crabbing (Roosenburg et al., 1997). Other states within the terrapins’ range should consider limiting commercial crab potting to deeper waters (at least during seasons when terrapins are active). They should also assess impacts that non-commercial (recreational) use of pots might have, and consider the modified tall pots for limited use. Pot height will need to vary from place to place, and in northeastern Florida pots over 3 m tall are necessary to prevent terrapins from drowning (Butler, 2000).

Another pot alteration with more potential for widespread use is the Bycatch Reduction Device (BRD) tested and proposed by Wood (1997) and adopted by the New Jersey Bureau of Marine Fisheries, and Maryland and Delaware Departments of Natural Resources. This is composed of a length of wire (pieces of coat hanger were used initially) bent into a rectangle and attached to the narrow opening of the pot inlet funnels to limit the size of the opening and therefore the organisms that can enter. The concept is to prevent terrapins from entering pots without impeding crabs. Several studies of BRD’s actually have demonstrated an increase in crab catch with the devices, probably as a result of crabs being less likely to find their way out of the smaller opening. The most effective size of the BRD’s varies from area to area based on terrapin size, which also varies throughout the range (Wood, 1997; Guillory and Prejean, 1998; Roosenburg and Green, 2000). As of April 1999 Maryland also requires the use of BRD’s, but only for noncommercial crab pots. These devices are inexpensive (< $0.50; New Jersey furnishes them to residents free of charge), easy to install, and they reduce terrapin bycatch while possibly enhancing crab catch.

Butler and Heinrich (in press) tested BRDs in eight Florida counties and determined that 73.2% of terrapins captured in their study would have been prevented from entering crab pots with these devices. Further, BRDs did not significantly alter crab capture. They suggested to the FFWCC that BRDs be required on all commercial and recreational crab pots in Florida (Butler and Heinrich, in press). Every state within the range of this species should consider requiring BRD's if crab potting is allowed in shallow waters. It should be noted that the BRD size that is most effective at preventing terrapin entrance without affecting crab capture does not prevent most male terrapins from entering. If males are more likely to drown than females, this could alter population structure.

We have noted that lost or abandoned "ghost" pots (also termed derelict traps) can kill terrapins for a long time after their original purpose has expired, and there needs to be some mechanism to limit this. Some pots are purposefully assembled with fastening devices that will rust and disintegrate over time, so lost pots eventually break apart. It might be advisable to hold crab fishermen accountable for their pots, or at least offer a bounty for salvaged ghost pots. Several states (North Carolina, Alabama, Mississippi, Louisiana, and Texas) have successful ongoing derelict trap removal programs, whereby crab trapping is halted for about two weeks, usually in the winter, and volunteer groups tag and collect these ghost pots (Guillory et al., 2001; GSMFC, 2003). In Florida, various groups under the supervision of the FFWCC have conducted derelict blue crab trap removals in Apalachicola Bay, Biscayne Bay, Crystal River, the Suwannee River and Tampa Bay (J.B. Dodson, FFWCC, *pers. comm.*). This effort should be expanded to cover all areas where terrapins are known to exist in the State, and its continuance should be assured.

Predation. — Although predation is a natural phenomenon, raccoons stand out as the major nest predators in many areas (Burger, 1977; Roosenburg, 1992; Goodwin, 1994; Butler, 2004). Raccoons take nests of other turtles, crocodilians, and ground nesting birds; and they adversely affect populations of several small mammals (MacLaren, 1992). In some cases human activities enhance raccoon densities (Hoffman and Gottschang, 1977), and it may be that in some areas raccoons have become so overabundant that they could be detrimental to the continued survival of their prey (Garrott et al., 1993). Conversely, terrapins and other species have been subjected to predation pressure from raccoons for a long time, and it is likely that their reproductive strategies have evolved under such influences. What appears to be excessive predation may, in fact, be normal, and removal or reduction in predation could cause negative consequences for terrapin populations over time. Before altering these relationships researchers need a better understanding of the intimate relationship between raccoons and terrapins (and other prey). We encourage all researchers interested in terrapins to consider evaluating predator densities and their impacts on populations.

Shoreline Development and Alteration. — Modification of tidal areas by humans requires monumental habitat alteration, and changes that are likely to be detrimental to terrapins and other species. Efforts must be made throughout the terrapins' range to identify nesting beaches, foraging areas, hibernacula, and other critical habitats with recommendations for protection from development. In areas where development must proceed, the effects of altering channel depth must be evaluated; deposition of spoil must be accomplished wisely so that terrapin habitat is not altered. Bulkheading, seawall construction, or any alterations that would impede terrapin movement to and from nesting areas must be avoided. If nesting areas are known, it may be possible to plan road construction in a way that would limit terrapin mortality in these areas.

Removal or planting of vegetation on nesting beaches can be detrimental to terrapins. Either could affect nest temperatures and thus impact sex determination. In some places vegetation is planted on nesting beaches to control erosion. These plants can have numerous detrimental effects such as depleting eggs of nutrients, trapping hatchlings as they attempt to leave nests, and causing females to risk inundation of nests by forcing them to nest closer to the tide line to avoid over-vegetated areas (Roosenburg, 1991a). Such beach alteration should be avoided or somehow accomplished wisely.

Shrimp Trawling. — Little is known about the impact of shrimp trawling on terrapin populations. Much trawling likely occurs in deeper waters where terrapins are less likely to be found. However, in northeastern Florida, female terrapins on their way to nesting areas must traverse waters that are being fished by shrimp trawlers. When trawlers are collecting shrimp to be sold live, they check trawls often and terrapins are unlikely to drown. Longer trawling periods result in more dead shrimp and, presumably, terrapins (Butler, 2000). The impact of this industry on terrapin populations is not known and needs to be studied.

Boat Traffic. — Local boating regulations may be necessary to prevent propeller-caused mortality to adult female terrapins (Roosenburg, 1991a; Gibbons et al. 2001). If nesting and aggregation areas and periods can be identified, boating regulations could be developed to prevent or decrease such encounters.

Pet Trade. — Terrapins are unique and very attractive to some pet enthusiasts. This coupled with the extreme vulnerability of females when they are on shore nesting leaves them in danger of exploitation by the pet trade. We suggest that nesting beach locations be kept strictly confidential among responsible conservationists. Additionally, Florida law prohibits buying terrapins and their possession for sale. Further, it restricts possession limits to two individuals. Other states should follow suit.

Education. — The only way most organisms are conserved is if people understand and appreciate them. Programs describing this unique turtle should be developed for all levels of university students, school children, nature centers, and parks.

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LITERATURE CITED

ALLEN, J.F. AND R.A. LITTLEFORD. 1955. Observations on the feeding habits and growth of immature diamondback terrapins. Herpetologica 11:77-80.

ARNDT, R.G. 1991. Predation on hatchling diamondback terrapin, *Malaclemys terrapin* (Schoepff), by the ghost crab, *Ocypode quadrata* (Fabricius). Florida Scientist 54:215- 217.

ARNDT, R.G. 1994. Predation on hatchling diamondback terrapin, *Malaclemys terrapin* (Schoepff), by the ghost crab, *Ocypode quadrata* (Fabricius). II. Florida Scientist 57:1-5.

AUGER, P.J. 1989. Sex ratio and nesting behavior in a population of *Malaclemys terrapin* displaying temperature-dependent sex determination. Ph. D. dissertation. Tufts Univ., Boston, MA.

AUGER, P.J. AND P. GIOVANNONE. 1979. On the fringe of existence, diamondback terrapins at Sandy Neck. Cape Naturalist 8:44-58.

AVISE, J.C. 1994. Molecular markers, natural history, and evolution. Chapman and Hall Publ., New York.

AVISE, J.C. 1995. Mitochondrial DNA polymorphism and a connection between genetics and demography of relevance to conservation. Conservation Biology 9:686-690.

AVISE, J.C. 1996. Toward a regional conservation genetics perspective: phylogeography of faunas in the southeastern United States. In: Avise, J. C. and J. L. Hamrick, (Eds.) Conservation Genetics: Case Histories from Nature. Chapman and Hall Publ., New York. pp. 431-470.

BALDWIN, J. D., L. A. LATINO, B. K. MEALEY, G. M. PARKS, AND M. R. J. FORSTNER. 2005. The diamondback terrapin in Florida Bay and the Florida Keys: insights into turtle conservation and ecology. In: Meshaka, Jr., W. E. and K. J. Babbitt, (Eds.) Amphibians and Reptiles: Status and Conservation in Florida, Krieger Publishing Co., Malabar, Florida pp. 180 – 186.

BARNEY, R.L. 1922. Further notes on the natural history and artificial propagation of the diamond-back terrapin. Bulletin of the U.S. Bureau of Fisheries 38:91-111.

BICKHAM, J.W., T. LAMB, P. MINX, AND J. C. PATTON. 1996. Molecular systematics of the genus *Clemmys* and the intergeneric relationships of emydid turtles. Herpetologica 52:89-97.

BISHOP, J.M. 1983. Incidental capture of diamondback terrapins by crab traps. Estuaries 6:426- 430.

BURGER, J. 1976a. Behavior of hatchling diamondback terrapins (*Malaclemys terrapin*) in the field. Copeia 1976:742-748.

BURGER, J. 1976b. Temperature relationships in nests of the northern diamondback terrapin, *Malaclemys terrapin terrapin*. Herpetologica 32:412-418.

BURGER, J. 1977. Determinants of hatching success in the diamondback terrapin, *Malaclemys terrapin*. American Midland Naturalist 97:444-464.

BURGER, J. 1989. Diamondback terrapin protection. Plastron Papers-Journal of the N.Y. Turtle and Tortoise Society 19:35-40.

BURGER, J. AND W. A. MONTEVECCHI. 1975. Nest site selection in the terrapin *Malaclemys terrapin*. Copeia 1975:113-119.

BURNS, T.A., AND K. L. WILLIAMS. 1972. Notes on the reproductive habits of *Malaclemys terrapin pileata*. Journal of Herpetology 6:237-238.

BUTLER, J.A. 2000. The status and distribution of the Carolina diamondback terrapin, *Malaclemys terrapin centrata*, in Duval Co.. Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida.

BUTLER, J.A. 2002. Population ecology, home range, and seasonal movements of the Carolina diamondback terrapin, *Malaclemys terrapin centrata*, in northeastern Florida. Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida.

Butler, J.A. and G.L. Heinrich. In Press. The effectiveness of bycatch reduction devices on crab pots at reducing capture and mortality of diamondback terrapins (*Malaclemys terrapin*) in Florida. Estuaries.

Butler, J.A., C. Broadhurst, M. Green, and Z. Mullin. 2004. Nesting, nest predation, and hatchling emergence of the Carolina diamondback terrapin, *Malaclemys terrapin centrata*, in northeastern Florida. American Midland Naturalist 152:145-155.

Butler, J.A., G. L. Heinrich, and R. A. Seigel. In Press. Third workshop on the ecology, status and conservation of diamondback terrapins: results and recommendations. Chelonian Conservation Biology.

Cagle, F.R. 1952. A Louisiana terrapin population (*Malaclemys*). Copeia 1952:74-76.

Carr, A.F., Jr. 1946. Status of the mangrove terrapin. Copeia 1946(3):170-172.

Carr, A.F., Jr. 1952. Handbook of Turtles. The Turtles of the United States, Canada, and Baja California. Comstock Publ. Assoc., Cornell University Press, Ithaca, New York. 542 pp.

Christiansen, J.L., and E. O. Moll. 1973. Latitudinal reproductive variation within a single subspecies of painted turtle, *Chrysemys picta bellii*. Herpetologica. 29:152-163.

Clark, W.S. 1982. Turtles as a food source of nesting bald eagles in the Chesapeake Bay Region. Journal of Field Ornithology 53:49-51.

Cochran, J.D. 1978. A note on the behavior of the diamondback terrapin, *Malaclemys t. terrapin* (Schoepff) in Maryland. Bulletin of the Maryland Herpetological Society 14:100.

Coker, R.E. 1906. The cultivation of the diamond-back terrapin. North Caroline Geological Survey Bulletin 14:1-169.

Coker, R.E. 1920. The diamondback terrapin: past, present, and future. Science Monthly 11:171-186.

Coker, R.E. 1951. The diamondback terrapin in North Carolina. In: Taylor, H. F. (Ed.). Survey of Marine Fishes of North Carolina. Univ. North Carolina Press, Chapel Hill. pp.219-230.

Cowan, F.B.M. 1981a. Short term acclimation of *Malaclemys terrapin* to saltwater. Comparative Biochemistry and Physiology 68A:55-59.

Cowan, F.B.M. 1981b. Effects of salt loading on salt gland function in the euryhaline turtle, *Malaclemys terrapin*. Journal of Comparative Physiology 145:101-108.

Cowan, F.B.M. 1990. Does the lachrymal gland of *Malaclemys terrapin* have a significant role in osmoregulation? Canadian Journal of Zoology 68:1520-1524.

Cunningham, B. 1939. Effect of temperature upon the development rate of the embryo of the diamondback terrapin (*Malaclemys centrata* Lat.). American Naturalist 73:381-384.

Davenport, J. and E.A. Macedo. 1990 Behavioral osmotic control in the euryhaline diamondback terrapin *Malaclemys terrapin*: responses to low salinity and rainfall. Journal of Zoology (London) 220:487-496.

Davenport, J., M. Spikes, S. M. Thornton, and B. O. Kelly. 1992. Crab-eating in the diamondback terrapin *Malaclemys terrapin*: dealing with dangerous prey. Journal of the Marine Biology Association, U. K. 72:835-848.

Davis, C.C. 1942. A study of the crab pot as a fishing gear. Chesapeake Biological Laboratory Publication No. 53. Solomons Island, MD. 20pp.

Dimond, M.T. 1987. The effects of incubation temperature on hatching time, sex, and growth of hatchlings of the diamondback terrapin, *Malaclemys terrapin* (Schoepff). Pranikee 8:1-5.

Dobie, J.L. 1981. The taxonomic relationship between *Malaclemys* Gray, 1844 and *Graptemys* Agassiz, 1857 (Testudines: Emydidae). Tulane Studies in Zoology and Botany 23:85-102.

Draud, M., M. Bossert, and S. Zimnavoda. 2004. Predation on hatchling and juvenile diamondback terrapins (*Malaclemys terrapin*) by the Norway rat (*Rattus norvegicus*). Journal of Herpetology 38:467-470.

Dunson, W.A. 1970. Some aspects of electrolyte and water balance in three estuarine reptiles, the diamondback terrapin, American and "salt water" crocodiles. Comparative Biochemistry and Physiology 32:161-164.

Dunson, W.A. 1985. Effect of water salinity and food salt content on growth and sodium efflux of hatchling diamondback terrapins (*Malaclemys*). Physiological Zoology 58:736-747.

Dunson, W.A. and F. J. Mazzotti. 1989. Salinity as a limiting factor in the distribution of reptiles in Florida Bay: a theory for the estuarine origin of marine snakes and turtles. Bulletin of Marine Science 44:229-244.

Enge, K.M. 1993. Herptile use and trade in Florida. Florida Game and Fresh Water Fish Comm. Nongame Wildlife Program Final Performance Report, Tallahassee, Fl. 102pp.

Ernst, C. H., J. E. Lovich, and R. W. Barbour. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington.

Ewert, M. A., and C. E. Nelson. 1991. Sex determination in turtles: diverse patterns and some possible adaptive values. Copeia 1991:50-69.

FFWCC. 2005. Florida's Wildlife Legacy Initiative. Florida's Comprehensive Wildlife Conservation Strategy. Gainesville: Florida Fish and Wildlife Conservation Commission.

Finneran, L.C. 1948. Diamond-back terrapin in Connecticut. Copeia 1948:138.

Frost, D.R. and D.M. Hillis. 1990. Species in concept and practice: Herpetological applications. Herpetologica 46:87-104.

Fowler, H.W. 1906. Some cold-blooded vertebrates of the Florida Keys. Proceedings of the Academy of Natural Sciences, Philadelphia 58:77-113.

Garrott, R.A., P.J. White, and C.A. Vanderbilt White. 1993. Overabundance: an issue for conservation biologists? Conservation Biology 7:946-949.

Gibbons, J.W., J.E. Lovich, A.D. Tucker, N.N. FitzSimmons, and J.L. Greene. 2001. Demographic and ecological factors affecting conservation and management of the diamondback terrapin (*Malaclemys terrapin*) in South Carolina. Chelonian Conservation and Biology 4:66-74.

Gilles-Baillien, M. 1973a. Isosmotic regulation in various tissues of the diamondback terrapin *Malaclemys centrata centrata* (Latreille). Journal of Experimental Biology 59:39-43.

Gilles-Baillien, M. 1973b. Seasonal variations and osmoregulation in the red blood cells of the diamondback terrapin *Malaclemys centrata centrata* (Latreille). Comparative Biochemistry and Physiology 46A:505-512.

Goodwin, C.C. 1994. Aspects of nesting ecology of the diamondback terrapin (*Malaclemys terrapin*) in Rhode Island. M. S. Thesis, Univ. Rhode Island.

Guillory, V. and P. Prejean. 1998. Effect of a terrapin excluder device on blue crab, *Callinectes sapidus*, trap catches. Marine Fisheries Review 60:38-40.

Guillory, V., A. McMillen-Jackson, L. Hartman, H. Perry, T. Floyd, T. Wagner, and G. Graham. 2001. Blue crab derelict traps and trap removal programs. Gulf States Marine Fisheries Commission, Ocean Springs, Mississippi, Publication Number 88, 13pp.

Gulf States Marine Fisheries commission (GSMFC). 2003. Guidelines for developing derelict trap removal programs in the Gulf of Mexico. GCMFC, Ocean Springs, Mississippi, Publication Number 110, 7 pp.

Hart, K.M. 2005. Population biology of diamondback terrapins (*Malaclemys terrapin*): defining and reducing threats across their geographic range. Ph.D. Dissertation, Duke University.

Harwood, V.J., J. Butler, D. Parrish, and V. Wagner. 1999. Isolation of fecal coliform bacteria from the diamondback terrapin (*Malaclemys terrapin centrata*). Applied Environmental Microbiology 65:865-867.

Hauswaldt, J.S. and Glenn, T.C. 2003. Microsatellite DNA from the diamondback terrapin (*Malaclemys terrapin*). Molecular Ecology Notes 3:174-176.

Hay, W.P. 1917. Artificial propagation of the diamond-back terrapin. Bulletin of the U.S. Bureau of Fisheries 24:1-20.

Hildebrand, S.F. 1929. Review of experiments on artificial culture of diamond-back terrapin. Bulletin of the U.S. Bureau of Fisheries 45:25-70.

Hildebrand, S.F. 1932. Growth of diamond-back terrapins: size attained, sex ratios and longevity. Zoologica 9:551-563.

Hoden, R., and K.W. Able. 2003. Habitat use and road mortality of diamondback terrapins (*Malaclemys terrapin*) in the Jacques Cousteau National Estuarine Research Reserve at Mullica River – Great Bay in southern New Jersey. Jacques Cousteau National Estuarine Research Reserve Technical Report #100-24.

Hoffman, C.O., and J.L. Gottschang. 1977. Numbers, distribution, and movements of a raccoon population in a suburban residential community. Journal of Mammalogy 58:623- 636.

Hoyle, M.E., and J.W. Gibbons. 2000. Use of a marked population of diamondback terrapins (*Malaclemys terrapin*) to determine impacts of recreational crab pots. Chelonian Conservation and Biology. 3:735-737.

Hurd, L.E., G.W. Smedes, and T.A. Dean. 1979. An ecological study of a natural population of diamondback terrapins (*Malaclemys t. terrapin*) in a Delaware salt marsh. Estuaries 2:28- 33.

IUCN. 2004. IUCN Red List. www.redlist.org.

Iverson, J.B. 1991. Patterns of survivorship in turtles (order Testudines). Canadian Journal of Biology. 69:385-391.

Iverson, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately printed, 363 pp.

Jackson, C.G., Jr., and A. Ross. 1971. Molluscan fouling of the ornate diamondback terrapin, *Malaclemys terrapin macrospilota*. Herpetologica 27:341-344.

Jackson, C.G., Jr., A. Ross, and G. Kennedy. 1973. Epifaunal invertebrates of the ornate diamondback terrapin, *Malaclemys terrapin macrospilota*. American Midland Naturalist 89:495-497.

Jeyasuria, P., W. M. Roosenburg, and A. R. Place. 1994. Role of P-450 aromatase in sex determination of the diamondback terrapin, *Malaclemys terrapin*. Journal of Experimental Zoology 270:95-111.

Johnson, W. R. 1952. Range of *Malaclemys terrapin rhizophorarum* on the west coast of Florida. Herpetologica 8:100.

Lamb, T. and J.C. Avise. 1992. Molecular and population genetic aspects of mitochondrial DNA variability in the diamondback terrapin, *Malaclemys terrapin*. Journal of Heredity 83:262-269.

Lamb, T. and M.F. Osentoski. 1997. On the paraphyly of *Malaclemys*: a molecular genetic assessment. Journal of Herpetology 31:258-265.

Lawler, A.R., and J.A. Musick. 1972. Sand beach hibernation by a northern Diamondback terrapin, *Malaclemys terrapin terrapin* (Schoepff). Copeia 1972:389-390.

Lazell, J.D., Jr. 1979. Diamondback terrapins at Sandy Neck. Aquasphere, Journal of the New England Aquarium 13:28-31.

Lazell, J.D., Jr. and P.J. Auger. 1981. Predation on diamondback terrapin (*Malaclemys terrapin*) eggs by dunegrass (*Ammophila breviligulata*). Copeia 1981:723-724.

Lovich, J.E. and J. W. Gibbons. 1990. Age at maturity influences adult sex ratio in the turtle *Malaclemys terrapin*. Oikos 59:126-134.

Lovich, J.E., A.D. Tucker, D.E. Kling, and J.W. Gibbons. 1991. Behavior of hatchling diamondback terrapins (*Malaclemys terrapin*) released in a South Carolina salt marsh. Herpetological Review 22:81-83.

MacLaren, P.A. 1992. Raccoon (*Procyon lotor*) depredation on listed and other species of native fauna. Florida DNR. Tallahassee, FL.

Mann, T.M. 1995. Population surveys for diamondback terrapins (*Malaclemys terrapin*) and Gulf salt marsh snakes (*Nerodia clarkii clarkii*) in Mississippi. Mississippi Museum of Natural Sciences Technical Report, No. 37. Jackson, MS.

Marion, K.R. 1986. Mississippi diamondback terrapin. In: Mount, R. H. (Ed.). Vertebrate Animals of Alabama in Need of Special Attention. Alabama Agricultural Experiment Station. Auburn University, Alabama. pp. 52-53.

McCauley, R.H., Jr. 1945. The Reptiles of Maryland and the District of Columbia. Printed privately, Hagerstown, Md.

Middaugh, D.P. 1981. Reproductive ecology and spawning periodicity of the Atlantic silverside, *Menidia menidia* (Pisces: Atherinidae). Copeia 1981:766-776.

Millsap, B.A., J.A. Gore, D.E. Runde, and S.I. Cerulean. 1990. Setting priorities for the conservation of fish and wildlife species in Florida. Wildlife Monographs 111:1-57.

Moll, E.O. 1973. Latitudinal and intersubspecific variation in reproduction of the painted turtle, *Chrysemys picta*. Herpetologica 29:307-318.

Moll, E.O. 1979. Reproductive cycles and adaptation. In: Harless, M. and Morlock, H. (Eds.). Turtles: Perspectives and Research. John Wiley and Sons, Inc. pp. 305-332.

Moll, E.O. and J.M. Legler. 1971. The life history of a neotropical slider, *Pseudemys scripta* (Schoepff), in Panama. Bulletin of the Los Angeles Co. Museum of Natural History, Sciences 11:1-102.

Montevecchi, W.A., and J. Burger. 1975. Aspects of the reproductive biology of the northern diamondback terrapin, *Malaclemys terrapin terrapin*. American Midland Naturalist 94:166-175.

Moritz, C. 1994. Applications of mitochondrial DNA analysis in conservation: a critical review. Molecular Ecology 3:401-411.

Morreale, S.J. 1992. The status and population ecology of the diamondback terrapin, *Malaclemys terrapin,* in New York. Report to the New York State Department of Environmental Conservation and the Nature Conservancy. Okeanos Ocean Research Foundation, Hampton Bays, New York.

Palmer, W. M., and C. L. Cordes. 1988. Habitat suitability index models: diamondback terrapin (nesting) - Atlantic coast. U.S. Fish and Wildlife Service Biological Report 82(10.151), Washington, D. C.

Powell, C.B. 1967. Female sexual cycles of *Chrysemys picta* and *Clemmys insculpta* in Nova Scotia. Canadian Field Naturalist 81:134-140.

Pitler, R. 1985. *Malaclemys terrapin terrapin* (northern diamondback terrapin). Behavior. Herpetological Review 16:82.

Pritchard, P.C.H. 1979. Encyclopedia of turtles. T. F. H. Publications, Inc. Neptune, New Jersey.

Reid, G.K. 1955. Reproduction and development in the northern diamondback terrapin, *Malaclemys terrapin terrapin*. Copeia 1955:310-311.

Robinson, G.D. and W.A. Dunson. 1976. Water and sodium balance in the estuarine diamondback terrapin (*Malaclemys*). Journal of Comparative Physiology 105:129-152.

Roosenburg, W.M. 1990. Final report: the Chesapeake diamondback terrapin investigations for the period 1987, 1988, 1989. Chesapeake Research Consortium, Solomons, MD, Publ. No. 133, 84pp.

Roosenburg, W.M. 1991a. The diamondback terrapin: habitat requirements, population dynamics, and opportunities for conservation. In: Chaney, A. and Mihursky, J. (Eds.). Proceedings of a Conference: New Perspectives in the Chesapeake System: A Research and Management Partnership. Chesapeake Research Consortium, Solomons, MD, Publ. No. 137. pp. 227- 234.

Roosenburg, W.M. 1991b. Final report: the Chesapeake diamondback terrapin investigations, 1991. Chesapeake Research Consortium, Solomons, MD, Publ. No. 140.

Roosenburg, W.M. 1992. Life history consequences of nest site choice by the diamondback terrapin, *Malaclemys terrapin*. Ph.D. dissertation. Univ. Pennsylvania. Philadelphia, PA.

Roosenburg, W.M. 1993. Final report: the Chesapeake diamondback terrapin investigations, 1992. Chesapeake Research Consortium, Solomons, MD, Publ. No. 146. 59pp.

Roosenburg, W.M. 1994. Nesting habitat requirements of the diamondback terrapin: a geographic comparison. Wetlands Journal 6(2):8-11.

Roosenburg, W.M. 1996. Maternal condition and nest site choice: an alternative for the maintenance of environmental sex determination? American Zoologist 36:157-168.

Roosenburg, W.M. 2004. The impact of crab pot fisheries on the terrapin, *Malaclemys terrapin*: Where are we and where do we need to go? In: Swarth, C., Roosenburg, W., and Kiviat, E. (Eds.). Conservation and Ecology of Turtles from the Mid-Atlantic Region: A Symposium. Proceedings of the Mid-Atlantic Turtle Symposium. Bibliomania, Salt Lake City, Utah. Pp 23-30 .

Roosenburg, W.M. and A.E. Dunham. 1997. Allocation of reproductive output: egg- and clutch-size variation in the diamondback terrapin. Copeia 1997:290-297.

Roosenburg, W.M. and J.P. Green. 2000. Impact of a bycatch reduction device on diamondback terrapin and blue crab capture in crab pots. Ecological Applications 10:882-889.

Roosenburg, W.M. and K.C. Kelley. 1996. The effect of egg size and incubation temperature on growth in the turtle *Malaclemys terrapin*. Journal of Herpetology 30:198-204.

Roosenburg, W.M. and P. Niewiarowski. 1998. Maternal effects and the maintenance of environmental sex determination. In: Mousseau, T. A. and Fox, C. W. (Eds.). Maternal Effects as Adaptations. Oxford Univ. Press., New York, pp. 307-322.

Roosenburg, W.M. and A.R. Place. 1994. Nest predation and hatchling sex ratio in the diamondback terrapin: implications for Management and conservation. In: Proceedings of a Conference: Toward a Sustainable Coastal Watershed: the Chesapeake Experiment. Chesapeake Research Consortium Publ. No. 149. Norfolk, VA. pp. 65-70.

Roosenburg, W.M., W. Cresko, M. Modesitte, and M.B. Robbins. 1997. Diamondback terrapin (*Malaclemys terrapin*) mortality in crab pots. Conservation Biology 11:1166-1172.

Roosenburg, W.M., K.L. Haley, and S. McGuire. 1999. Habitat selection and movements of diamondback terrapins, *Malaclemys terrapin*, in a Maryland estuary. Chelonian Conservation and Biology 3:425-429.

Ross, A. and C.G. Jackson, Jr. 1972. Barnacle fouling of the ornate diamondback terrapin, *Malaclemys terrapin macrospilota*. Crustaceana 22:203-205.

Sachsse, W. 1984. Long term studies of the reproduction of *Malaclemys terrapin centrata*. Acta Zoologica et Pathologica Antverpiensia 78:297-308.

Schwartz, A. 1955. The diamondback terrapins (*Malaclemys terrapin*) of peninsular Florida. Proceedings of the Biological Society of Washington 68:157-164.

Seigel, R.A. 1980a. Predation by raccoons on diamondback terrapins, *Malaclemys terrapin tequesta*. Journal of Herpetology 14:87-89.

Seigel, R.A. 1980b. Courtship and mating behavior of the diamondback terrapin, *Malaclemys terrapin tequesta*. Journal of Herpetology 14:420-421.

Seigel, R.A. 1980c. Nesting habits of diamondback terrapins (*Malaclemys terrapin*) on the Atlantic coast of Florida. Transactions of the Kansas Academy of Sciences 83:239-246.

Seigel, R.A. 1983. Occurrence and effects of barnacle infestations on diamondback terrapins (*Malaclemys terrapin*). American Midland Naturalist 109:34-39.

Seigel, R.A. 1984. Parameters of two populations of diamondback terrapins (*Malaclemys terrapin*) on the Atlantic coast of Florida. In: Siegel, R., Hunt, L., Knight, J. L., Malaret, L., and Zuschlag, N. L. (Eds.). Vertebrate Ecology and Systematics: A Tribute to Henry S. Fitch. Museum of Natural History, University of Kansas, Special Publication No.10. pp. 77-87.

Seigel, R.A. 1993. Apparent long-term decline in diamondback terrapin populations at the Kennedy Space Center, Florida. Herpetological Review 24:102-103.

Seigel, R.A. and J.W. Gibbons. 1995. Workshop on the ecology, status, and management of the diamondback terrapin (*Malaclemys terrapin*), Savannah River Ecology Laboratory, 2 August 1994: final results and recommendations. Chelonian Conservation and Biology 1:240-243.

Spagnoli, J. J., and B. I. Marganoff. 1975. New York's marine turtle. Conservationist (New York) 29:17-19.

Stegmann, E.W., R.B. Primark, and G.S. Ellmore. 1988. Absorption of nutrient exudates from terrapin eggs by roots of *Ammophila breviligulata*. Canadian Journal of Botany 66:714-718.

Stephens, P.R. and J.J. Wiens. 2003. Ecological diversification and phylogeny of emydid turtles. Biological Journal of the Linnean Society 79:577-610.

Szerlag, S., and S.P. McRobert. 2006. Road occurrence and mortality of the northern diamondback terrapin. Applied Herpetology 3:27-37.

Tinkle, D.W. 1961. Geographic variation in reproduction, size, sex ratio, and maturity of *Sternothaerus odoratus* (Testudinata: Chelydridae). Ecology 42:68-76.

Tucker, A.D., N. N. FitzSimmons, and J. W. Gibbons. 1995. Resource partitioning by the estuarine turtle *Malaclemys terrapin*; trophic, spatial, and temporal foraging constraints. Herpetologica 51:167-181.

Wood, R.C. 1977. Evolution of the emydine turtles *Graptemys* and *Malaclemys* (Reptilia, Testudines, Emydidae). Journal of Herpetology 11:415-421.

Wood, R.C. 1981. The mysterious mangrove terrapin. Florida. Naturalist. 54:6-7.

Wood, R.C. 1992. Mangrove terrapin. In: Moler, P. (Ed.). Rare and Endangered Biota of Florida. Vol. III. Amphibians and Reptiles. University Press of Florida, Gainesville. pp. 204-209.

Wood, R.C. 1997. The impact of commercial crab traps on diamondback terrapins. In: Van Abbema, J. (Ed.). Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles- An International Conference. New York Turtle and Tortoise Society. pp. 21-27.

Wood, R.C. and R. Herlands. 1996. Terrapins, tires and traps: conservation of the northern diamondback terrapin (*Malaclemys terrapin terrapin*) on the Cape May Peninsula, New Jersey, USA. Proceedings of the International Congress of Chelonian Conservation. Gonfaran, France. July 1995. SOPTOM. pp. 254-256.

Wood, R.C. and R. Herlands.1997. Turtles and tires: the impact of roadkills on northern diamondback terrapin, *Malaclemys terrapin terrapin*, populations on the Cape May Peninsula, southern New Jersey, USA. In: Van Abbema, J. (Ed.). Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles-An International Conference. New York Turtle and Tortoise Society. pp. 46-53.

Yearicks, E.G., R.C. Wood, and W.S. Johnson. 1981. Hibernation of the northern diamondback terrapin, *Malaclemys terrapin terrapin*. Estuaries 4:78-80.

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Trachemys scripta – Slider or Yellow-Bellied Slider

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Summary. – The slider, *Trachemys scripta,* is a relatively common turtle species both within Florida and throughout its distribution. Sliders are not listed as rare or endangered by any state or federal agency. Partly due to its abundance, and partly due to its availability from scientific suppliers, this species has been the subject of relatively extensive study by researchers, and there is much known about its biology. The yellow-bellied slider (*Trachemys scripta scripta*) is native to the panhandle and the northern one-quarter of peninsular Florida. Non-native red-eared sliders (*T. s. elegans*) have been introduced to Florida largely as a result of their popularity in the pet trade. However, the negative impacts on native species have not been studied within the state. Adult females are (on average) larger than adult males, and the males usually have longer tails and foreclaws. Sliders inhabit a diverse array of habitats, but are most abundant in soft-bottomed habitats with minimal flow and abundant sunlight. Courtship may involve so-called "titillation" behaviors and/or biting and chasing behaviors with the peak of courtship activities probably occurring during autumn. Females usually nest in relatively open areas anytime between March and July, with reports of average clutch size ranging from 5–20 eggs. The species is largely omnivorous but the adults typically consume more plant material than the relatively carnivorous juveniles. Some of the potential threats to this species include the pet trade, habitat alteration/destruction, and road-associated mortality. The potential threats posed by exotic *T. s. elegans* (e.g., competition, genetic pollution) to native *T. s. scripta* are discussed.

Conservation Status. – FNAI Global - G5 (Demonstrably Secure), State - S5 (Demonstrably Secure); ESA Federal - Not Listed; State - Not Listed; CITES - Not Listed; IUCN Red List - Not Listed (LC-Least Concern).

Species Recognition. — The yellow-bellied slider, *Trachemys scripta scripta*, the subspecies native to Florida, is an aquatic turtle of moderate size with adult male plastron length (PL) ranging from about 9.0 to over 23.0 cm (ca. 9.4-24.0 cm carapace length [CL]), and adult females ranging from ca. 15.0-29.0 cm PL (ca. 19.0-30.0 cm CL) (Fig. 21.1) (Iverson, 1977; Jackson, 1988; Gibbons and Lovich, 1990; Thomas 1993; Mitchell, 1994; Tucker et al., 1998a; Platt and Rainwater, 2003; Aresco, 2004). The plastron is unhinged, the carapace exhibits a modest mid-dorsal keel, and the marginals of the posterior carapace are moderately serrated. The plastron is usually yellow and may exhibit one to several pairs of dark blotches (Figs. 21-2, 21-3). Color of the carapace and skin varies, but usually ranges from olive to brown with yellow striping. The lower jaw is ventrally rounded and there is a conspicuous yellow blotch on each side of the head (Fig. 21-4) (Brimley, 1907; Ernst et al., 1994).

The red-eared slider (*Trachemys s. elegans*) is not native to Florida, but has been introduced at many locations (King and Krakauer, 1966; Bancroft et al., 1983; Wilson and Porras, 1983; Iverson and Etchberger, 1989; Hutchison, 1993; Butterfield et al., 1994; Townsend et al., 2002; Emer, 2004). This subspecies can be distinguished from *T. s. scripta* by the presence of a distinct red bar behind the eye (Fig. 21-5), which is absent in *T. s. scripta* (Brimley, 1907; Ernst et al., 1994). In locations where *T. s. elegans* has been introduced, the two subspecies may successfully interbreed (see Mitchell, 1994).

Taxonomic History. — The slider has at one time or another been placed in the following genera: *Testudo*, *Emys*, *Chrysemys*, *Pseudemys*, and *Trachemys* (see Ernst, 1990; Seidel and Jackson, 1990, for detailed summaries). Likewise, the recognition of subspecies within *T. scripta* is a source of controversy. Ernst (1990) recognized 14 subspecies, and others have recognized as many as 17 (Legler, 1990). Legler (1990) placed the various subspecies of *T. scripta* into three groups: (1) United States, (2) Mesoamerican, and (3) Antillean, with the United States group being made up of three subspecies: (1) *T. s. elegans*, (2) *T. s. scripta*, and (3) *T. s. troostii*.

Seidel (2002) proposed a more restricted view of this "megaspecies" (i.e., *T. scripta*) and partitioned the group into 15 species, 8 of which were polytypic. In this proposal, *T. scripta* was viewed as a polytypic species with three subspecies (*T. s. elegans*, *T. s. scripta*, and *T. s. troostii*). The two subspecific groups formerly known as the "Mesoamerican" and "Antillean" groups (see Legler, 1990) were viewed as a collection of 14 species separate and distinct from the "United States" group.

Figure 21-1. Adult female yellow-bellied slider, *Trachemys scripta scripta*, from Leon Co., Florida. This subspecies is native to Florida. Photo by Matt Aresco.

Herein, I follow the taxonomic revisions for *T. scripta* native to the United States as outlined in Seidel (2002).

DISTRIBUTION

Geographic Distribution. — The natural range of *Trachemys scripta* (*sensu* Seidel, 2002) includes a large portion of North America that extends southward from southern Michigan to the northeastern border of Mexico, to eastern New Mexico in the west and from the Atlantic coast of Virginia to northern Florida in the east (Ernst et al., 1994; Seidel, 2002). However, one subspecies (*T. s. elegans*) has been introduced across the globe via the pet trade (Grant, 1936; Da Silva and Blasco, 1995; Ernst et al., 1994; Luiselli et al., 1997; Chen and Lue, 1998; Spinks et al., 2003).

Trachemys s. scripta is found throughout the panhandle and the northern one-quarter of the peninsula (Fig. 21-6) (Iverson and Etchberger, 1989; Ernst et al., 1994; Johnston and Johnston, 2003a). *Trachemys s. elegans* has been introduced in many locations throughout the state (Fig. 21-6) (King and Krakauer, 1966; Bancroft et al., 1983; Wilson and Porras, 1983; Iverson and Etchberger, 1989; Hutchison, 1993; Butterfield et al., 1994; Townsend et al., 2002; Johnston and Johnston, 2003b; Emer, 2004).

Ecological Distribution. — Throughout its range, *T. scripta* occupies a diverse array of aquatic habitats, and may be found within almost any body of water. It is usually most abundant in soft-bottomed habitats with minimal flow, abundant sunlight, and an abundance of aquatic plants (Cagle, 1950; Ernst et al., 1994; Anderson et al., 2002). Adult *T. scripta* may prefer deeper waters while juveniles prefer shallow waters (Hart, 1983), and habitat use may vary seasonally in some situations (Bodie and Semlitsch, 2000a).

Figure 21-2. Plastral view of juvenile yellow-bellied slider, *Trachemys scripta scripta*, from Gilchrist Co., Florida. Photo by John Iverson.

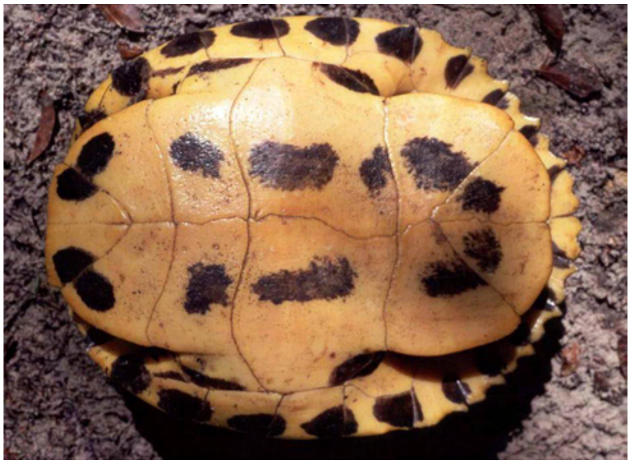

Figure 21-3. Plastral view of adult female yellow-bellied slider, *Trachemys scripta scripta*, from Wakulla Co., Florida. Photo by George Heinrich.

Figure 21-4. Juvenile yellow-bellied slider, *Trachemys scripta scripta,* from Alachua Co., Florida. Photo by Dick Bartlett.

Florida populations of *T. s. scripta* also occupy a diversity of aquatic habitats. Habitats often associated with high population densities include hydric hammocks, limestone sinkhole ponds covered with duckweed (Lemnaceae), and shallow ponds (D. Auth, *pers. obs*.). They are also abundant in some lakes (Aresco, 2002), rivers and spring runs (P. Meylan, *pers. obs*.).

HABITAT RELATIONS

Activity and Seasonality. — *Trachemys scripta* is most active diurnally, and may rest on the bottom or passively float at the surface nocturnally (Cagle, 1950; Ernst et al., 1994). The existence of an endogenous circadian rhythm influenced by photoperiod has been suggested (Jarling et al., 1989), while others have doubted the existence of such a pattern (Cloudsley-Thompson, 1982).

Trachemys scripta may remain in the water (sitting on the bottom) during winter (Cagle, 1950; Mitchell, 1994; Thomas, *pers. obs*.), or seek shelters such as muskrat (*Ondatra sibethica*) burrows (Cagle, 1950; Mitchell, 1994). The notion that *T. scripta* is inactive when water temperatures were < 10ºC (Cagle, 1950) has not been supported by subsequent research, and winter activity may be more common than previously thought (Auth, 1975; Lardie, 1980; Schubauer and Parmenter, 1981; Anton, 1987; Nijs and Janssen, 1993; Thomas, *pers. obs*.). It is clear that the influence of temperature and photoperiod on activity levels has not been adequately addressed (Burger, 1937; Cash, 2000). Likewise, latitudinal variation in the length and timing of the active season has not been adequately examined. The preferred body temperature of *T. scripta* is influenced by a number of factors (e.g., nutritional status) but ranges from about 24–29ºC (Gatten, 1974) with the upper end of that range serving as the optimal temperature in terms of ingestion rate (Parmenter, 1980).

Figure 21-5. Adult female red-eared slider, *Trachemys scripta elegans*, from Leon Co., Florida. This subspecies is introduced (invasive) in Florida. Photo by Matt Aresco.

Movements and Home Range. — Movement and habitat use by *T. scripta* may vary seasonally (Bodie and Semlitsch, 2000a), and adult males usually exhibit both a larger total and aquatic home range area than females or juveniles (Schubauer et al., 1990). Estimates of home range size are highly variable ranging from 0.66–104 ha (see Schubauer et al, 1990), with some individuals including more than one aquatic habitat as part of their home range (Cagle, 1944a; Burke et al., 1995; Thomas and Parker, 2000). Some of this variation may have been related to the different methods used to estimate home range size, as well as differences in overall size of the specific aquatic habitats examined in these studies.

Terrestrial Activity. — Overland movements of *T. scripta* have been well documented (Cagle, 1944a; Gibbons, 1970; Bennett et al., 1970). *Trachemys scripta* may respond to stressors such as declines in habitat quality/quantity (e.g., drought) by emigrating in search of better conditions (Cagle, 1950; Gibbons et al., 1983; Cash and Holberton, 1999, 2005; Cash, 2000; Aresco, 2002). Terrestrial foraging by *T. scripta* has been observed (Cagle, 1944a; Thomas, *pers. obs*.), but the frequency and relative importance of such forays are not known. Females must move overland in order to nest (Gibbons et al., 1990; Rose and Manning, 1996; Buhlmann and Gibbons, 2001), and hatchling *T. scripta* must move overland to water after emerging from the nest (Tucker, 2000a).

Smaller hatchling sliders are probably subject to greater risk of mortality relative to larger neonates (Tucker, 2000a; Janzen et al., 2000a, b), and all hatchling *T. scripta* are probably subject to greater risk of mortality than that experienced by adults during overland movements. Fortunately, terrestrial movements, other than initial travel from nest to aquatic habitat, are not characteristic of hatchling *T. scripta* (Gibbons, 1990a). Most new colonists to a recently constructed farm pond in Clay County, Mississippi, were juveniles (but not necessarily hatchlings), and the few adults that colonized the pond were more likely to emigrate than juveniles (Parker, 1990).

Adult male *T. scripta* may participate in overland movements more frequently and move greater distances than females or juveniles (Parker, 1984; Morreale et al., 1984). The greater mobility of males is thought to represent mate-searching activities, and may increase individual fitness by increasing the probability of encountering females (Parker, 1984; Morreale et al., 1984; Tuberville et al., 1996; Thomas and Parker, 2000). In contrast, some studies have reported that female *T. scripta*

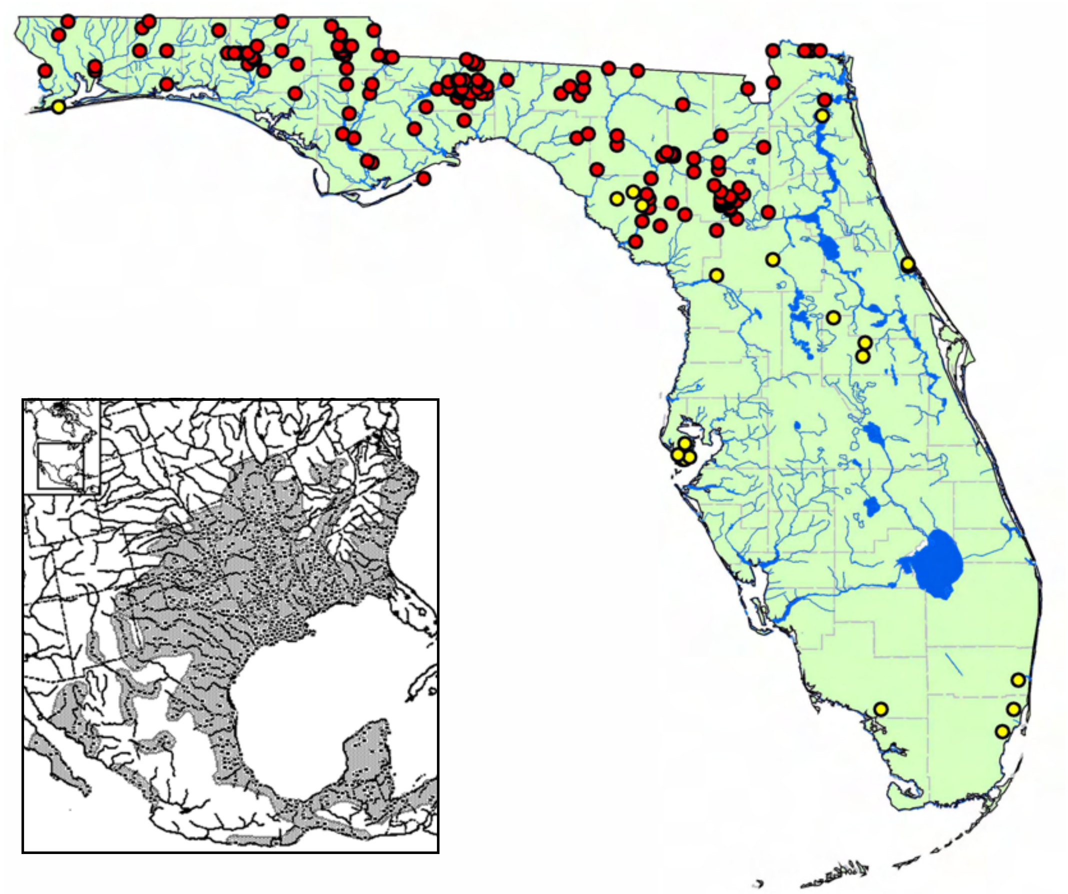

Figure 21-6. Available distribution records (red dots) for yellow-bellied sliders, *Trachemys scripta scripta,* from Florida. Yellow dots indicate records for the introduced red-eared slider, *Trachemys scripta elegans*. Inset: distribution records from most of the range of *T. scripta* (*sensu* Legler, 1990) (adapted from Iverson, 1992a; distribution in inset map not current for Florida as presented here).

were more likely than males to move overland, suggesting that terrestrial activity may be somewhat context dependent (Rose and Manning, 1996; Aresco, 2005). Intrasexual variation in the frequency of overland movements among male *T. scripta* has been observed with melanistic males moving overland among/between aquatic habitats more often than the smaller (on average) nonmelanistic males (Thomas and Parker, 2000).

Temperature Relationships. — Thermoregulation is often accomplished via aerial (i.e., atmospheric) basking. Aerial basking may also provide secondary benefits such as drying of the skin, and/or encouraging the synthesis of vitamin D (Boyer, 1965; Auth, 1975; Spotila et al., 1984). Basking behaviors are well developed in *T. scripta* (Cagle, 1950; Boyer, 1965; Auth, 1975), and even hatchlings participate in such behaviors (Janzen et al., 1992; Lindeman, 1993). Hatchling *T. scripta* often bask on narrower and more steeply sloped structures than adults (Hart, 1983, Dreslik and Kuhns, 2000). Aerial basking activity may occur at anytime of day, but usually peaks during mid-morning or mid-afternoon (Cagle, 1950; McDonald, 1992), and the specific timing of these peaks may vary seasonally (Auth, 1975; Spotila et al., 1984; Dreslik and Kuhns, 2000). Both basking duration and frequency may be influenced by digestive state, acclimation, season, sex, and body size (Auth, 1975; Hammond et al., 1988; Thomas et al., 1999; Grayson and Dorcas, 2004).

In a pond near Gainesville, Florida, the daily number of individual *T. scripta* participating in aerial basking, as well as daily basking frequency of individual *T. scripta* peaked at a daily water temperature of 28.5ºC (Auth, 1975). Operative environmental temperature (T_e) is an index of the thermal environment, and is often positively correlated with air temperature, substrate temperature, short-wave solar radiation, and total solar radiation (see Crawford et al., 1983). Operative environmental temperatures are often good predictors of basking behavior in *T. scripta*, with individuals usually avoiding basking behaviors when T_e is < 28ºC (Crawford et al., 1983). *Trachemys scripta* may limit basking activities when air temperatures exceed 35ºC (McDonald, 1992). Some *T. scripta* bask during winter, especially on relatively warm, sunny days (Auth, 1975; Thomas, *pers. obs*.), but basking has been observed at air temperatures of 2ºC (Schubauer and Parmenter, 1981). Intersexual variation in basking frequency has been observed in *T. scripta,* with males basking more frequently in the fall and winter and females basking more frequently during spring (Auth, 1975; Thomas et al., 1999).

Trachemys scripta may exhibit both inter- and intraspecific aggressive interactions while basking. The frequency of such interactions may increase with the density of the congregation, and larger individuals are more likely to initiate and succeed during such interactions (McDonald, 1992; Lindeman, 1999). However, the relative importance or impact of inter- and intra-specific competition for basking sites has not yet been adequately examined (see Cadi and Joly, 2003, for discussion).

Alternatively, *T. scripta* may thermoregulate within the aquatic environment via aquatic basking or by seeking areas of aquatic habitat that more closely approximate preferred temperature (Boyer, 1965; Auth, 1975; Bury et al., 2000). For example, *T. scripta* selects specific temperatures within aquatic thermal gradients (Crawshaw et al., 1980; Jarling et al., 1984; 1989; Bury et al., 2000). Extreme high temperatures (i.e., > 41ºC) are potentially lethal for *T. scripta* (Brattstrom, 1965), and they may burrow into mud, enter stumps, seek shaded waters, or migrate overland to escape such conditions (Cagle, 1950). Likewise, extreme cold temperatures are potentially fatal (particularly for smaller individuals; Bodie and Semlitsch, 2000b), and the relative effectiveness of seeking "shelter" (Cagle, 1950; Mitchell, 1994) during winter is not known.

GROWTH AND REPRODUCTION

Growth. — The growth pattern of *T. scripta* is characterized by a rapid juvenile growth rate punctuated by an abrupt decline at onset of maturity (Cagle, 1948a, 1950; Tucker and Moll, 1997). Growth rate varies (Cagle, 1946; Tucker and Moll, 1997; Tucker et al., 1995a, 1999a) and several factors may influence growth, e.g., temperature (Christy et al., 1974; Avalos, 1975; Thornhill, 1982; Avery et al., 1993; Thomas, 1993), food availability (Parmenter, 1980), and food quality (Christy et al., 1974; Parmenter, 1980; Avery et al., 1993).

Dimorphism and Size at Maturity. — On average, adult females are larger than males (Cagle, 1950; Gibbons and Lovich, 1990). Males usually become sexually mature between 9.0 and 11.0 cm PL, and females between 15.0 and 19.5 cm PL (Cagle, 1948b; Cagle, 1950; Gibbons and Greene, 1990; Aresco, 2004). Males usually attain sexual maturity between 3–5 yrs and females between 5–8 yrs (Gibbons et al. 1981; Gibbons and Greene, 1990; Tucker and Moll, 1997). Substantial variation in age and size at sexual maturity may exist within and among populations (Cagle, 1948b; Gibbons et al., 1981; Gibbons and Greene, 1990; Thomas, 1993; Tucker et al., 1995b), and minimum size at sexual maturity may be influenced by the size at which the risk of predation decreases (see Tucker et al., 1999a). Secondary sexual characters (e.g., elongated foreclaws and tail) become apparent in male *T. scripta* as they approach sexual maturity, and females usually have relatively shorter foreclaws and tails throughout life (Grant, 1936; Evans, 1951; Gibbons and Greene, 1990). Males become melanistic at a size and age well beyond sexual maturity (Viosca, 1933; Cagle, 1950; McCoy, 1966; Lovich et al., 1990; Tucker et al., 1995b). Most male *T. scripta* eventually become melanistic (Lovich et al., 1990), but female melanism is usually restricted to a slight overwash of the carapace, while the striped pattern of the head, neck, legs, and tail remain unchanged (Lovich et al., 1990). However, the degree of melanin expression in some female sliders can sometimes be much more extensive (F. Rose, *pers. obs*.). The age and size at onset of male melanism varies among populations of *T. scripta* (Cagle, 1950). Average size at onset of melanism coincides with population-specific female size at sexual maturity and not male size at sexual maturity (Tucker et al., 1995b). Also, onset of melanism coincides with maximal development of male foreclaw length (Terrell and Garstka, 1984; Lovich et al., 1990). The adaptive advantages (if any) of ontogenetic melanism in male *T. scripta* remain speculative (see Lovich et al., 1990, for discussion).

Longevity. — Some authors have suggested that adult *T. scripta* follow a Type II survivorship curve with constant rates of mortality at all ages (Gibbons and Semlitsch, 1982; Tucker and Moll, 1997), but recent evidence suggests that adult survivorship may not be constant at all ages and sizes (Tucker et al., 1999b; Bodie and Semlitsch, 2000b). Speculation that natural longevity for *T. scripta* ranged from 50–75 yrs (Cagle, 1950) has not been validated by subsequent research. For example, survivorship curves based on the results of long-term studies at the Savannah River Site near Aiken, South Carolina, estimated probable maximum longevity in natural populations at ca. 30 yrs (Gibbons and Semlitsch, 1982). Also, average minimum ages for *T. scripta* in a Mississippi farm pond were 17.4 and 18.7 yrs for males and females, respectively, and individuals > 30 yrs of age were rare (Parker, 1996).

Male Reproductive Cycle. — The spermatogenic cycle of *T. scripta* can be divided into five phases (see Moll, 1979, for definitions) as follows: (1) germinal quiescence, (2) gonial proliferation, (3) spermatocytogenesis, (4) spermiogenesis, and (5) spermiation. Germinal quiescence begins during late November, and continues until the beginning of a new cycle during the following spring, with minimal seminiferous tubule diameter usually occurring during May (Brewer and Killebrew, 1986). Gonial proliferation begins around mid-May and ends by mid-June (Brewer and Killebrew, 1986). Spermatocytogenesis usually occurs from mid-June through early September with the peak of this phase occurring from mid-July through early August (Brewer and Killebrew, 1986). Spermiogenesis generally peaks during August and ends by mid-November with maximal diameter of the seminiferous tubules occurring during August (Brewer and Killebrew; 1986). Total cell volume is reduced by 79% as spermatids develop into mature spermatozoa (Sprando and Russell, 1988). Some studies report spermiation to begin as early as mid-September, peak during October, and conclude by November (Brewer and Killebrew, 1986; Gist et al., 2001). However, the germ cells of *T. scripta* progress through spermatogenesis in a temporal (rather than spatial) pattern which results in a single massive spermiation event in November (Gross and Garstka, 1984; Gribbins et al., 2003). The potential for geographic and/or subspecific variation in the timing of the spermatogenic cycle of *T. scripta* has not been adequately examined. Likewise, the proximate environmental cues that stimulate the spermatogenic cycle of *T. scripta* are not fully understood, but limited evidence suggests that photoperiod may play a role (Burger, 1937).

Sperm are stored in the epididymides of male *T. scripta*, which may contain viable sperm throughout the year even when testes are fully regressed (Gist et al., 2001). The sperm of *T. scripta* exhibit relatively low motility and remain viable for relatively long periods (e.g., > 40 days in vitro; Gist et al., 2001). Considering the narrow window of time that gametes are produced by male *T. scripta* (Gribbins et al., 2003), these characteristics (i.e., longevity and low motility) may allow for successful copulations over an extended period of time (Gist et al., 2001). Unfortunately, the paucity of detailed information on the seasonal patterns of mating activity in the wild prevents confident assignment of the spermatogenic cycle of *T. scripta* to either an associated or disassociated pattern (Moore and Lindzey, 1992).

Female Reproductive Cycle. — The reproductive cycle of female *T. scripta* can be divided into four phases (see Moll, 1979, for definitions) as follows: (1) follicular enlargement, (2) ovulation and intrauterine period, (3) nesting period, and (4) latent period. The accumulation of yolk protein (vitellogenesis) results in the growth of follicles (Kuchling, 1999). Follicular enlargement usually begins during late summer or fall but may not end until the following spring (Cagle, 1950; Moll, 1979; Congdon and Gibbons, 1990; Moll and Moll, 1990). The follicles tend to enlarge in groups, and several distinct size-groups may be present prior to the nesting season, and these are thought to represent successive clutches (Moll, 1979; Jackson, 1988; Moll and Moll, 1990). Ovulation probably occurs a few weeks prior to nesting (Gibbons and Greene, 1990), and the length of intrauterine period is probably variable (see Moll, 1979). The nesting season of *T. scripta* seems to be similar across its entire distribution and usually begins during spring and ends by midsummer (Cagle, 1950; Jackson, 1988; Gibbons and Greene, 1990; Aresco, 2004). The ovaries are at minimal size during the latent period (Moll, 1979), which usually occurs from June through July (Moll, 1979; Moll and Moll, 1990).

Sperm Storage. — Fertilization is presumed to occur during the short period of time (perhaps < 24 hrs) between ovulation and secretion of the albuminous envelope around the yolk (Kuchling, 1999), while ovulation probably occurs a few weeks prior to nesting (Gibbons and Greene, 1990). The ability of female *T. scripta* to store sperm may be necessary because the timing of sperm transfer does not necessarily coincide with ovulation (see Gist and Congdon, 1998; Pearse and Avise, 2001; Sever and Hamlett, 2002, for discussion). The ability of female *T. scripta* to store sperm may be further necessitated by the fact that females often produce multiple clutches during a single year. The relatively short internesting interval of this species permits very little time for mating (Gist and Congdon, 1998; Tucker, 2001a). Female *T. scripta* possess sperm storage tubules that are found within the posterior portion of the albumen-secreting section of the oviduct, and sperm have been found within the tubules of *T. scripta* held in isolation for > 79 days (Gist and Jones, 1989).

The sperm storage capabilities of *T. scripta* coupled with their particular suite of life-history characteristics make this species an ideal candidate for the application of various models of sperm allocation strategies (e.g., see Reinhold et al., 2002). Specific application of such models to *T. scripta* may assist researchers in their attempts to identify the peak time of sperm transfer, and speed progress toward developing a better understanding of *T. scripta* reproductive strategies and fitness relationships.

Courtship and Mating Behavior. — Courtship behaviors of male *T. scripta* may include biting, chasing (Davis and Jackson, 1973; Thomas, 1999, 2002), and so-called “titillation” behaviors that involve facing the female and vibrating the foreclaws across or near the face of the female (Taylor, 1933; Grant, 1936; Cagle, 1950; Jackson and Davis, 1972; Thomas, 1999, 2002). Male *T. scripta* may use a conditional mating strategy (as defined in Gross, 1996) with larger and older melanistic males courting females with biting and chasing behaviors coupled with a greater precopulatory display rate, while nonmelanistic males use titillation behaviors and a lower precopulatory display rate (Thomas, 2002). However, there is much that is not understood regarding the courtship behaviors of *T. scripta* (Cagle, 1955; Rives, 1978; Gist et al., 1990; Kuchling, 1999; Thomas, 1999, 2002; Cash, 2000; Pearse and Avise, 2001; Thomas and Altig, 2006).

During what has been assumed to represent a typical copulation, the male moves to the rear of the female, while the female is positioned horizontally and motionless. The male lowers his tail and moves the rear medial portion of his shell close to that of the female. The tails of the two interlock and the male moves into an almost vertical position relative to the horizontally positioned female (Davis and Jackson, 1970).

Mating Season. — Traditionally, it has been assumed that courtship activities of male *T. scripta* peak during spring, with some authors recognizing a second (and often assumed as less important) peak occurring during the fall (see Cagle, 1950; Carr, 1952; Ernst and Barbour, 1989; Ernst et al., 1994; Buhlmann and Gibbons, 2001; Gribbins et al., 2003). However, some authors have noted that courtship activities may occur (to some degree) at any time of year (e.g., Lardie, 1980; Gibbons and Greene, 1990; Nijs and Janssen, 1993); others have concluded that the most important peak of courtship activities for *T. scripta* occurred during fall (Thomas et al., 1999; Thomas, 1999, 2002; Cash, 2000). To further complicate the issue, studies of sperm storage in adult *T. scripta* (both sexes) indicate that any of these scenarios are physically possible (Gist and Congdon, 1998; Gist et al., 2000, 2001). My interpretation of the available evidence is that while courtship activities may occur at any time of year, the peak of such activity probably occurs during fall with mating activities continuing (to some degree) into winter and the following spring. However, the possibility of geographic variation in the timing and performance of courtship behaviors of *T. scripta* has not been properly examined (see Foster and Endler, 1999), and the behaviors that we commonly associate with courtship (e.g., titillation) are not fully understood (Rives, 1978; Kramer and Burghardt, 1998; Kuchling, 1999; Thomas, 2002; Thomas and Altig, 2006). Because the communicative functions of titillation displays are not fully understood, some have proposed that the term titillation is inappropriate and should be replaced with "foreclaw display" which is neutral with respect to communicative purpose (Thomas and Altig, 2006).

Nesting Season / Nest Sites / Nesting Behavior. — *Trachemys scripta* usually nest in relatively open areas during early morning or late evening (Cagle, 1937; Tucker, 1997). Female *T. scripta* may partially excavate several "trial" holes before actually nesting (Cagle, 1950), and may remain stationary in a concealed position for short periods of time (Buhlmann and Gibbons, 2001). The female may press her head and neck against the substrate (i.e., ground-nuzzling behavior) at several locations prior to nest construction, which may represent a mechanism to assess nest-site characteristics (e.g., temperature, moisture) prior to nest construction (Morjan and Valenzuela, 2001). Female *T. scripta* may also exhibit a certain degree of nest-site fidelity (Tucker, 2001b).

During nest construction, the forelimbs are planted firmly against the substrate while the hindlimbs are used for excavation (Cagle, 1937). Female *T. scripta* may release urine onto the soil (presumably) to facilitate excavation (Cagle, 1937, 1950). Excavation of the nest may take anywhere from 26–187 min (Cagle, 1950), and eggs are laid into the nest at ca. 40 sec intervals (Cahn, 1937). The posterior portions of the shell and the hindlimbs are then used to cover the nest (Cagle, 1937). The typical nest of *T. scripta* has been described as a jug-shaped cavity plugged with soil (Cagle, 1950). The form of the nest can be highly variable and may be somewhat dependent on soil characteristics (Cagle, 1950) and/or female body size (Congdon and Gibbons, 1985; Tucker, 1997).

In Florida, most sliders nest between mid-March and mid-July (Jackson, 1988, 1994; Aresco, 2004). Aresco (2004) noted that 55% of all observations of nesting sliders in northwestern Florida occurred in May, but a small number of females were observed nesting as late as August. Throughout their entire range, the nesting season of *T. scripta* is variable, however, most nesting occurs from mid-April to mid-July with a peak period from late May to early June (Cagle, 1950; Gibbons and Greene, 1990; Palmer and Braswell, 1995; Tucker, 1997; Buhlmann and Gibbons, 2001). There is some evidence that maternal body mass may influence the timing of oviposition (Tucker, 1999a). The proximate cues (e.g., rainfall, temperature, photoperiod) that stimulate nesting excursions by female *T. scripta* are not fully understood, but there is evidence that temperature and rainfall are important (see Tucker, 1997, for discussion).

Female *T. scripta* may construct nests anywhere from < 10 m to > 500 m from the maternal aquatic habitat (Cagle, 1950; Buhlmann and Gibbons, 2001; Tucker, 1997, 2000a; Burke et al., 1998). Studies of *T. scripta* inhabiting west-central Illinois revealed that overall internesting interval ranged from 6–41 days, and significant variation (among sites) in internesting interval, but found no evidence of year-to-year variation in the internesting interval (Tucker, 2001a).

Eggs. — The eggs of *T. scripta* are ovoid with a flexible white shell that becomes more rigid as water is absorbed (Cagle, 1950), and are about 72.2% water (Congdon and Gibbons, 1990). Egg size is variable with egg length usually ranging from 23.0–44.2 mm, egg width from 18.0–25.4 mm, and egg mass from 9.0–13.9 g (Cagle, 1950; Iverson, 1977; Jackson, 1988; Congdon and Gibbons, 1983, 1985, 1990; Tucker and Moll, 1997; Tucker and Janzen, 1998; Tucker et al., 1998a, b; Marlen and Fischer, 1999; Tucker and Warner, 1999). Egg mass may even vary among sites within relative close proximity to each another (Tucker and Warner, 1999). Body size is usually positively correlated with egg mass and egg width, but not egg length (Congdon and Gibbons, 1983). The shape of *T. scripta* eggs (but not the mass) varies with order of oviposition within a given clutch, and the first and last two eggs are significantly longer than those laid intermediately (Tucker and Janzen, 1998).

Clutch Size and Relative Clutch Mass. — Average clutch size for *T. scripta* usually ranges from 5–20 eggs (Cahn, 1937; Cagle, 1950; Webb, 1961; Iverson, 1977; Congdon and Gibbons, 1983; Fitch, 1985; Jackson, 1988; Frazer et al., 1990; Mitchell and Pague, 1990; Thomas, 1993; Tucker and Moll, 1997; Tucker and Janzen, 1998; Tucker et al., 1998a, b; Marlen and Fischer, 1999; Tucker and Warner, 1999; Li and Tang, 2001; Aresco, 2004), with a maximum clutch size of 31 eggs (Thomas, 1993). Clutch size varies, however, the proportional investment per clutch apparently remains fairly constant among populations even among those with differing growth rates and body sizes (Congdon and Gibbons, 1983). Numerous authors have documented the relationship between clutch size and maternal body size in *T. scripta* (e.g., Cagle, 1950; Congdon and Gibbons, 1983, 1985; Gibbons, 1982; Jackson, 1988; Gibbons and Greene, 1990; Mitchell and Pague, 1990; Iverson, 1992b; Tucker et al., 1998a, b; Thomas, 1993; Tucker and Moll, 1997; Aresco, 2004). Average relative clutch mass typically ranges between 0.056–0.097, but is not usually correlated with female body size (Jackson, 1988; Thomas, 1993; Tucker et al., 1998b).

Reproductive Potential. — Estimates of annual reproductive potential for female *T. scripta* are highly variable, ranging from 6.88 to 38.8 eggs/season (Cagle, 1950; Jackson, 1988; Frazer et al., 1990; Thomas, 1993). Maternal body size is usually a good predictor of variation in reproductive output within *T. scripta*, however, significant year-to-year variation in reproductive output may exist independent of body size (Tucker et al., 1998a).

Throughout their range, annual clutch frequency of *T. scripta* usually ranges from 0–3 clutches per year (Cagle, 1950; Moll and Legler, 1971; Thornhill, 1982; Jackson, 1988; Mitchell and Pague, 1990; Moll and Moll, 1990;

Gibbons and Greene, 1990; Frazer et al., 1990; Li and Tang, 2001; Tucker, 2001a). Iverson (1977) suspected that *T. s. scripta* produced multiple clutches in northern Florida, which is consistent with subsequent reports that these sliders may produce 3–5 clutches per season (Jackson, 1988). In contrast, evidence of multiple clutches was not observed in a study of sliders in northwestern Florida, but this could have been related (directly or indirectly) to a severe drought that occurred during the study period (Aresco, 2004). There is some evidence that clutch frequency may decrease with decreasing latitude (Tucker et al., 1998a), however, interpretation of such patterns is difficult because estimates of clutch frequency may vary depending on the particular technique used to estimate clutch frequency (Tucker, 2001a). Not all female *T. scripta* nest annually, with as many as 37% of females failing to nest during a particular year (Frazer et al., 1990; Gist and Congdon, 1998). There is currently no evidence of reproductive senescence in *T. scripta* (Tucker and Moll, 1997), and it is assumed that reproductive activity continues throughout their lives. This assumption is consistent with what has been observed in other species (e.g., *Terrapene carolina*; Miller, 2001).

Incubation and Hatching. — The incubation period for *T. scripta* eggs is variable but may range from 60–91 days (Cagle, 1950; Iverson, 1977; Congdon and Gibbons, 1990; Jackson, 1994; Tucker and Warner, 1999; Tucker and Paukstis, 1999). *Trachemys scripta* eggs incubated at temperatures ranging from 24 to 30ºC usually hatch, while incubation temperatures > 40ºC may be lethal (Cagle, 1950). Soil moisture during both incubation and overwintering may influence hatchling mass, hydration, and survivorship (Tucker and Paukstis, 1999). Early-stage *T. scripta* embryos (19–22 days) are less susceptible to excessive moisture than late-stage embryos (39–42 days), and nest flooding probably results in greater nest mortality for late-staged embryos (Tucker et al., 1997).

Trachemys scripta exhibits temperature-dependent sex determination (TSD) with relatively cool temperatures producing males and relatively warm temperatures producing females, and the pivotal temperature (temperature that produces 1:1 sex ratio) is about 29.0 to 29.5ºC (Bull et al., 1982). The middle-third of the incubation period is thought to represent the thermosensitive period (see Wibbels et al., 1998, for review). Factors other than temperature (e.g., CO_2 levels; pH) may play a role in sex-determination (Etchberger et al., 1991, 1992, 2002), and many questions regarding the evolutionary significance of TSD remain unanswered (Valenzuela et al., 2003).

Trachemys scripta usually hatch sometime between July and September, however, some remain in the nest (i.e., overwinter) and emerge sometime between February and May of the following year (Cagle, 1944b, 1950; Mount, 1975; Gibbons and Nelson, 1978; Jackson, 1994; Tucker, 1997, 1999b, 2000b; Tucker and Packard, 1998; Aresco, 2004). In either case, there is minimal (if any) overlap between the time of hatchling emergence and the nesting season (see Tucker, 1997, for discussion).

Most hatchling *T. scripta* emerge and move overland to the aquatic habitat diurnally (Tucker, 1997). The timing of the emergence of *T. scripta* hatchlings that have overwintered is positively correlated with both daily low and high temperatures (Tucker, 1999b). Emergence of hatchling *T. scripta* is not directly correlated with rainfall, but emergence usually occurs subsequent to a precipitation event (Tucker, 1999b). Also, hatchling *T. scripta* are more likely to emerge when the temperature at the top of nest exceeds that of the bottom (Tucker, 1999b). Young *T. scripta* escape the egg by using their egg tooth, their foreclaws, or by pushing through the shell with their head and/or limbs (Cagle, 1950). Yolk resorption usually occurs immediately prior to or shortly after hatching (Cagle, 1944b, 1950), and the egg tooth is usually retained for only a few days after hatching (Cagle, 1944b).

Hatchling Size. — Hatchling body size ranges from 22.5–35.4 mm CL and 3.94–10.02 g (Iverson, 1977; Tucker, 1997, 2000b; Jackson, 1988; Tucker and Moll, 1997; Marlen and Fischer, 1999; Tucker and Warner, 1999; Aresco, 2004). Variation in environmental factors (e.g., moisture, severity of winter, etc.), and maternal investment may result in significant variation in hatchling body sizes (Congdon and Gibbons, 1990; Tucker, 2000b). Initial egg mass, egg width, and maternal body size may also influence hatchling body size (Tucker and Moll, 1997; Tucker and Warner, 1999).

Parental investment by female turtles occurs prior to ovulation and primarily consists of producing yolk material (e.g., lipids) in excess of the amount necessary to produce a hatchling (Congdon and Gibbons, 1985). Maternally transferred non-polar lipids provide enough stored lipids to support *T. scripta* hatchlings for ca. 58 days (Marlen and Fischer, 1999). Therefore, egg lipid proportions may influence the length of time hatchlings delay emergence (Congdon and Gibbons, 1983, 1985). Hatchling *T. scripta* lose mass while overwintering, and this loss may represent the use of residual yolk (Tucker and Paukstis, 1999). These lipids may also facilitate survival of hatchling *T. scripta* when caloric demands exceed caloric intake (e.g., overwintering or migration from nest to aquatic habitat; Tucker et al., 1998c; Tucker and Paukstis, 1999).

POPULATION BIOLOGY

Density and Biomass. — In general, *T. scripta* is common across its range (Ernst et al., 1994; Mitchell, 1994), and it is often the most abundant species within its preferred habitats (Parker, 1939; Cagle, 1942, 1950; Cagle and Chaney, 1950; Congdon et al., 1986; Anderson et al., 2002). The density and biomass of this species may exceed that of the remainder of the turtle community within some habitats (Congdon et al., 1986). Sliders comprised 41.9% (2097) of the 5000 turtles captured while exiting the rapidly drying Lake Jackson, Leon Co., Florida, during a drought (Aresco, 2002). Studies of the temporal dynamics of turtle assemblages in Alabama farm ponds suggest that overall abundance of *T. scripta* either remained stable or increased over time (Stone et al., 1993), however, these results cannot necessarily be extrapolated to other populations (see Frazer et al., 1990).

Population Structure. — Estimates of sex ratios within wild populations of *T. scripta* vary, but most indicate a predominance of males (see Gibbons, 1990b; Aresco, 2005), although a predominance of females within some populations has been reported (Rose and Manning, 1996). Estimates of sex-ratios are usually biased because of various problems associated with methods of collection (see Cagle and Chaney, 1950; Ream and Ream, 1966; Thomas et al., 1999). Thus, actual sex ratios among populations of *T. scripta* are not usually known. Actual sex ratios within *T. scripta* populations are probably influenced by four factors: (1) sex ratios of hatchlings, (2) differential mortality of the sexes, (3) differential emigration and immigration rates of the sexes, and (4) differences in age at maturity of the sexes (Gibbons, 1990b).

INTERSPECIFIC INTERACTIONS

Community Structure. — Across their distribution, sliders may be found in association with a number of other species, e.g., *Chelydra serpentina*, *Chrysemys picta*, *Pseudemys concinna*, *P. floridana*, *Deirochelys reticularia*, *Sternotherus odoratus*, *Apalone spinifera*, *A. ferox*, *Kinosternon subrubrum*, *Macrochelys temminckii*, and *Graptemys geographica* (Cagle, 1942; Cagle and Chaney, 1950; Iverson, 1977; Jackson, 1988; Thomas et al., 1994; Bodie and Semlitsch, 2000a; Bodie, et al., 2000; Anderson et al., 2002; Aresco, 2002). This species was found with approximately equal numbers of *Pseudemys nelsoni* and *P. floridana* in a drying lake (wet prairie) near Gainesville, Florida (Fig. 21-7) (B. Taylor and P.A. Meylan, unpubl. data).

Diet and Feeding. — *Trachemys scripta* is an omnivore and consumes a diverse array of both plants and animals (Parker, 1939; Marchand, 1942; Cagle, 1950; Webb, 1961; Avalos, 1975; Parmenter, 1980; Schubauer and Parmenter, 1981; Bjorndal, 1991; Thomas, 1993; Thomas et al., 1994; Ernst et al., 1994; Chen and Lue, 1998; Dreslik, 1999; Johnston and Johnston, 2003c). Digestive physiology of this species suggests frequent consumption and digestion of small meals (Secor and Diamond, 1999). Most *T. scripta* locate and ingest their food within the aquatic environment. Terrestrial foraging has been reported (Cagle, 1944a; Thomas, *pers. obs.*), but the relative importance of this mode of foraging is not known. Feeding activities are usually concentrated during the early morning hours (Cagle, 1950), and may occur at any time of year (Schubauer and Parmenter, 1981).

The diet of *T. scripta* may vary seasonally (Clark and Gibbons, 1969; Schubauer and Parmenter, 1981; Dreslik, 1999), and/or ontogenetically with a switch from carnivory in juveniles to herbivory in adults (Clark and Gibbons, 1969; Hart, 1983). However, not all observations have been consistent with an ontogenetic switch from carnivory to herbivory (see Dreslik, 1999).

Maximum ingestion rates for *T. scripta* occur at ca. 29°C and decrease with higher and lower temperatures; and elevated body temperatures decrease digestive turnover times and increase assimilation efficiencies (Parmenter, 1980). Composition of the diet may influence digestive efficiency, for example, *T. scripta* may obtain significantly more energy from duckweed (Lemnaceae) when consumed with insects than when ingested alone (Bjorndal, 1991).

Predation. — Skunks (*Mephitus* sp.), raccoons (*Procyon lotor*), rice rats (*Oryzomys palustris*), various snakes, and shrews (*Blarina brevicauda*, *Cryptotis parva*) commonly consume *T. scripta* eggs (Cagle, 1949, 1950; Goodpaster and Hoffmeister, 1952; Burke et al., 1998; Hamilton et al., 2002; Aresco, 2004). Nest predation rates are usually high with estimates ranging from 84.2 to > 90% (Cagle, 1950; Burke et al., 1998; Hamilton et al., 2002; Aresco, 2004). Armadillos (*Dasypus novemcinctus*) have been suspected as predators of slider nests, but documentation appears to be lacking (Hamilton et al., 2002). Various fungi, ants, and larval dipterans may pose additional threats to nests of *T. scripta* (Cagle, 1937; Aresco, 2004). Cagle

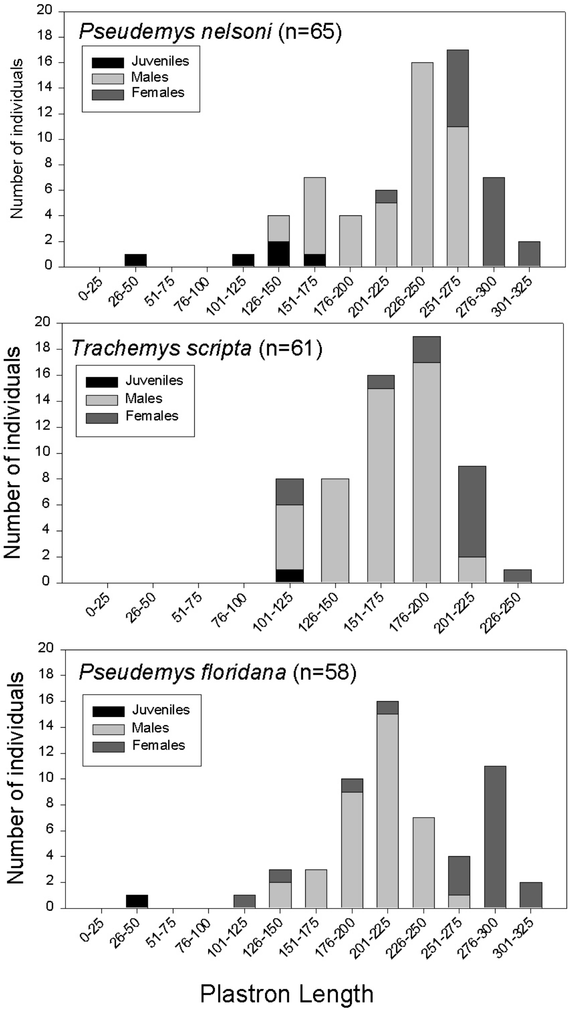

Figure 21-7. Population structure for three species of emydid turtles from a drying pool in Lake Kanapaha, Alachua County, Florida, during a drought in 1981–82 (B. Taylor and P.A. Meylan, unpubl. data).

(1950) speculated that nest density increases risk of predation on *T. scripta* eggs, but subsequent studies have found no evidence that predation rate is influenced by nest density, general habitat type, or distance from the maternal aquatic habitat (Burke et al., 1998). However, there is evidence that the presence of deer feeders increases the risk of predation to the nests of *T. s. scripta* in northern Florida (Hamilton et al., 2002).

Both hatchling and small juvenile *T. scripta* face relatively high levels of predation (Frazer et al., 1990) by a diversity of predators (Cagle, 1950; Goodpaster and Hoffmeister, 1952; Burke et al., 1998; Janzen et al., 2000a). For example, juvenile mortality rates were estimated at ca. 89.5% in a South Carolina population of *T. scripta* (Frazer et al., 1990). Historically, it was assumed that large predatory fish (e.g., largemouth bass) were common predators of hatchling turtles, however, largemouth bass (*Micropterus salmoides*) do not commonly prey upon *T. scripta* of any size (Semlitsch and Gibbons, 1989; Britson, 1998).

During post-emergent migrations to water, large neonatal *T. scripta* usually have a greater chance of survival than smaller individuals (see Filorama and Janzen, 2002, for possible exception), with diurnal avian predators being the most likely source of predation. The enhanced survival of large hatchlings may be related to their ability to move more rapidly than smaller hatchlings (Janzen et al., 2000a, b). Hatchling turtles may use alternative strategies during their post-emergent migrations to water, which may reflect a tradeoff between risk of predation and risk of desiccation (see Kolbe and Janzen, 2002). A “fast” trip may result in greater water loss that impairs locomotor abilities and/or increased desiccation mortality, but decreased risk of predation, while “slow” travel may decrease rate of water loss and increase risk of predation. When compared to hatchling *Chrysemys picta*, *T. scripta* minimized water loss by moving relatively slowly toward water, but moved more quickly when favorable weather conditions reduced desiccation risks (Finkler, 1999; Tucker, 2000a; Kolbe and Janzen, 2002). Hatchling *T. scripta* may (to some degree) be able to avoid both desiccation and predation by burying themselves underneath soil when post-emergent migrations occur under xeric conditions (Filorama and Janzen, 2002).

Adult sliders have few natural enemies (other than humans), but some are taken by alligators (*Alligator mississippiensis*; Cagle, 1950), large gar (*Lepisosteidae*; Cagle, 1950), crows (*Corvis* sp.; Cagle, 1950), mink (*Mustela vison*; Cagle, 1950), otter (*Lutra canadensis*; Stophlet, 1947; Cagle, 1950), and raccoons (*P. lotor*; Cagle, 1950; Rose and Manning, 1996; Tucker et al., 1999b). In spite of the fact that population stability in turtles is probably most sensitive to the loss of adults (Congdon et al., 1993; Tucker and Moll, 1997), the proportional population level impacts of each of these potential predators are not known. Adult survivorship is usually relatively high (Frazer et al., 1990; Tucker and Moll, 1997), and risk of predation to nesting *T.* scripta decreases as body size increases (Tucker et al., 1999b).

Parasites and Disease. — *Trachemys scripta* commonly serves as a host to a variety of both internal and external parasites, e.g., intestinal helminths and nematodes (Esch et al., 1990; Thomas et al., 1994; Johnson et al., 1998), leeches (Boyer, 1965; Thomas, *pers. obs*.), and algae (Proctor, 1958; Boyer, 1965; Thomas, *pers. obs*.). Some of these parasites are potentially harmful or even fatal (see Johnson et al., 1998), but the relative danger posed by most turtle parasites remains largely speculative. Likewise, the possibility that some of these organisms are not actually parasitic but rather symbiotic has not been adequately explored.

Necrotic shell disease is sometimes common among captive *T. scripta* (Li and Tang, 2001), as well as within some wild populations (i.e., as high as 35%; Lovich et al., 1996). Necrotic shell disease has been observed in several turtle species, including species that aerially bask as well as those often considered as non-baskers (Ernst et al., 1999). The expression of necrotic shell disease may vary geographically, but usually involves (some or all) of the following: (1) lesions on the skin; (2) lesions and eroded patches on the shell; and (3) sores on the skin that resemble leprosy-like lesions (Ernst et al., 1999; Li and Tang, 2001). The macroscopic appearance of the lesions varies, however, a series of histological changes are usually associated with the progression of the disease. Initial signs of the disease usually involve acute segmental necrosis of the epidermis, followed by ulceration, necrosis of dermis and dermal bone, and exaggerated remodeling of bone (Garner et al., 1997). Currently, there is very limited information on the cause(s), prevalence, progression, and impact(s) of necrotic shell disease in turtles. Contact with environmental pollutants (e.g., PCB’s, dioxins, furans, heavy metals) may play a role by facilitating secondary bacterial, fungal, or protozoan infections, and ectoparasites (e.g., algae) on the shell may contribute to the damage that results from the disease (Garner et al., 1997; Ernst et al., 1999). Further study is needed to assess the impact(s) of necrotic shell disease in turtles.

THREATS

Man probably poses the greatest threat (either directly or indirectly) to *T. scripta* (Cagle, 1937, 1950; Ernst et al., 1994; Close and Siegel, 1997; Aresco, 2005). Juvenile *T. scripta* have been collected for sale as pets (Cagle, 1950), fishermen sometimes collect eggs for use as fish bait (Cagle, 1937), and some fishermen destroy *T. scripta* due to the common (but erroneous) belief that they are harmful to fish populations (Cagle, 1950; Thomas, *pers. obs*.). Fishermen in northern Florida occasionally catch sliders while fishing, and have been observed killing these animals with pliers, machetes, and other blunt objects (M. Aresco, *pers. obs*.). Enge (1994) reported that more than 2300 live *T. s. scripta* were collected from the wild in Florida and sold in the pet trade during a two-year period (1990–92). In 1999, the United States exported ca. 8,000,000 hatchlings to 60 different nations (Williams, 1999), mainly from turtle farms. Negative impacts on some local populations of *T. scripta* as a direct result of commercial harvest have been suspected (Close and Seigel, 1997). Efforts at captive propagation of *T.*

scripta have received criticism for a variety of reasons (Williams, 1999). In particular, turtle farmers often remove large female *T. scripta* from wild populations for the purpose of supplementing breeding stock (Warwick, 1986; Warwick et al., 1990). This practice is of concern because turtle populations are probably more sensitive to the loss of large adults than other life stages (Tucker and Moll, 1997).

Modeling of road-mortality suggests that road-associated mortality may not threaten populations of "small-bodied" pond turtles such as *T. scripta* (Gibbs and Shriver, 2002). In spite of these models, many turtles (including *T. scripta*) are killed on our roads (Aresco, 2002, 2003, 2005; see *P. floridana* account for further discussion), and such problems may worsen as human populations continue to increase. Likewise, alteration (or outright destruction) of aquatic habitats and adjacent terrestrial zones for anthropogenic purposes often negatively impacts resident wildlife, and such conversion will likely increase along with our population. The habitat requirements of *T. scripta* are very general which allows them to occupy a diverse array of aquatic habitats, but studies have demonstrated their dependence on both the aquatic as well as adjacent terrestrial habitat (see Burke and Gibbons, 1995).

The threat of imported fire ants (*Solenopsis invicta*) is generally thought to be serious for turtles, but has not been specifically assessed for *T. scripta* (Moulis, 1997). Many of the potential impacts of introduced *T. s. elegans* on native *T. s. scripta* (or any other turtle species) through competition or any other mechanism remain speculative (Luiselli et al., 1997; Chen and Lue, 1998). However, recent research has provided evidence that the presence of exotic *T. s. elegans* negatively impacts at least some native species (e.g., Cadi and Joly, 2003, 2004). Exotic *T. s. elegans* may outcompete some species (e.g., *Emys orbicularis*, *Actinemys marmorata*) for preferred basking sites, however, the consequences of such competition remains speculative (Cadi and Joly, 2003; Spinks et al., 2003). Interbreeding populations of the various subspecies of *Trachemys* (due to human introductions) are known (see Ernst and Jett, 1969; Mitchell, 1994), but the impacts of this genetic pollution are not known. Numerous studies have documented negative impacts of introduced species on native wildlife (see Devine, 1998; Cox, 1999; Elton, 2000), and I believe that the abundance of such varied examples coupled with the specific evidence provided by Cadi and Joly (2003, 2004) are sufficient to at least warrant concern over the potential impacts of exotic *T. s. elegans* on native species.

Numerous man-made pollutants are known to negatively influence endocrine function and development in vertebrates (see Crisp et al., 1998). Studies designed to specifically examine potential population-level impacts of endocrine disrupting compounds (e.g., chlordane, DDT, and polychlorinated biphenyls) on turtles (e.g., *T. scripta*) are needed (Willingham and Crews, 2000; Willingham et al., 2000). In general, toxicological studies often neglect to investigate possible sublethal effects of pesticides and/or other pollutants, but these could be important (e.g., Hall, 1980; Willingham and Crews, 2000; Willingham, 2001). For example, chronic exposure to sublethal levels of pesticides may influence the growth of hatchlings (Willingham, 2001). Juvenile growth rates influence size and age at sexual maturity of *T. scripta* (Gibbons et al., 1981), and altering life-history traits such as average size/age at sexual maturity within a population of turtles may influence average fecundity/fitness within that population (Iverson, 1992b; Congdon et al., 1993). Therefore, pesticides may have long-term consequences on the population dynamics of *T. scripta*, but I am unaware of any study documenting such impacts on turtle populations.

STATUS

Considered relatively abundant throughout its natural range in Florida as well as across its entire distribution. *Trachemys scripta* is not currently listed by CITES, USFWS, FCREPA, or IUCN.

CONSERVATION OPTIONS AND SOLUTIONS

Trachemys scripta is not listed as a protected species, and at present, is considered quite common. However, steps should be taken to insure that this common species remains common. Education of the public may be the most powerful tool available for conserving turtle populations (see also *P. floridana* account). For example, increasing the awareness of both pet dealers and pet owners about the potential dangers of releasing non-native pets (e.g., *T. scripta*) could be required (or at least strongly encouraged).

Maintenance of appropriate terrestrial buffer zones surrounding wetlands may help protect nesting habitat and overland migration corridors (Bodie and Semlitsch, 2000a; Buhlmann and Gibbons, 2001). Federal wetland protection statutes are sometimes inadequate to protect the necessary terrestrial habitats of freshwater turtles (including *T. scripta*; Burke and Gibbons, 1995). Therefore, it is important to re-evaluate current terrestrial buffer zone requirements with the specific needs of turtles in mind (see also Bodie, 2001). Also, monitoring the impact of road mortality to locate specific crossing areas with high rates of mortality might allow for more effective placement of structures that permit safe passage. Quantitative assessment of the relative effectiveness of such structures is needed in order to more effectively protect turtles from road-associated mortality (e.g., Aresco, 2003). Reducing mortality of adult *T. scripta* during overland migrations is particularly important given that protection of adults (particularly large females) is probably more effective at maintaining turtle populations than measures that strictly focus on the protection of eggs and/or hatchlings (Tucker and Moll, 1997; Congdon et al., 1993).

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LITERATURE CITED

Anderson, R. V., Gutierrez, M.L., and Romano, M.A. 2002. Turtle habitat use in a reach of the upper Mississippi River. Journal of Freshwater Ecology 17:171-178.

Anton, T. G. 1987. Notes on winter activity in a red-eared slider, *Trachemys scripta elegans*. Bulletin of the Chicago Herpetological Society 22:131.

Aresco, M. J. 2002. Surviving drought: Lake Jackson's turtles. Florida Wildlife 56:26-28.

Aresco, M. J. 2003. Highway mortality of turtles and other herpetofauna at Lake Jackson, Florida, USA and the efficacy of a temporary fence/culvert system to reduce road kills. In: Irwin, C. L., Garrett, P., and McDermott, K.P. (Eds.). Proceedings on the International Conference on Ecology and Transportation. North Carolina State University, Raleigh, NC, pp. 433-449.

Aresco, M. J. 2004. Reproductive ecology of *Pseudemys floridana* and *Trachemys scripta* (Testudines: Emydidae) in northwestern Florida. Journal of Herpetology 38:89-96.

Aresco, M. J. 2005. The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. Biological Conservation 123:37-44.

Auth, D. L. 1975. Behavioral ecology of basking in the yellow-bellied turtle, *Chrysemys scripta scripta* (Schoepff). Bulletin of the Florida State Museum of Biological Sciences 20:1-45.

Avalos, D. 1975. The growth of the red-ear turtle *Pseudemys scripta elegans* in a thermal lake in southwestern Illinois. M.S. Thesis, Eastern Illinois University, Charleston. 22 pp.

Avery, H. W., Spotila, J.R., Congdon, J.D., Fischer, Jr., R.U., Standora, E.A., and Avery, S.B. 1993. Roles of diet protein and temperature in the growth and nutritional energetics of juvenile slider turtles, *Trachemys scripta*. Physiological Zoology 66:902-925.

Bancroft, G. T., Godley, J.S., Gross, D.T., Rojas, N.N., Sutphen, D.A., and McDiarmid, R.W. 1983. Large scale operations management test of the use of the white amur for control of problem aquatic plants; the herpetofauna of Lake Conway, Florida: species accounts. U.S. Army Engineers Water Experimental Station, CE, Vicksburg, Mississippi. 304 pp.

Bennett, D. H., Gibbons, J.W., and Franson, J.C. 1970. Terrestrial activity in aquatic turtles. Ecology 51:738-740.

Bjorndal, K. A. 1991. Diet mixing: nonadditive interactions of diet items in an omnivorous freshwater turtle. Ecology 72:1234-1241.

Bodie, J. R. 2001. Stream and riparian management for freshwater turtles. Journal of Environmental Management 62:443-455.

Bodie, J. R., and Semlitsch, R.D. 2000a. Spatial and temporal use of floodplain habitats by lentic and lotic species of aquatic turtles. Oecologia 122:138-146.

Bodie, J. R., and Semlitsch, R.D. 2000b. Size-specific mortality and natural selection in freshwater turtles. Copeia 2000:732-739.

Bodie, J. R., Semlitsch, R.D., and Renken, R.B. 2000. Diversity and structure of turtle assemblages: associations with wetland characters across a floodplain landscape. Ecography 23:444-456.

Boyer, D. R., 1965. Ecology of the basking habit in turtles. Ecology 46:99-118.

Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist 73:376-422.

Brewer, K., and Killebrew, F. C. 1986. The annual testicular cycle of *Pseudemys scripta elegans* (Emydidae) in the Texas panhandle. Southwestern Naturalist 31:299-305.

Brimley, C. S. 1907. Notes on some turtles of the genus *Pseudemys*. Journal of the Elisha Mitchell Scientific Society 23:76-84.

Britson, C. A. 1998. Predatory responses of largemouth bass (*Micropterus salmoides*) to conspicuous and cryptic hatchling turtles: a comparative experiment. Copeia 1998:383-390.

Buhlmann, K. A., and Gibbons, J.W. 2001. Terrestrial habitat use by aquatic turtles from a seasonally fluctuating wetland: implications for wetland conservation boundaries. Chelonian Conservation and Biology 4:115-127.

Bull, J. J., Vogt, R.C., and McCoy, C.J. 1982. Sex determining temperatures in turtles: a geographic comparison. Evolution 36:326-332.

Burger, J. W. 1937. Experimental sexual photoperiodicity in the male turtle, *Pseudemys elegans* (Wied). American Naturalist 71:481-487.

Burke, V. J., and Gibbons, J.W. 1995. Terrestrial buffer zones and wetland conservation: a case study of freshwater turtles in a Carolina bay. Conservation Biology 9:1365-1369.

Burke, V. J., Greene, J.L., and Gibbons, J.W. 1995. The effect of sample size and study duration on metapopulation estimates for slider turtles (*Trachemys scripta*). Herpetologica 51:451-456.

Burke, V. J., Rathbun, S.L., Bodie, J.R., and Gibbons, J.W. 1998. Effect of density on predation rate for turtle nests in a complex landscape. Oikos 83:3-11.

Bury, R. B., Nebeker, A.V., and Adams, M.J. 2000. Response of hatchling and yearling turtles to thermal gradients: comparison of *Chelydra serpentina* and *Trachemys scripta*. Journal of Thermal Biology 25:221-225.

Butterfield, B. P., Meshaka, Jr., W.E., and Hauge, J.B. 1994. Two turtles new to the Florida keys. Herpetological Review 25:81.

Cadi, A., and Joly, P. 2003. Competition for basking places between the endangered European pond turtle (*Emys orbicularis galloitalica*) and the introduced red-eared slider (*Trachemys scripta elegans*). Canadian Journal of Zoology 81:1392-1398.

Cadi, A., and Joly, P. 2004. Impact of the introduction of the red-eared slider (*Trachemys scripta elegans*) on survival rates of the European pond turtle (*Emys orbicularis*). Biodiversity and Conservation 13:2511-2518.

Cagle, F. R. 1937. Egg laying habits of the slider turtle (*Pseudemys troostii*), the painted turtle (*Chrysemys picta*), and the musk turtle (*Sternotherus odoratus*). Journal of the Tennessee Academy of Science 12:87-95.

Cagle, F. R. 1942. Turtle populations in southern Illinois. Copeia 1942:155-162.

Cagle, F. R. 1944a. Home range, homing behavior, and migration in turtles. Miscellaneous Publications of the Museum of Zoology, University of Michigan 61:1-34.

Cagle, F. R. 1944b. Activity and winter changes of hatchling *Pseudemys*. Copeia 1944:105-109.

Cagle, F. R. 1946. The growth of the slider turtle, *Pseudemys scripta elegans*. American Midland Naturalist 36:685-729.

Cagle, F. R. 1948a. The growth of turtles in Lake Glendale, Illinois. Copeia 1948:197-203.

Cagle, F. R. 1948b. Sexual maturity in the male turtle, *Pseudemys scripta troostii*. Copeia 1948:108-111.

Cagle, F. R. 1949. Notes on the raccoon, *Procyon lotor megalodus* Lowery. Journal of Mammalogy 30:45-47.

Cagle, F. R. 1950. The life history of the slider turtle, *Pseudemys scripta troostii* (Holbrook). Ecological Monographs 20:31-54.

Cagle, F. R. 1955. Courtship behavior of juvenile turtles. Copeia 1955:307.

Cagle, F. R., and Chaney, A.H. 1950. Turtle populations in Louisiana. American Midland Naturalist 43:383-388.

Cahn, A. R. 1937. The turtles of Illinois. University of Illinois Bulletin 35:1-218.

Cash, W. B. 2000. Behavioral and physiological ecology of the slider turtle: laboratory and field studies integrating hormonal and behavioral aspects. Ph.D. Dissertation, Univ. Mississippi, Oxford. 153 pp.

Cash, W. B., and Holberton, R.L. 1999. Effects of exogenous corticosterone on locomotor activity in the red-eared slider turtle, *Trachemys scripta elegans*. Journal of Experimental Biology 284:637-644.

Cash, W. B., and Holberton, R.L. 2005. Endocrine and behavioral response to a decline in habitat quality: effects of pond drying on the slider turtle, *Trachemys scripta*. Journal of Experimental Zoology 303A:872-879.

Carr, A. 1952. Handbook of Turtles: The Turtles of the United States, Canada, and Baja California. New York:Comstock Publ. Assoc., Cornell University Press, 542 pp.

Chen, T., and Lue, K. 1998. Ecological notes on feral populations of *Trachemys scripta elegans* in northern Taiwan. Chelonian Conservation and Biology 3:87-90.

Christy, E. J., Farlow, J.O., Bourque, J.E., and Gibbons, J.W. 1974. Enhanced growth and increased body size of turtles living in thermal and post-thermal aquatic systems. In: Gibbons, J.W., and Sharitz, R.R. (Eds.). Thermal Ecology. AEC Symposium Series (CONF-730505), pp. 277-284.

Clark, D. B., and Gibbons, J.W. 1969. Dietary shift in the turtle *Pseudemys scripta* (Schoepff) from youth to maturity. Copeia 1969:704-706.

Close, L. M., and Seigel, R.A. 1997. Differences in body size among populations of red-eared sliders (*Trachemys scripta elegans*) subjected to different levels of harvesting. Chelonian Conservation and Biology 2:563-566.

Cloudsley-Thompson, J. L. 1982. Rhythmic activity in young red-eared terrapins (*Pseudemys scripta elegans*). British Journal of Herpetology 6:188-194.

Congdon, J. D., and Gibbons, J.W. 1983. Relationships of reproductive characteristics to body size in *Pseudemys scripta*. Herpetologica 39:147-151.

Congdon, J. D., and Gibbons, J.W. 1985. Egg components and reproductive characteristics of turtles: relationships to body size. Herpetologica 41:194-205.

Congdon, J. D., and Gibbons, J.W. 1990. Turtle eggs: their ecology and evolution. In: Gibbons, J. W.(Ed.). Life History and Ecology of the Slider Turtle. Washington DC: Smithsonian Institution Press, pp. 109-123.

Congdon, J. D., Greene, J.L., and Gibbons, J.W. 1986. Biomass of freshwater turtles: a geographic comparison. American Midland Naturalist 115:165-173.

Congdon, J. D., Dunham, A.E., and Van Loben Sels, R.C. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation of long-lived organisms. Conservation Biology 7:826-833.

Cox, G. W. 1999. Alien Species in North America and Hawaii: Impacts on Natural Ecosystems. Washington DC: Island Press, 400 pp.

Crawford, K. M., Spotila, J.R., and Standora, E.A. 1983. Operative environmental temperatures and basking behavior of the turtle *Pseudemys scripta*. Ecology 64:989-999.

Crawshaw, L. I., Johnston, M.H., and Lemmons, D.E. 1980. Acclimation, temperature selection, and heat exchange in the turtle, *Chrysemys scripta*. American Journal of Physiology 238:R443-R446.

Crisp, T. M., Clegg, E.D., Cooper, R.L., Wood, W.P., Anderson, D.G., Baetcke, K.P., Hoffman, J.L., Morrow, M.S., Rodier, D.J., Shaeffer, J.E., Touart, L.W., Zeeman, M.G., and Patel, Y.M. 1998. Environmental endocrine disruption: an effects assessment analysis. Environmental Health Perspectives 106(supplement):11-56.

Da Silva, E., and Blasco, M. 1995. *Trachemys scripta* in southwestern Spain. Herpetological Review 26:133-134.

Davis, J. D., and Jackson, Jr., C.G. 1970. Copulatory behavior in the red-eared turtle, *Pseudemys scripta elegans*. Herpetologica 26:238-240.

Davis, J. D., and Jackson, Jr., C.G 1973. Notes on the courtship of a male *Chrysemys scripta taylori*. Herpetologica 29:62-64.

Devine, R.S. 1998. Alien Invasion: America's Battle with Non-native Animals and Plants. Washington DC: National Geographic Society, 288 pp.

Dreslik, M. J. 1999. Dietary notes on the red-eared slider (*Trachemys scripta*) and river cooter (*Pseudemys concinna*) from Southern Illinois. Transactions of the Illinois State Academy of Sciences 92:233-241.

Dreslik, M. J., and Kuhns, A.R. 2000. Early season basking in the red-eared slider, *Trachemys scripta*. Transactions of the Illinois State Academy of Sciences 93:215-220.

Elton, C. S. 2000. The Ecology of Invasions by Animals and Plants. Chicago:University of Chicago Press, 182 pp.

Emer, S. 2004. Growth of an introduced population of *Trachemys scripta elegans* at Fox Pond, Eckerd College, Pinellas County, Florida. Herpetological Review 35:34-35.

Enge, K. M. 1994. Herptile use and trade in Florida. Florida Game and Freshwater Fish Comm. Nongame Wildlife Program Final Performance Report. Tallahassee, Florida. 102 pp. + iii.

Ernst, C. H. 1990. Systematics, taxonomy, variation, and geographic distribution of the slider turtle. In: Gibbons, J. W.(Ed.). Life History and Ecology of the Slider Turtle. Washington DC: Smithsonian Institution Press, pp. 57-67.

Ernst, C. H., and Jett, B.J. 1969. An intergrade population of *Pseudemys scripta elegans* x *Pseudemys scripta troostii* in Kentucky. Journal of Herpetology 3:103-105.

Ernst, C. H., and Barbour, R.W. 1989. Turtles of the World. Washington DC: Smithsonian Institution Press, 313 pp.

Ernst, C. H., Barbour, R.W., and Lovich, J.E. 1994. Turtles of the United States and Canada. Washington DC: Smithsonian Institution Press, 578 pp.

Ernst, C. H., Akre, T.S.B., Wilgenbusch, J.C.,Wilson, T.P., and Mills, K. 1999. Shell disease in turtles in the Rappahannock River, Virginia. Herpetological Review 30:214-215.

Esch, G. W., Marcogliese, D.J., Goater, T.M., and Jacobson, K.C. 1990. Aspects of the evolution and ecology of helminth parasites in turtles: A review. In: Gibbons, J. W.(Ed.). Life History and Ecology of the Slider Turtle. Washington DC: Smithsonian Institution Press, pp. 299-307.

Etchberger, C. R., Phillips, J.B., Ewert, M.A., Nelson, C.E., and Prange, H.D. 1991. Effects of oxygen concentration and clutch on sex determination and physiology in red-eared slider turtles (*Trachemys scripta*). Journal of Experimental Zoology 258:394-403.

Etchberger, C. R., Ewert, M.A., Phillips, J.B., Nelson, C.E., and Prange, H.D 1992. Physiological responses to carbon dioxide in embryonic red-eared slider turtles, *Trachemys scripta*. Journal of Experimental Zoology 264:1-10.

Etchberger, C. R., Ewert, M.A., Phillips, J.B., and Nelson, C.E., 2002. Carbon dioxide influences environmental sex determination in two species of turtles. Amphibia-Reptilia 23:169-175.

Evans, L. T. 1951. Effects of male hormones upon the tail of the slider turtle, *Pseudemys scripta troostii*. Science 114:277-279.

Filorama, N. I., and Janzen, F.J. 2002. An experimental study of the influence of embryonic water availability, body size, and clutch on survivorship of neonatal red-eared sliders, *Trachemys scripta* *elegans*. Herpetologica 58:67-74.

Finkler, M. S. 1999. Influence of water availability during incubation on hatchling size, body composition, desiccation tolerance, and terrestrial locomotor performance in the snapping turtle *Chelydra serpentina*. Physiological and Biochemical Zoology 72:714-722.

Fitch, H. S. 1985. Variation in clutch and litter size in New World reptiles. University of Kansas Museum of Natural History Miscellaneous Publication no. 76., 76 pp.

Foster, S. A., and Endler, J.A. 1999. Geographic Variation in Behavior: Perspectives on Evolutionary Mechanisms. New York: Oxford University Press, 336 pp.

Frazer, N. B., Gibbons, J.W., and Green, J.L. 1990. Life tables of a slider turtle population. In: Gibbons, J. W.(Ed.). Life History and Ecology of the Slider Turtle. Washington DC: Smithsonian Institution Press, pp. 183-200.

Garner, M. M., R. Herrington, and Jacobson, E.R. 1997. Shell disease in river cooters (*Pseudemys concinna*) and yellow-bellied turtles (*Trachemys scripta*) in a Georgia (USA) lake. Journal of Wildlife Diseases 33:78-88.

Gatten, R. E., Jr. 1974. Effect of nutritional status on the preferred body temperature of the turtles *Pseudemys scripta* and *Terrapene ornata*. Copeia 1974:912-917.

Gibbs, J. P., and Shriver, G. 2002. Estimating the effects of road mortality on turtle populations. Conservation Biology 16:1647-1652.

Gibbons, J. W. 1970. Terrestrial activity and the population dynamics of aquatic turtles. American Midland Naturalist 83:404-414.

Gibbons, J. W. 1982. Reproductive patterns in freshwater turtles. Herpetologica 38:222-227.

Gibbons, J. W. 1990a. The slider turtle. In: Gibbons, J. W.(Ed.). Life History and Ecology of the Slider Turtle. Washington DC: Smithsonian Institution Press, pp. 3-18.

Gibbons, J. W. 1990b. Sex ratios and their significance among turtle populations. In: Gibbons, J. W.(Ed.). Life History and Ecology of the Slider Turtle. Washington DC: Smithsonian Institution Press, pp. 171-182.

Gibbons, J. W., and Greene, J.L. 1990. Reproduction in the slider and other species of turtles. In: Gibbons, J. W.(Ed.). Life History and Ecology of the Slider Turtle. Washington DC: Smithsonian Institution Press, pp. 124-134.

Gibbons, J. W., and Lovich, J.E. 1990. Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). Herpetological Monographs 4:1-29.

Gibbons, J. W., and Nelson, D.H. 1978. The evolutionary significance of delayed emergence from the nest by hatchling turtles. Evolution 32:297-303.

Gibbons, J. W., and Semlitsch, R.D. 1982. Survivorship and longevity of a long-lived vertebrate species: how long do turtles live? Journal of Animal Ecology 51:523-527.

Gibbons, J. W., Semlitsch, R.D., Greene, J.L., and Schubauer, J.P. 1981. Variation in age and size at maturity of the slider turtle (*Pseudemys scripta*). American Naturalist 117:841-845.

Gibbons, J. W., Greene, J.L., and Congdon, J.D. 1983. Drought-related responses of aquatic turtle populations. Journal of Herpetology 17:242-246.

Gibbons, J. W., Greene, J.L., and Congdon, J.D. 1990. Temporal and spatial movement patterns of sliders and other turtles. In: Gibbons, J. W. (Ed.). Life History and Ecology of the Slider Turtle. Washington DC: Smithsonian Institution Press, pp. 201-215.

Gist, D. H., and Congdon, J.D. 1998. Oviductal sperm storage as a reproductive tactic of turtles. Journal of Experimental Zoology 282:526-534.

Gist, D. H., and Jones, J.M. 1989. Sperm storage within the oviduct of turtles. Journal of Morphology 199:379-384.

Gist, D. H., Michaelson, J.A., and Jones, J.M. 1990. Autumn mating in the painted turtle, *Chrysemys picta*. Herpetologica 46:331-336.

Gist, D. H., Turner, T.W., and Congdon, J.D. 2000. Chemical and thermal effects on the viability of spermatozoa from the turtle epididymis. Journal of Reproduction and Fertility 119:271-277.

Gist, D. H., Dawes, S.M., Turner, T.W., Sheldon, S., and Congdon, J.D. 2001. Sperm storage in turtles: a male perspective. Journal of Experimental Zoology 292:180-186.

Goodpaster, W. W., and Hoffmeister, D.F. 1952. Notes on the mammals of western Tennessee. Journal of Mammalogy 33:362-371.

Grant, C. 1936. Breeding of *Pseudemys elegans* in California and notes on other captive reptiles. Copeia 1936:112-113.

Grayson, K.L. and Dorcas, M. E. 2004. Seasonal temperature variation in the painted turtle (*Chrysemys picta*). Herpetologica 60:325-336.

Gribbins, K.M., Gist, D.H., and Congdon, J.D. 2003. Cytological evaluation of spermatogenesis and organization of the germinal epithelium in the male slider turtle, *Trachemys scripta*. Journal of Morphology 255:337-346.

Gross, M. 1996. Alternative reproductive strategies and tactics: diversity within the sexes. Trends in Ecology and Evolution 11:92-98.

Gross, M., and Garstka, W.R. 1984. Sperm storage and capacitation in the male slider turtle, *Pseudemys scripta*. Journal of the Alabama Academy of Science 55:144.

Hall, R. J. 1980. Effects of environmental contaminants on reptiles: A review. U.S. Fish and Wildlife Service, Special Science Report Wildlife 228:1-12.

Hart, D.W. 1983. Dietary and habitat shift with size of red-eared turtles (*Pseudemys scripta*) in a southern Louisiana population. Herpetologica 39:285-290.

Hamilton, A.M., Freedman, A.H., and Franz, R. 2002. Effects of deer feeders, habitat and sensory cues on predation rates on artificial turtle nests. American Midland Naturalist 147:123-134.

Hammond, K.A., Spotila, J.R., and Standora, E.A. 1988. Basking behavior of the turtle *Pseudemys scripta*: effects of digestive state, acclimation temperature, sex, and season. Physiological Zoology 61:69-77.

Hutchison, A.M. 1993. A reproducing population of *Trachemys scripta elegans* in southern Pinellas County, Florida. Herpetological Review 23:74-75.

Iverson, J.B. 1977. Reproduction in freshwater and terrestrial turtles of north Florida. Herpetologica 33:205-212.

Iverson, J.B. 1992a. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately printed, 363 pp.

Iverson, J.B. 1992b. Correlates of reproductive output in turtles (order Testudines). Herpetological Monographs 6:25-42.

Iverson, J.B., and Etchberger, C.R. 1989. The distributions of the turtles of Florida. Florida Scientist 52:119-144.

Jackson, C.G., Jr., and Davis, J.D. 1972. A quantitative study of the courtship display of the red-eared turtle, *Chrysemys scripta elegans* (Weid). Herpetologica 28:58-64.

Jackson, D. R. 1988. Reproductive strategies of sympatric freshwater emydid turtles in northern peninsular Florida. Bulletin of the Florida State Museum, Biological Science 33:113-158.

Jackson, D. R. 1994. Overwintering of hatchling turtles in northern Florida. Journal of Herpetology 28:401-402.

Janzen, F. J., Paukstis, G.L., and Brodie, III, E.D. 1992. Observations on basking behavior of hatchling turtles in the wild. Journal of Herpetology 26:217-219.

Janzen, F. J., Tucker, J.K., and Paukstis, G.L. 2000a. Experimental analysis of an early life-history stage: avian predation selects for larger body size of hatchling turtles. Journal of Evolutionary Biology 13:947-954.

Janzen, F. J., Tucker, J.K., and Paukstis, G.L. 2000b. Experimental analysis of an early life-history stage: selection on size of hatchling turtles. Ecology 81:2290-2304.

Jarling, C., Scarperi, M., and Bleichert, A. 1984. Thermoregulatory behavior of the turtle, *Pseudemys scripta elegans*, in a thermal gradient. Comparative Biochemistry and Physiology 77A:675-678.

Jarling, C., Scarperi, M., and Bleichert, A. 1989. Circadian rhythm in the turtle, *Chrysemys* (=*Pseudemys*) *scripta elegans*, in a thermal gradient. Journal of Thermal Biology 14:173-178.

Johnson, C. A., Griffith, J.W., Tenario, P., Hytrek, S., and Lang, C.M. 1998. Fatal trematodiasis in research turtles. Lab Animal Science 48:340-343.

Johnston, G. R., and Johnston, J.C. 2003a. Geographic distribution. *Trachemys scripta scripta*. Herpetological Review 34:164.

Johnston, G. R., and Johnston, J.C 2003b. Geographic distribution. *Trachemys scripta elegans*. Herpetological Review 34:164.

Johnston, G. R., and Johnston, J.C 2003c. *Trachemys scripta elegans* (red-eared slider). Diet. Herpetological Review 34:242.

King, W., and Krakauer, T. 1966. The exotic herpetofauna of southeast Florida. Quarterly Journal of Florida Academy of Science 29:144-154.

Kolbe, J. J., and Janzen, F.J. 2002. Experimental analysis of an early life-history stage: water loss and migrating hatchling turtles. Copeia 2002:220-226.

Kramer, M., and Burghardt, G.M. 1998. Precocious courtship and play in emydid turtles. Ethology 104:38-56.

Kuchling, G. 1999. The Reproductive Biology of the Chelonia. Berlin: Springer, 223 pp.

Lardie, R. L. 1980. Winter activity of *Chrysemys scripta elegans* (Wied-Neuwied) in north central Texas. Bulletin of the Oklahoma Herpetological Society 4:72-76.

Legler, J. M. 1990. The genus *Pseudemys* in Mesoamerica: taxonomy, distribution, and origins. In: Gibbons, J. W. (Ed.). Life History and Ecology of the Slider Turtle. Washington DC: Smithsonian Institution Press, pp. 82-105.

Li, G., and Tang, D. 2001. Breeding of *Trachemys scripta elegans*. Journal of Jinan University (Natural Science): 22:127-130.

Lindeman, P. V. 1993. Aerial basking by hatchling freshwater turtles. Herpetological Review 24:84-87.

Lindeman, P. V. 1999. Aggressive interactions during basking among four species of Emydid turtles. Journal of Herpetology 33:214-219.

Lovich, J. E., McCoy, C.J., and Garstka, W.R. 1990. The development and significance of melanism in the slider turtle. In: Gibbons, J. W.(Ed.). Life History and Ecology of the Slider Turtle. Washington DC: Smithsonian Institution Press, pp. 233-254.

Lovich, J. E., Gotte, S.W., Ernst, C.H., Harshbarger, J.C., Laemmerzahl, A.F., and Gibbons, J.W. 1996. Prevalence and histopathology of shell disease in turtles from Lake Blackshear, Georgia. Journal of Wildlife Diseases 32:259-265.

Luiselli, L., Capula, M., and Anibaldi, C. 1997. Problems for conservation of pond turtles (*Emys orbicularis*) in central Italy: is the introduced red-eared turtle (*Trachemys scripta*) a serious threat? Chelonian Conservation and Biology 2:417-419.

Marchand, L. J. 1942. A contribution to the knowledge of the natural history of certain freshwater turtles. M.S. Thesis, University of Florida, Gainesville. 83 pp.

Marlen, M. D., and Fischer, R.U. 1999. Parental investment in the red-eared slider turtle, *Trachemys scripta elegans*. Journal of Herpetology 33:306-309.

McCoy, C. J. 1966. The development of melanism in an Oklahoma population of *Chrysemys scripta elegans* (Reptilia: Testudinidae). Proceedings of the Oklahoma Academy of Sciences 47:84-87.

McDonald, L. M. 1992. The basking behavior of *Trachemys scripta elegans*. M.S. Thesis, Texas A&M University. 85 pp.

Miller, J. K. 2001. Escaping senescence: demographic data from the three-toed box turtle (*Terrapene carolina triunguis*). Experimental Gerontology 36:829-832.

Mitchell, J. C. 1994. The Reptiles of Virginia. Washington DC: Smithsonian Institution Press, 352 pp.

Mitchell, J. C., and Pague, C.A. 1990. Body size, reproductive variation, and growth in the slider turtle at the northeastern edge of its range. In: Gibbons, J. W.(Ed.). Life History and Ecology of the Slider Turtle. Washington DC: Smithsonian Institution Press, pp. 146-151.

Moll, E. O. 1979. Reproductive cycles and adaptations. In: Harless, M. and H. Morlock (Eds.). Turtles: perspectives and research. New York: John Wiley, pp. 305-331.

Moll, E. O., and Legler, J.M. 1971. The life history of a neotropical slider turtle, *Pseudemys scripta* (Schoepff), in Panama. Bulletin of the Los Angeles County Museum of Natural History Science 11:1-102.

Moll, D., and Moll, E.O. 1990. The slider turtle in the neotropics: adaptation of a temperate species to a tropical environment. In: Gibbons, J. W.(Ed.). Life History and Ecology of the Slider Turtle. Washington DC: Smithsonian Institution Press, pp. 152-161.

Moore, M. C., and Lindzey, J. 1992. The physiological basis of sexual behavior in male reptiles. In: C. Gans and D. Crews (Eds.). Biology of the Reptilia; Vol. 18; Physiology E; Hormones, Brain, and Behavior. Chicago: University of Chicago Press, pp. 70-113.

Morjan, C. L., and Valenzuela, N. 2001. Is ground-nuzzling by female turtles associated with soil surface temperatures? Journal of Herpetology 35:668-672.

Morreale, S. J., Gibbons, J.W., and Congdon, J.D. 1984. Significance of activity and movement in the yellow-bellied turtle (*Pseudemys scripta*). Canadian Journal of Zoology 62:1038-1042.

Moulis, R. A. 1997. Predation by the imported fire ant (*Solenopsis invicta*) on loggerhead sea turtle (*Caretta caretta*) nests on Wassaw National Wildlife Refuge, Georgia. Chelonian Conservation and Biology 2:433-436.

Mount, R. H. 1975. The reptiles and amphibians of Alabama. Auburn: Auburn University Press, 345 pp.

Nijs, J., and Janssen, H. 1993. Sexual activity and copulation at low temperature in the red-eared slider, *Trachemys scripta elegans* (Wied, 1839). Bulletin of the Chicago Herpetological Society 28:102-103.

Palmer, W. M., and Braswell, A.L. 1995. Reptiles of North Carolina. Chapel Hill: University of North Carolina Press, 412 pp.

Parker, M. V. 1939. The amphibians and reptiles of Reelfoot Lake and vicinity, with a key for the separation of species and subspecies. Journal of Tennessee Academy of Science 14:72-101.

Parker, W. S. 1984. Immigration and dispersal of slider turtles *Pseudemys scripta* in Mississippi farm ponds. American Midland Naturalist 112:280-293.

Parker, W. S. 1990. Colonization of a newly constructed farm pond in Mississippi by slider turtles and comparisons with established populations. In: Gibbons, J. W.(Ed.). Life History and Ecology of the Slider Turtle. Washington DC: Smithsonian Institution Press, pp. 216-222.

Parker, W. S. 1996. Age and survivorship of the slider (*Trachemys scripta*) and the mud turtle (*Kinosternon subrubrum*) in a Mississippi farm pond. Journal of Herpetology 30:266-268.

Parmenter, R. R. 1980. Effects of food availability and water temperature on the feeding ecology of pond sliders (*Chrysemys s. scripta*). Copeia 1980:503-514.

Pearse, D. E., and Avise, J.C. 2001. Turtle mating systems: behavior, sperm storage, and genetic paternity. Journal of Heredity 92:206-211.

Platt, S. G., and Rainwater, T.R. 2003. *Trachemys scripta elegans* (red-eared slider). Maximum size. Herpetological Review 34:242.

Proctor, V. W. 1958. The growth of *Basicladia* on turtles. Ecology 39:634-645.

Ream, C., and Ream, R. 1966. The influence of sampling methods on the estimation of population structure in painted turtles. American Midland Naturalist 75:325-338.

Reinhold, K., Kurtz, J., and Engqvist, L. 2002. Cryptic male choice: sperm allocation strategies when female quality varies. Journal of Evolutionary Biology 15:201-209.

Rives, J.D. 1978. A comparative study of the courtship related behavior in immature emydid turtles of two species. M.S. Thesis, University of Southwestern Louisiana, Lafayette, 114 pp.

Rose, F.L., and Manning R.W. 1996. Notes on the biology of the slider, *Trachemys scripta elegans* (Reptilia: Emydidae), inhabiting man-made cattle ponds in west Texas. Texas Journal of Science 48:191-206.

Schubauer, J.P., and Parmenter, R.R. 1981. Winter feeding by aquatic turtles in a southeastern reservoir. Journal of Herpetology 15:444-447.

Schubauer, J.P., Gibbons, J.W., and Spotila, J.R. 1990. Home range and movement patterns of slider turtles inhabiting Par Pond. In: Gibbons, J. W. (Ed.). Life History and Ecology of the Slider Turtle. Washington DC: Smithsonian Institution Press, pp. 223-232.

Secor, S.M., and Diamond, J. 1999. Maintenance of digestive performance in the turtles *Chelydra serpentina*, *Sternotherus odoratus*, and *Trachemys scripta*. Copeia 1999:75-84.

Seidel, M.E. 2002. Taxonomic observations of extant species and subspecies of slider turtles, genus *Trachemys*. Journal of Herpetology 36:285-292.

Seidel, M.E., and Jackson, D.R. 1990. Evolution and fossil relationships of slider turtles. In: Gibbons, J. W.(Ed.). Life History and Ecology of the Slider Turtle. Washington DC: Smithsonian Institution Press, pp. 68-73.

Semlitsch, R.D., and Gibbons, J.W. 1989. Lack of largemouth bass predation on hatchling turtles (*Trachemys scripta*). Copeia 1989:1030-1031.

Sever, D.M., and Hamlett, W.C. 2002. Female sperm storage in reptiles. Journal of Experimental Zoology 292:187-199.

Spinks, P.Q., Pauly, G.B., Crayon, J.J., and Shaffer, H.B. 2003. Survival of the western pond turtle (*Emys marmorata*) in an urban California environment. Biological Conservation 113:257-267.

Spotila, J.R., Foley, R.E., Schubauer, J.P., Semlitsch, R.D., Crawford, K.M., Standora, E.A., and Gibbons, J.W. 1984. Opportunistic behavioral thermal regulation of turtles, *Pseudemys scripta*, in response to microclimatology of a nuclear reactor cooling reservoir. Herpetologica 40:299-308.

Sprando, R.L., and Russell, L.D. 1988. Spermiogenesis in the red-ear turtle (*Pseudemys scripta*) and the domestic fowl (*Gallus domesticus*): a study of cytoplasmic events including cell volume changes and cytoplasmic elimination. Journal of Morphology 198:95-118.

Stone, P.A., Hauge, J.B., Scott, A.F., Guyer, C., and Dobie, J.L. 1993. Temporal changes in two turtle assemblages. Journal of Herpetology 27:13-23.

Stophlet, J.J. 1947. Florida otters eat large terrapin. Journal of Mammalogy 28:183.

Taylor, E.H. 1933. Observations on the courtship of turtles. University of Kansas Science Bulletin. 21:269-271.

Terrell, C.W., and Garstka, W.R. 1984. Melanism and reproduction in the male slider turtle, *Pseudemys scripta*. Journal of the Alabama Academy of Science 55:141.

Thomas, R.B. 1993. Growth, diet, and reproduction of the red-eared slider (*Trachemys scripta*) inhabiting a reservoir receiving a cold effluent. M.S. Thesis, Southwest Missouri State University, Springfield. 42 pp.

Thomas, R.B. 1999. Intraspecific variation in the behavior of adult slider turtles (*Trachemys scripta*). Ph.D. Dissertation, Mississippi State University, Mississippi State. 80 pp.

Thomas, R.B. 2002. Conditional mating strategy in a long-lived vertebrate: ontogenetic shifts in the mating tactics of male slider turtles *Trachemys scripta*). Copeia 2002:456-461.

Thomas, R.B., and R. Altig. 2006. Characteristics of the foreclaw display behaviors of female slider turtles (*Trachemys scripta*). Southeastern Naturalist 5:227-234.

Thomas, R.B., and Parker, W.S. 2000. Intrasexual variations in overland movements of slider turtles (*Trachemys scripta*). Journal of Herpetology 34:469-472.

Thomas, R.B., Moll, D., and Steiert, J. 1994. Evidence of a symbiotic relationship between cellulolytic bacteria and a freshwater herbivorous turtle. Southwestern Naturalist 39:386-388.

Thomas, R.B., Vogrin, N., and Altig, R. 1999. Sexual and seasonal differences in behavior of *Trachemys scripta* (Testudines: Emydidae). Journal of Herpetology 33:511-515.

Thornhill, G.M. 1982. Comparative reproduction of the turtle, *Chrysemys scripta elegans*, in heated and natural lakes. Journal of Herpetology 16:347-353.

Townsend, J.H., Krysko, K.L., and Reppas, A.T. 2002. Noteworthy records for introduced reptiles and amphibians from Florida, USA. Herpetological Review 33:75.

Tuberville, T. D., Gibbons, J.W., and Greene, J.L. 1996. Invasion of new aquatic habitats by male freshwater turtles. Copeia 1996:713-715.

Tucker, J.K. 1997. Natural history notes on nesting, nests, and hatchling emergence in the red-eared slider turtle, *Trachemys scripta elegans*, in west-central Illinois. Illinois Natural History Survey Biological Notes 140:1-13.

Tucker, J.K. 1999a. Seasonal variation in reproduction in the red-eared slider (*Trachemys scripta elegans*). Bulletin of the Maryland Herpetological Society 35:43-55.

Tucker, J.K. 1999b. Environmental correlates of hatchling emergence in the red-eared turtle, *Trachemys scripta elegans*, in Illinois. Chelonian Conservation and Biology 3:401-406.

Tucker, J.K. 2000a. Body size and migration of hatchling turtles: inter- and intraspecific comparisons. Journal of Herpetology 34:541-546.

Tucker, J.K. 2000b. Annual variation in hatchling size in the red-eared slider turtle (*Trachemys scripta elegans*). Herpetologica 56:8-13.

Tucker, J.K. 2001a. Clutch frequency in the red-eared slider (*Trachemys scripta elegans*). Journal of Herpetology 35:664-668.

Tucker, J.K. 2001b. Nesting red-eared sliders (*Trachemys scripta elegans*) exhibit fidelity to their nesting areas. Journal of Herpetology 35:661-664.

Tucker, J.K., and Janzen, F.J. 1998. Order of oviposition and egg size in the red-eared slider turtle (*Trachemys scripta elegans*). Canadian Journal of Zoology 76:377-380.

Tucker, J.K., and Moll, D. 1997. Growth, reproduction, and survivorship in the red-eared turtle, *Trachemys scripta elegans*, in Illinois, with conservation implications. Chelonian Conservation and Biology 2:352-357.

Tucker, J.K., and Packard, G.C. 1998. Overwinter survival by hatchling sliders (*Trachemys scripta*) in west-central Illinois. Journal of Herpetology 32:431-434.

Tucker, J.K., and Paukstis, G.L. 1999. Post-hatching substrate moisture and overwintering hatchling turtles. Journal of Herpetology 33:608-615.

Tucker, J.K., and Warner, D.A. 1999. Microgeographic variation in response of red-eared slider (*Trachemys scripta elegans*) embryos to similar incubation environments. Journal of Herpetology 33:549-557.

Tucker, J.K., Maher, R.J., and Theiling, C.H. 1995a. Year-to-year variation in growth of the red-eared turtle, *Trachemys scripta elegans*. Herpetologica 51:354-358.

Tucker, J.K., Maher, R.J., and Theiling, C.H. 1995b. Melanism in the red-eared slider turtle (*Trachemys scripta elegans*). Journal of Herpetology 29:291-296.

Tucker, J. K., Janzen, F.J., and Paukstis, G.L. 1997. Response of embryos of the red-eared turtle (*Trachemys scripta elegans*) to experimental exposure to water-saturated substrates. Chelonian Conservation and Biology 2:345-351.

Tucker, J. K., Paukstis, G.L, Janzen, F.J. 1998a. Annual and local variation in reproduction in the red-eared slider turtle, *Trachemys scripta elegans*. Journal of Herpetology 32:515-526.

Tucker, J. K., Janzen, F.J., and Paukstis, G.L. 1998b. Variation in carapace morphology and reproduction in the red-eared slider *Trachemys scripta elegans*. Journal of Herpetology 32:294-298.

Tucker, J. K., Filorama, N.I., Paukstis, G.L, and Janzen, F.J. 1998c. Residual yolk in captive and wild-caught hatchlings of the red-eared slider turtle (*Trachemys scripta elegans*). Copeia 1998:488-492.

Tucker, J. K., Moll, D., and Moll, E.O. 1999a. Growth of slider turtles (*Trachemys scripta*) from temperate and tropical populations. Chelonian Conservation and Biology 3:464-467.

Tucker, J. K., Filorama, N.I., and Janzen, F.J. 1999b. Size-biased mortality due to predation in a nesting freshwater turtle, *Trachemys scripta*. American Midland Naturalist 141:198-203.

Valenzuela, N., Adams, D.C., and Janzen, F.J. 2003. Pattern does not equal process: exactly when is sex environmentally determined? American Naturalist 161:676-683.

Viosca, P., Jr. 1933. The *Pseudemys troostii-elegans* complex, a case of sexual dimorphism. Copeia 1933:208-210.

Warwick, C. 1986. Red-eared terrapin farms and conservation. Oryx 20:237-240.

Warwick, C., Steedman, C., and Holford, T. 1990. Ecological implications of the red-eared turtle trade. Texas Journal of Science 42:419-422.

Webb, R. G. 1961. Observations on the life histories of turtles (Genus *Pseudemys* and *Graptemys*) in Lake Texoma, Oklahoma. American Midland Naturalist 65:193-214.

Wibbels, T., Cowan, J., and LeBoeuf, R. 1998. Temperature-dependent sex determination in the red-eared slider turtle, *Trachemys scripta*. Journal of Experimental Zoology 281:409-416.

Williams, T. 1999. The terrible turtle trade. Audubon 101:44-51.

Willingham, E. 2001. Embryonic exposure to low-dose pesticides: effects on growth rate in the hatchling red-eared slider turtle. Journal of Toxicology and Environmental Health Part A 64:257-272.

Willingham, E., and Crews, D. 2000. The red-eared slider turtle: an animal model for the study of low doses and mixtures. American Zoologist 40:421-428.

Willingham, E., Rhen, T., Sakata, J.T., and Crews, D. 2000. Embryonic treatment with xenobiotics disrupts steroid hormone profiles in hatchling red-eared slider turtles (*Trachemys scripta elegans*). Environmental Health Perspectives 108:329-332.

Wilson, L. D., and Porras, L. 1983. The ecological impact of man on the south Florida herpetofauna. University of Kansas Museum of Natural History, Special Publication 9:1-89.

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Pseudemys nelsoni – Florida Red-Bellied Turtle

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SUMMARY. – **The Florida red-bellied turtle, *Pseudemys nelsoni*, is a large, aquatic, hard-shelled turtle, one of three species of the genus *Pseudemys* occurring in Florida. The species is sexually dimorphic in body size, with females achieving larger sizes. Males reach maturity at a minimum plastron length (PL) of 170–210 mm but can exceed 260 mm PL (290 mm carapace length, CL) and weigh nearly 3 kg. Females mature at approximately 260–270 mm PL but can reach 300 mm (330 mm CL) or more and weigh greater than 5 kg. The species' thick, highly domed shell may be an adaptation to resist the biting force of the American alligator, with which this turtle shares much of its habitat. Florida red-bellies typically occupy lakes and marshes, as well as the slower stretches of some rivers. The species' range includes the entire Florida peninsula, with a poorly known and apparently disjunct population in the Apalachicola River region of the Florida panhandle. Like other *Pseudemys*, the Florida red-belly feeds upon aquatic plants; its basking habit is well developed and may aid it in digesting its food by raising its body temperature. Females may lay several large clutches of small eggs (average about 14, but up to 32 eggs per clutch) during the late spring and summer; a favorite nesting site is the nest of alligators. At a constant temperature of 30°C, eggs may hatch in as few as 45 days, one of the most rapid developmental rates among turtles. Cooler incubation temperatures (to 25°C) may extend the period to 80 days. Insufficient data are available to characterize most populations, but at least some achieve high densities and biomasses. Adults seem to predominate in some populations, although age structures may vary locally. Despite wetland habitat losses, the species' conservation status is generally considered to be secure at present.**

CONSERVATION STATUS. – **FNAI Global - G5 (Demonstrably Secure), State - S5 (Demonstrably Secure); ESA Federal - Not Listed; State - Not Listed; CITES - Not Listed; IUCN Red List - Not Listed (LC-Least Concern).**

Species Recognition. — The Florida red-bellied turtle, or Florida red-belly, *Pseudemys nelsoni*, is a large (record 37.5 cm carapace length [CL]) hard-shelled turtle with a black or very dark, highly domed shell with a single dominant vertical bar of lighter color on each costal scute (Fig. 22-1). The vertical bars, which may branch at the top or bottom of the scute to form Y-shaped figures, vary in width and in color from red to yellow-orange. The shell surface is frequently sculptured with numerous fine parallel ridges. The plastrons of adults and older juveniles are usually unmarked and yellow-orange to reddish in color. Submarginal spots vary in number but are typically solid rather than concentric or hollow (Fig. 22-2). Adults of both sexes can develop reticulate melanism, a pattern in which scattered deposits of black pigment obscure some of the red to yellow regions of the carapace and plastron (Fig. 22-3). The carapace of very young red-bellied turtles is greenish rather than black but still bears a single major vertical bar (light green to yellowish) on each costal scute (Figs. 22-4, 22-5); the plastron is orange tinted and often bears numerous black markings, many in the shape of solid spots or semicircles with their straight edges along scute seams (Fig. 22-6) (Carr, 1952; Conant and Collins, 1991).

The skin of the legs and head is black with yellow to cream stripes. The head stripes are fewer in number than those in other species of *Pseudemys* and often include an arrow-like marking on top of the head, with its point over the snout. A distinct median notch at the front of the upper jaw is typically flanked by a strong cusp on each side (Fig. 22-7), although the cusps are poorly developed in very young and even a few older turtles; similar though less pronounced cusps occur occasionally in *P. concinna* and *Trachemys scripta.* Males do not grow as large as females and are characterized by much longer foreclaws, larger tails, and shells that usually are less highly domed.

Taxonomic History. — *Pseudemys nelsoni* is one of a small group of turtles collectively referred to as red-bellied turtles. Although Carr (1938) was the first to characterize the disjunct population of red-bellied turtles in peninsular Florida as a distinct species, others had previously noted their existence. Loennberg (1894) assigned specimens from north-central peninsular Florida to *P. rubriventris,* and subsequently, DeSola (1935) referred the Everglades population to *P. alabamensis.* Although some later authors (e.g., Mertens, 1951; Crenshaw, 1955) considered *P. nelsoni* to be a subspecies of one of those two species, all recent authors have followed Carr (1938) in recognizing it as a full species. No subspecies of *P. nelsoni* are recognized, although geographic variation has not been examined.

Figure 22-1. Adult Florida red-bellied turtle, *Pseudemys nelsoni,* from Glades County, Florida. Photo by Robert T. Zappalorti.

The priority of the name *nelsoni* may be in question. Two species of fossil emydids, *Deirochelys floridana* Hay 1908 and *Trachemys? jarmani* Hay 1908, both appear to represent *P. nelsoni* (Jackson, 1978). As a junior homonym of *Pseudemys floridana* (LeConte), the name *floridana* is unavailable. However, the name *P. jarmani* remains potentially available as a senior synonym of *P. nelsoni*. However, because it has not been used for this species for more than 50 years, this change seems inadvisable.

Most authorities agree that the three species of red-bellied turtles—*P. alabamensis* (Mobile Bay drainage, Alabama, and Pascagoula River system, Mississippi; Dobie,1985; Leary et al., 2003), *P. nelsoni* (peninsular and lower Apalachicola regions of Florida, extreme southeastern Georgia), and *P. rubriventris* (Atlantic coastal states from Massachusetts to North Carolina)—form a closely related (monophyletic) group, the *P. rubriventris* series, also termed by some (e.g., Ward, 1984) as the subgenus *Ptychemys.* These three species are presently allopatric, and no intergrades are known; thus, their treatment as species seems warranted at least on geographic grounds, although few morphological and molecular data exist to corroborate this. Ward's (1984) alignment of *P. texana* with the red-bellied turtles does not appear to be valid (Seidel, 1994). Rather, it appears morphologically to be more closely allied with the river cooter, *P. concinna,* and its allies.

DISTRIBUTION

Geographic Distribution. — Pleistocene fossils reveal that *P. nelsoni* formerly occurred as far north as coastal South Carolina (Dobie and Jackson, 1979). Present native

Figure 22-2. Plastral view of adult male Florida red-bellied turtle, *Pseudemys nelsoni,* from Levy County, Florida. Note elongated front claws (right) that characterize males. Photo by John Iverson.

Figure 22-3. Plastral view of adult male Florida red-bellied turtle, *Pseudemys nelsoni,* from Lee County, Florida, showing reticulate melanism that is common in older males of this species. Photo by Dick Bartlett.

populations, however, are restricted to northern and peninsular Florida (Fig. 22-8) and extreme southeastern Georgia. The confirmed range of the species extends from Cape Sable and Florida Bay in extreme southern Florida, northward to the Okefenokee Swamp and Cumberland Island, Georgia (Duellman and Schwartz, 1958; Powers and Smith, 1977; Vitt and Dunham, 1980; Dunson and Seidel, 1986; Shoop and Ruckdeschel, 1986; Dunson and Mazzotti, 1989). Within peninsular Florida, red-bellied turtles presumably occupy hundreds of lakes and slow-moving rivers. Although the species' principal distribution lies east of the Suwannee River, limited evidence (below) supports the existence of possibly isolated populations in the Apalachicola River basin of the Florida panhandle. Red-bellied turtles apparently are absent from the Florida Keys, where permanent freshwater bodies are scarce (Duellman and Schwartz, 1958). Rose et al. (1998) noted the establishment of an introduced population in the San Marcos River, Texas.

The status of *P. nelsoni* west of the Suwannee River is problematic (Conant and Collins, 1991; Iverson, 1992) and requires further investigation. Numerous biologists (e.g., Crenshaw, 1955; Carr and Crenshaw, 1957; Means, 1977; Pritchard, 1980; Dobie, 1985; Lewis et al., 2001; J. Dobie, J. Crenshaw, Jr., R. Mount, and R. Zappalorti, *pers. comm.*) have reported *P. nelsoni* from the Apalachicola region of the Florida panhandle, although some of these reports may have been based on misidentifications. Further, it remains to be determined whether the few positively identified red-bellied turtles represent true populations or isolated individuals (perhaps releases or waifs). Because of the small number of documented records, I summarize below all confirmed specimens known to me.

Several records exist for St. Vincent Island, a barrier island and National Wildlife Refuge off the mouth of the Apalachicola River. Blaney (1971) observed (but did not collect) *Pseudemys* from several of the island's ponds but referred them to *P. floridana* based on head striping observed via telescope; however, his emphasis of the highly arched carapaces of these turtles suggests that he actually may have observed *P. nelsoni*. I recorded a large *P. nelsoni* shell (lacking scutes) on display at the island's old lodge during a 1983 visit to the island, but the source of the shell could not be verified at that time. The Florida Museum of Natural History (UF) herpetology collection contains a similar shell of a large female (UF 56347; CL 363 mm, PL 332 mm; "St. Vincent Island, beach on southwest corner, probably washed in dead; Steve Christman, winter 1983") that may, in fact, be the same specimen. Dobie (1985) reported two specimens (AUM 32541, a live adult male, and AUMP 2698, an adult female shell with scutes) that he collected on the island and for which he subsequently provided me with confirmatory photographs; both have very dark carapaces and are indeed *P. nelsoni*. Lewis et al. (2001) later published another record of a carcass found in a dry pond basin on the island. A recent photograph by K. Brandt shows a female *P. nelsoni* that was observed nesting on the island in April 2002.

Several additional specimens have been collected or photographed on the nearby mainland of the Apalachicola River delta in Franklin County. J. Dobie provided a photograph of a brightly marked mature female taken from within the city limits of Apalachicola. In 1992, I recorded the shell of an adult male *P. nelsoni* among the remains of 63 butchered cooters (*P. concinna*) that had been discarded in a dump near Eastpoint; presumably these turtles had been collected in the lower Apalachicola (and/or Chipola) River drainage. At least two other *P. nelsoni* specimens derive from this coast (UF 67791, head of juvenile found dead in 1968, ca. 5 miles southwest of Carrabelle Beach; USNM 101090 [not examined by me], near Apalachicola). Likewise, several records from the Chipola River (Gulf and Calhoun counties), a tributary of the Apalachicola River, have been assigned to *P. nelsoni*. Photographs provided to me by R. Zappalorti show a female *P. nelsoni* nesting at Dead Lake on the lower Chipola River. The same site is the provenience of a juvenile specimen (UF 67757; CL 95 mm, PL 82 mm) collected by C. Longden in 1975 (note: a second specimen catalogued as *P. nelsoni*, UF 67750, actually is *P. floridana*). Carr and Crenshaw (1957) noted four juvenile

Figure 22-4. Hatchling Florida red-bellied turtle, *Pseudemys nelsoni*, from Alachua Co., Florida. The egg tooth, used by hatchlings to open their egg shell, is visible in this view. Photo by John Iverson.

Figure 22-5. Post-hatchling Florida red-bellied turtle, *Pseudemys nelsoni*, from Lee Co., Florida. Photo by Dick Bartlett.

Figure 22-6. Variation in plastral pattern within a clutch of Florida red-bellied turtle, *Pseudemys nelsoni,* hatchlings from Alachua Co., Florida. Photo by Dale Jackson.

specimens (UF 440-3; identity confirmed by me) from the Chipola-Apalachicola region just above Dead Lake (Scotts Ferry to Blountstown); data accompanying these specimens state that they hatched in about 1953 from two clutches of 9 and 12 eggs, but because they were given to the museum by W.T. Neill who received them from an unknown collector, there is reason to question the accuracy of the locality data (a mix-up with *Graptemys barbouri* specimens is possible).

Very recently, an adult male red-bellied turtle was caught in the Wacissa River, Jefferson County (Jackson and Stearns, 2005). This represents the only confirmed record in the relatively large hiatus between the Suwannee and Apalachicola basins. Whether the animal is part of a natural population or represents an escaped or released individual is problematic.

Thus, although Ward (1984) doubted the occurrence of the species in the Florida panhandle, and my experience likewise suggests that it is very rare in the region, it seems that a population exists minimally in the lower Apalachicola River basin, including the lower Chipola River and at least one barrier island. Still, at least some older reports (e.g., Carr and Crenshaw, 1957) may have been based on misidentified *P. concinna*, which in western Florida can resemble *P. nelsoni* in plastral coloration and development of cusped jaws. Even *P. floridana* at some Florida panhandle sites may be quite dark above while somewhat reddish below (e.g., Jackson, 2002). Carr and Crenshaw (1957) emphasized the *nelsoni*-like characteristics often seen in cooters of the *concinna-floridana* complex in this region. Mislabeling of museum specimens may also play a role; besides the four juveniles noted above, my examination of at least one Florida panhandle specimen (USNM 95765, Leon County) reveals it to represent an incorrect association of a shell of *P. nelsoni* with the skull of a *P. floridana*. Clearly, there is need for further field documentation of the status of this species' northwestern-most populations. The rare and isolated nature of red-bellied turtles in the Florida panhandle suggests that they may represent relictual populations from a once more continuous distribution that joined the species' predominantly peninsular range with that of the closely related *P. alabamensis* roughly 480 km to the west. Molecular studies might prove especially rewarding in elucidating relationships among these and all populations of the entire red-bellied turtle complex (i.e., *P. rubriventris* series or subgenus *Ptychemys*).

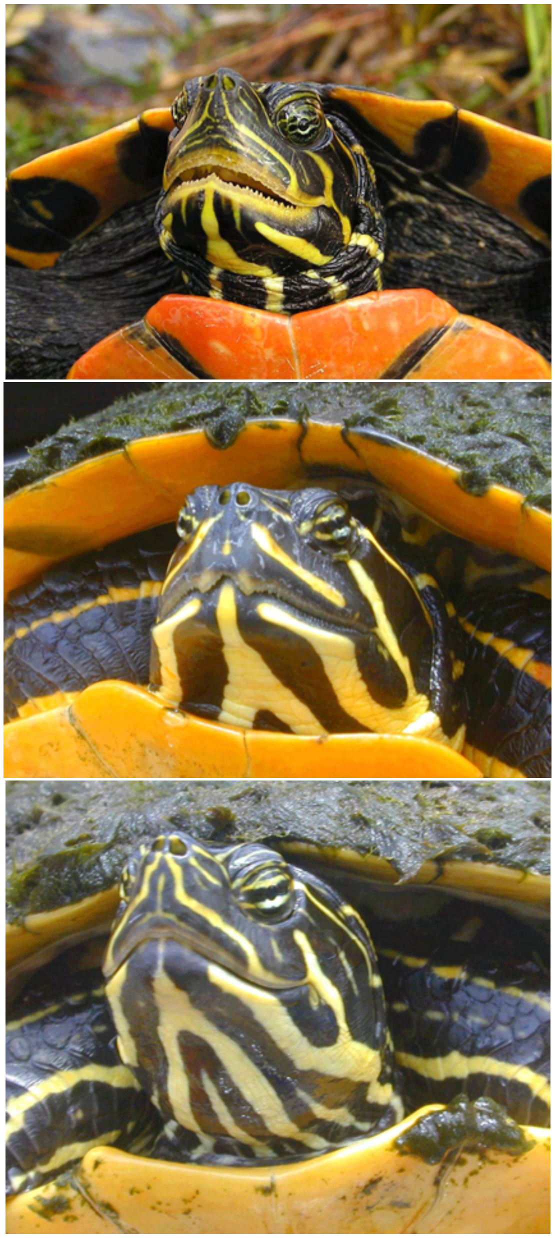

Figure 22-7. Anterior views of (A) Suwannee Cooter, *Pseudemys concinna*, (B) Florida red-bellied turtle, *Pseudemys nelsoni*, and (C) peninsula cooter, *Pseudemys floridana*, all from Marion Co., Florida; note cusp in upper jaw of *Pseudemys nelsoni* (B). Photos by Tim Walsh (A) and Steve Johnson (B, C).

Ecological Distribution. — Florida red-bellied turtles inhabit freshwater marshes, ponds, lakes, canals, low-gradient rivers and spring runs, and even some mangrove-bordered coastal creeks. Optimal habitat is characterized by permanent, non-flowing water with abundant aquatic vegetation. In lakes with both open water and a vegetated littoral zone, red-bellied turtles typically remain in the latter. They seem to prefer areas with water lilies (*Nymphaea*) while

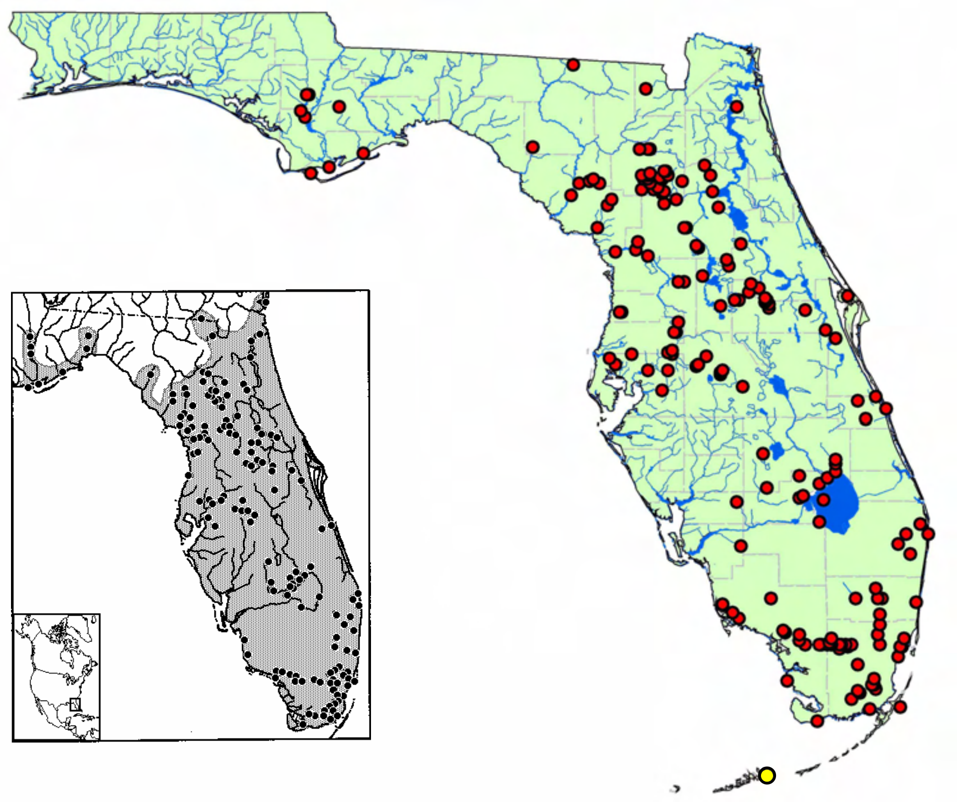

Figure 22-8. Available distribution records for the Florida red-bellied turtle, *Pseudemys nelsoni,* from Florida. Inset: distribution records from entire range of *P. nelsoni* (adapted from Iverson, 1992; distribution in inset map not current for Florida as presented here). Record from Lower Keys (yellow dot) may represent an escaped individual.

avoiding grasses (*Panicum*). These patterns may help to separate the species ecologically from its close relative, the Florida cooter, *P. floridana* (Bancroft et al., 1983). In heterogeneous habitats, red-bellied turtles seem to be more abundant in areas that offer physical support (e.g., aquatic vegetation, submerged branches and trees) for animals resting near the surface (Kramer, 1989). These turtles also commonly inhabit the trails and holes carved out of marshes and lakes by the American alligator (*Alligator mississippiensis*). In the Everglades, red-bellied turtles seem to be abundant in the few "deep" water systems but are virtually absent from the extensive sawgrass (*Cladium*) marsh (W. Meshaka, *pers. comm.*). They likewise seem to be rare or absent in the oligotrophic, sand-bottomed, sparsely vegetated lakes of northern and central peninsular Florida, and also appear incapable of maintaining populations in isolated, temporary ponds (in contrast to *Deirochelys* and *Kinosternon*). Dunson and Seidel (1986) recorded red-bellied turtles as present but uncommon in brackish waters (up to 30% sea water) in Florida Bay at the southern tip of the peninsula, and Shoop and Ruckdeschel (1986) found specimens on a barrier island beach in Georgia. P. Meylan (*pers. comm.*) has noted the ability of this species to survive in permanent lakes and ponds within developed areas such as downtown St. Petersburg (Pinellas County) and on the grounds of the former Crandon Park Zoo (Miami-Dade County), and J. Ward (*pers. comm.*) has observed large populations in stormwater retention ponds in Brevard County. However, neither this nor other species of *Pseudemys* seems as adept as *Trachemys scripta* at thriving in highly disturbed and even polluted situations.

HABITAT RELATIONS

Activity. — Florida red-bellied turtles are fully aquatic, although they may spend long hours basking, either singly or in groups, under sunny skies and even occasionally under cloudy or shaded conditions. Basking sites include mats of vegetation as well as logs, stumps, and occasionally rocks (Pritchard and Greenwood, 1968; Kramer, 1989; Jackson, *pers. obs.*). Most basking occurs at air temperatures above 21°C (Giovanetto, 1992); it occurs year-round at least in southern Florida (Duellman and Schwartz, 1958). Basking individuals may share sites with turtles of other ages as well as the opposite sex and even other species of *Pseudemys* (*P. floridana*, *P. concinna*). They are easily disturbed by passing canoes and boats that approach too closely (Kramer 1989); however, Giovanetto (1992) believed them to be less wary than other *Pseudemys* and more able to acclimate to passing boats and human activity. Overland movements are limited principally to nesting forays by females, and occasional inter-pond movements by both sexes.

Home Range. — Although unproven, it is likely that most individuals maintain restricted home ranges of a few hectares even within larger lakes. Kramer (1986, 1989, 1995) conducted one of the few mark-release studies of this species in a 980-m section of central Florida's Rock Springs Run (Orange County), an atypical habitat for *P. nelsoni*. Based on 126 marked animals (74 males, 52 females), he suggested that turtles in this population normally maintained rather small home ranges (smaller than sympatric *P. floridana*) averaging only 120–200 m of spring run (less than 3 ha of surface area), with no differences between the sexes. He also radiotracked three individuals in a marsh-lake system (Payne's Prairie, Alachua County), where he estimated much larger home ranges (10–21 ha); one male moved more than 2 km following release. However, these greater movements may have been in response to handling stress or alternatively to drying lake conditions (Kramer, 1989, 1995). Home ranges overlap extensively with those of other conspecific turtles of both sexes. Although true territoriality (defended home areas) is unlikely, observations of short fights consisting of gaping and biting suggest the possible existence of dominance hierarchies among males (Kramer, 1984, 1986, 1989; Kramer and Fritz, 1989; Meshaka and Deyrup, 1999).

GROWTH AND REPRODUCTION

Size, Dimorphism, Growth, and Longevity. — The Florida red-bellied turtle is one of the largest North American emydid turtles. The species is sexually dimorphic in body size, with females achieving larger sizes. Jackson (1988 and unpubl. data) recorded the following parameters for adult turtles, mostly from northern peninsular Florida. Males reach maturity at a minimum PL of 170–210 mm; the largest sampled male measured 260 mm PL, 287 mm CL, and 2.77 kg body mass. Females mature at approximately 260–270 mm PL; a sample of adults ranged from 270–303 (mean 290) mm PL, 280–333 mm CL, and 3.2–5.2 (mean 4.02) kg body mass. Bancroft et al. (1983) believed that males reach maturity in 3 yrs, and females in 7–8 yrs, in a central Florida population, but these probably were underestimates based on an assumption that sexually distinguishable turtles were mature (foreclaws and basal region of tail begin to enlarge in older juveniles). No data are available for longevity, but there is little question that maximum age can exceed 20 yrs, and probably more than 30. I have maintained a captive male, hatched in 1976, for 30 years.

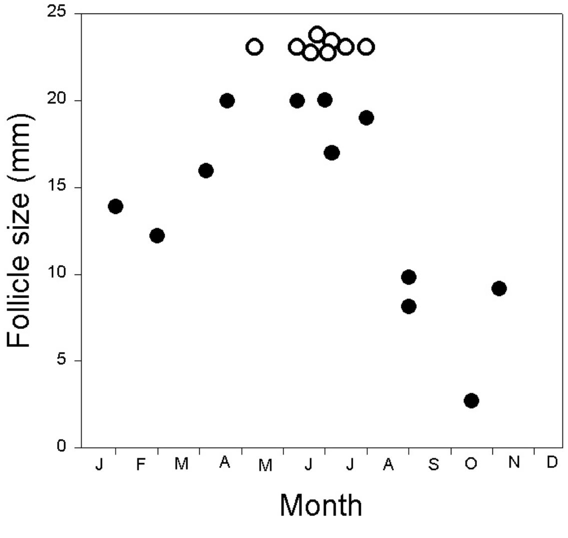

Figure 22-9. Maximum diameter of yolked follicles throughout the year for Florida red-bellied turtles, *Pseudemys nelsoni,* from the vicinity of Alachua County, Florida. Solid circles, within ovaries; open circles, within shelled eggs. Redrawn from Jackson (1988).

Male Reproductive Cycle. — The reproductive cycle of male red-bellied turtles is incompletely known. A sample of mature males from northern Florida showed largest testicular masses in August, with moderate masses through November, and lower masses from March to July. Epididymides of one male were swollen with mature sperm in February, whereas those from two males in March and July contained far fewer sperm (Jackson, unpubl. data). Peak spermatogenesis in late summer, as suggested by these data, is characteristic of most other North American turtles known to have a postnuptial spermatogenic cycle (Moll, 1979).

Female Reproductive Cycle. — The female reproductive cycle in northern peninsular Florida follows a pattern of oogenesis through ovulation and oviposition typical of most North American turtles (Moll, 1979). Vitellogenesis (yolk buildup in the eggs) appears to begin in the fall, but the majority of lipid is sequestered as yolk stores during the spring prior to ovulation and egg-laying (Fig. 22-9). Because red-bellied turtles produce multiple clutches in a season, follicles within the ovaries are usually in several stages of development simultaneously, with corpora lutea formed by the ovulation of earlier clutches present with subsequent clutches in various stages of vitellogenesis. A relatively quiescent period of unknown duration follows oviposition of the final clutch before the cycle starts anew for the following year (Jackson, 1988).

Courtship and Mating Behavior. — Observations of courtship in the wild are insufficient to determine the exact timing and duration of the mating season; in fact, it may extend from spring through fall. However, like most turtles, female red-bellied turtles presumably are able to store viable sperm for long periods, so the mating period is not directly linked to reproduction. Courtship, as described by Jackson (1977) and Kramer and Fritz (1989), is similar to that recorded by Jackson and Davis (1972) for the Suwannee cooter (*P. concinna suwanniensis*). It occurs in water, with the male performing a series of stereotyped movements designed to gain a female's acceptance and cooperation in mating. Following a period of investigative trailing and circling, the male positions himself over the female's back and reaches down with his front legs alongside her head. This is in contrast to the face-to-face posture used by sliders (*Trachemys*). The male then rapidly vibrates his greatly elongated foreclaws against or near the female's head, a process known as titillation. If successful, the pair may then sink to the bottom to mate. Interestingly, neonates and juveniles also use foreclaw titillation, a practice of uncertain significance. Larger males may replace or supplement the titillation phase with biting and dragging of the female (Kramer, 1989).

Nesting. — Much of our knowledge about reproduction in this species stems from Jackson's (1988) studies in

Figure 22-10. Alligator nest on Payne's Prairie, Alachua County, Florida, opened to expose seven clutches of Florida red-bellied turtle, *Pseudemys nelsoni,* eggs and one clutch of Florida softshell, *Apalone ferox,* eggs (lower right) surrounding a partial clutch of alligator eggs (largest eggs, middle-right). Most of the alligator eggs had been destroyed earlier by raccoons. Photo by Dale R. Jackson.

northern Florida in the vicinity of Alachua County. Nesting there occurs from May through August, with a June–July peak (Fig. 22-9). A similar seasonal pattern characterizes southern Florida populations as well (Kushlan and Kushlan, 1980; Jackson, 1988). Although they typically nest in well drained soils within 250 m of fresh water, female red-bellied turtles also show a strong proclivity for nesting in alligator nest mounds (Fig. 22-10) (Goodwin and Marion, 1977; Deitz and Jackson, 1979; Kushlan and Kushlan, 1980; Hunt, 1987; Enge et al., 2000). In a study of seven large lakes and wetlands, Enge et al. (2000) found that 26.6% of 1586 active alligator nests contained red-bellied turtle eggs, with some nests containing > 150 eggs (> 10 clutches). Turtles used an even higher percentage of nests that contained no alligator eggs and which presumably were undefended by alligators. The use of alligator nests may greatly reduce the distance (and hence energy expenditure) that a gravid female turtle may need to travel to find a well drained nest site within an extensive wetland system. In contrast to other Florida *Pseudemys*, the nest of *P. nelsoni* consists of a single chamber (no accessory holes; see account for *P. concinna*).

Eggs, Clutch Size, and Reproductive Potential. — Jackson (1988) recorded a mean clutch size of 14.3 eggs (range, 7–26), although Enge et al. (2000) documented clutches as large as 32. Each female may lay 3–6 clutches per season. Based on these figures, mean annual reproductive potential per female may be in the range of 60–70 eggs. Eggs average 10.2 g and 34.8 x 23.2 mm. Mean clutch mass is 146.3 g, which, when compared to female mass, yields a relative clutch mass (clutch mass/gravid female mass) estimate of 0.044.

Incubation and Hatchlings. — Development of eggs is very rapid compared to most turtles, with hatching usually occurring 45 to 60 days (but sometimes as long as 80 days) after oviposition, for eggs incubated at constant temperatures of 25 to 30°C (Jackson, 1988). As with many other turtles, incubation temperature determines offspring sex in this species; the pivotal temperature is approximately 28.5ºC (males cooler, females warmer; Ewert et al., 2004). Hatchlings are relatively small, averaging 7.4 g and 30.4 mm PL.

POPULATION BIOLOGY

Population Size and Density. — No statewide population size estimates are available for the Florida red-bellied turtle. The species occurs in appropriate habitat throughout its range and is often locally abundant, but no specific inventory has been conducted to document precise distribution, trends, or population sizes. Studies of behavior and reproduction (Kramer, 1986, 1989; Jackson, 1988), including use of alligator nests, as well as recent commercial egg-collecting ventures in southern Florida (P. Moler, *pers. comm.*), suggest that red-bellied turtles are common at least locally.

Population density estimates are not available for red-bellied turtles within their more usual lake and marsh habitats. However, Giovanetto (1992) estimated densities of 22.2 turtles (all ages) per ha (estimated population size of 138 turtles in 0.7 km or 6.22 ha) in the Homosassa River (Citrus County), and 4.6 per ha (population estimate of 25 in 0.7 km or 5.42 ha) in the Rainbow River (Marion County). Kramer (1995) estimated a much denser population of 231 adult and subadult red-bellied turtles in a 980 x 30 m stretch (ca. 78.6 turtles per ha) of Rock Springs Run.

Population Structure. — The few data available for the distribution of body sizes (loosely correlated with age) in red-bellied turtle populations present somewhat contrasting pictures. A sample of more than 100 living turtles captured during a three-year study of Lake Conway, Orange County, was roughly bimodal, with peaks at 40–90 mm CL (juveniles) and 260–270 mm CL (adult/subadult females), and a minor peak at 160 mm CL (adult/subadult males) (Bancroft et al., 1983). However, it appears that adult turtles may predominate in at least some local populations of red-bellied turtles. In an assemblage of dead turtles that had succumbed to the drying of a shallow lake (Station Pond, Levy County, Florida) during a severe drought in 1977, 76.5% of 153 red bellied turtles were > 240 mm PL (Fig. 22-11) (D.R. Jackson and D. Deitz, unpubl. data). Whether smaller individuals were truly rare, versus having been removed by predators and scavengers or perhaps having successfully buried in the mud, could not be determined. However, the much greater relative abundance of small *P. floridana* in the same assemblage (Fig. 22-11; only 19% of individuals > 240 mm PL, with 64% < 200 mm PL) suggests that the scarcity of small *P. nelsoni* was real. If so, this may have related to a higher incidence of predation by alligators on the latter, due to microhabitat differences, or alternatively to a more rapid rate of growth by juvenile male *P. nelsoni*, which do not achieve sexual maturity at the small size of male *P. floridana* (Jackson, 1988). The likelihood that marsh populations of *P. nelsoni* are characteristically skewed toward subadults and adults

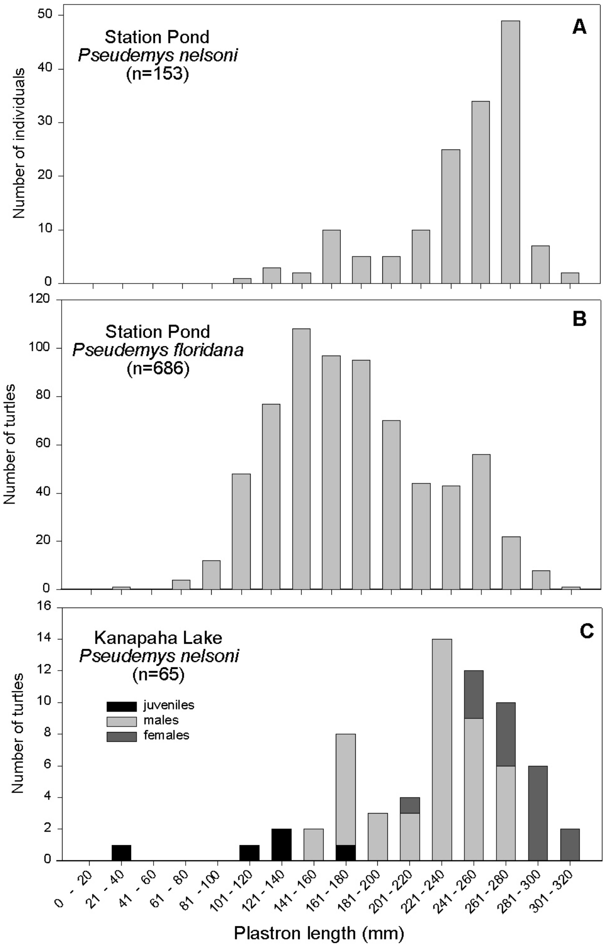

Figure 22-11. Plastron lengths for two species of *Pseudemys* from two localities in northern Florida. **(A)** Florida red-bellied turtle, *Pseudemys nelsoni*, from a death assemblage found during a severe drought at Station Pond, Levy County, Florida, in 1977, **(B)** Florida Cooter, *Pseudemys floridana* from the same death assemblage, **(C)** distribution by size and sex of 65 *Pseudemys nelsoni* recovered alive from a drying pool in Lake Kanapaha, Alachua County, Florida, during a drought in 1981-1982 (A, B, unpubl. data collected by D.R. Jackson and D. Deitz; C, unpubl. data collected by B. Taylor and P. Meylan).

is supported by a second sample of turtles recovered alive from a drying lake in adjacent Alachua County (Fig. 22-11; B. Taylor and P. Meylan, unpubl. data).

Few reliable sex ratio data exist for red-bellied turtles, but all indicate a preponderance of males. The two available samples from populations inhabiting spring runs are remarkably similar. Giovanetto's (1992) sample from the Rainbow River had a male:female sex ratio of 1:0.67. Kramer's (1995) sample of adult and subadult turtles also included more males (74 vs. 52), for a male:female ratio of 1:0.70. The male:female ratio was even more disparate (1:0.36) in an all-age sample (adults, subadults, sexable juveniles) of turtles collected from a drying marsh lake (Lake Kanapaha) in Alachua County (Fig. 22-11; B. Taylor and P. Meylan, unpubl. data). Because males mature at smaller sizes and presumably younger ages than females, they are expected to predominate, as many young females of comparable age would likely be classified as unsexable juveniles. However, even if the few juveniles in the Lake Kanapaha sample were all females, males still would have exceeded females there by more than a 2:1 ratio.

INTERSPECIFIC INTERACTIONS

Community Relations. — Pseudemys nelsoni often coexists with one or more other emydids, including *P. floridana*, *Deirochelys reticularia*, the riverine *P. concinna*, and least frequently *Trachemys s. scripta* (the range of which lies principally to the north of that of *P. nelsoni*). The species shares habitat in the canals of southern Florida with the introduced red-eared slider, *T. s. elegans* (W. Meshaka, *pers. comm.*). Non-emydid co-habitants often include the Florida softshell (*Apalone ferox*), the common snapping turtle (*Chelydra serpentina*), and any of the state's four kinosternids (mud and musk turtles).

Existing data about the relative representation of red-bellied turtles within local turtle faunas suggest great variation in the degree to which this species can dominate a site. Whether *P. nelsoni* is more or less common than other species seems to be site- and habitat-specific. Although not quantified, my subjective impression is that *P. nelsoni* comprises more than 90% of the emydid turtle fauna in some marshy sites (presumably optimal habitat) such as Payne's Prairie and parts of south Florida's Everglades. Duellman and Schwartz (1958) likewise considered it to be far more abundant than *P. floridana* in southern Florida. In lakes with more extensive open water, though still common, *P. nelsoni* tends to be outnumbered substantially by *P. floridana*. Such was the case both among living turtles collected at Lake Conway (3–6 times as many *P. floridana* collected yearly: Bancroft et al., 1983) and among turtle carcasses at Station Pond (ca. 70% *P. floridana* vs. 15% *P. nelsoni*: D.R. Jackson and D. Deitz, unpubl. data). *Pseudemys nelsoni*, *P. floridana*, and *T. scripta* each comprised roughly one-third of the emydid turtles (65, 58, and 61 individuals, respectively) retrieved in 1981–82 from a residual pool in a drying lake bed in Alachua County, Florida (B. Taylor and P. Meylan, unpubl. data); this site (Lake Kanapaha) occurs within the narrow zone of overlap between red-bellied turtles and sliders.

Florida red-bellied turtles are generally less dominant in riverine sites, although there are exceptions in central and southern Florida. Giovanetto (1992) found *P. nelsoni* to be the sixth most abundant (3% of sample) of seven species of native turtles in the Rainbow River, a large spring run that is more optimal for the Suwannee cooter (*P. concinna suwanniensis*). In the same river, Marchand (1942) and Meylan et al. (1992) respectively estimated that *P. nelsoni* comprised only 2.1% and 0.2% of turtles, and 2.8% and 2.6% of *Pseudemys*, with both *P. concinna* and *P. floridana* being more abundant. In the very low-gradient Homosassa River, Giovanetto (1992) found *P. nelsoni* to be less abundant (32% of sample) than *P. floridana* (65%) but more abundant than *P. concinna* (3%). Kramer (1995), however, collected 3.2 times as many *P. nelsoni* as *P. floridana* in

Rock Springs Run, part of an Atlantic Coast drainage that lies outside of the range of *P. concinna*, which dominates similar spring-run habitats in Gulf Coast drainages.

The red-bellied turtle's interactions with the alligator clearly extend beyond a predator-prey relationship and seem to be unique among Florida turtles. Although young *P. nelsoni* must remain wary of the jaws of these crocodilians, the thick, highly domed shells of adult turtles allow them to live in intimate association with alligators. They are thereby able to take advantage of the survival benefits, especially during drought, offered by the alligator's habit of excavating deep "gator holes" and bank caves. Furthermore, maternal protection of alligator nests may secondarily enhance the survival rate of turtle eggs laid in those structures. According to one hypothesis (P.C.H. Pritchard, *pers. comm.*), increased alligator populations as a result of greater protection for the species in recent decades may have indirectly allowed the red-bellied turtle to increase its range and numbers, perhaps even at the expense of other emydids.

Diet. — Except for its early juvenile stages, which are poorly studied, *P. nelsoni* is strictly herbivorous. The diet includes such aquatic plants as *Cabomba, Lemna, Nuphar, Nymphaea, Potamogeton, Sagittaria, Vallisneria, Wolffia* and the invasive exotics *Egeria* (elodea) and *Hydrilla* (Ward, 1980; Bancroft et al., 1983; Bjorndal et al., 1997; Giovanetto, 1992; Jackson, unpubl. data). In the canals of southern Florida, this turtle exploits the flowers of at least one exotic ornamental tree (*Bauhinia*; W. Meshaka, *pers. comm.*). Red-bellied turtles have also been observed grazing on algae growing on the carapaces of other cooters (Meshaka, 1988; Meshaka and Deyrup, 1999). Small juveniles may include at least some animal matter (insects, crustaceans, worms) in their diets (Carr, 1952; Ernst and Barbour, 1972; Bancroft et al., 1983; Bjorndal, 1986; Jackson, *pers. obs.* of captive turtles). With the capability of consuming more than 10% of its body weight in aquatic vegetation per day (Bancroft et al., 1983), the red-bellied turtle may exert a profound influence on the community dynamics of aquatic ecosystems.

Predation. — Like most freshwater turtles within its range, this species is subject to predation by alligators (Delany and Abercrombie, 1986; Delany et al., 1988) and carnivorous mammals such as otters and raccoons. Nesting females are especially vulnerable while they are on land. Red-bellied turtles may even comprise a major component of the diet of large (especially male) alligators in some lakes (Delany and Abercrombie, 1986). This risk may be reduced in the southern Everglades, where alligators tend to be smaller (Jacobsen and Kushlan, 1989; Dalrymple, 1996). Ross (1989) additionally recorded young *P. nelsoni* in the diets of at least three species of North American raptorial birds. As for many turtles, nest predation is heavy, with most eggs being taken by such broad omnivores as raccoons and crows. Humans must also be considered as predators, and currently no regulations limit the number of red-bellied turtles that may be harvested.

Recent experimental evidence suggests that the red imported fire ant (*Solenopsis invicta*) has the potential to be an important predator of red-bellied turtle hatchlings, and perhaps of all species of turtles in Florida. Allen et al. (2001) found that 71% of an experimental group of *P. nelsoni* exposed to fire ants during hatching died from ant attacks. This may be ecologically significant, as approximately 20% of alligator nests, a preferred nesting microhabitat of red-bellied turtles, are infested with fire ants in central Florida (Allen et al. 1997). The ubiquity of this exotic species throughout Florida, coupled with its proclivity for attacking newly hatched eggs, makes it a major threat to much of the state's herpetofauna.

Parasites and Disease. — As with most freshwater turtles, red-bellied turtles commonly support a few minor parasites and commensals. Among these are leeches (*Placobdella*) and algae (*Basicladia*). Neither seems to be debilitating except in turtles whose health is already compromised for other reasons.

THREATS

Although red-bellied turtles are taken occasionally by divers and fishers for food, this does not appear to be common. Apparently the species' contribution to human cuisine was greater historically, as Carr (1940) noted that the Seminole Indians valued this turtle highly. In open water systems, impact from boat propellers is a documented source of mortality, although perhaps a less significant threat than it is to the Florida cooter because of microhabitat and shell thickness differences between the species (Bancroft et al., 1983). Until recently, southern Florida supported a small commercial industry of collection of freshwater turtle eggs, presumably for the pet trade. This industry, which focused on Florida red-bellied turtles and Florida softshells, was at least temporarily curtailed in 1999 by a Florida Fish and Wildlife Conservation Commission regulation prohibiting possession of more than 50 eggs as well as their sale (P. Moler, *pers. comm.*)

Like much of Florida's herpetofauna, the dependence of the red-bellied turtle upon wetlands ties its status and survival prospects directly to the condition and maintenance of sufficient freshwater habitat. Wetlands throughout Florida are threatened by pollution (both point and non-point source, including acid rain), drainage, destruction of shoreline vegetation in association with residential development, and general shrinkage from lowered water tables as a result of withdrawal for human consumption and use of excessive water from underground aquifers. Rapid decline of one population of red-bellied turtles as a result of destruction of littoral zone and shoreline vegetation has already been documented in one central Florida lake system (McDiarmid et al., 1983). Construction of roads across, between, and around wetlands causes an ever-increasing rate of mortality for all aquatic turtles, including *P. nelsoni*, that at least occasionally wander terrestrially. This includes adult females in search of upland nesting sites, hatchlings that must make a perilous migration from the nest to the wetland, and dispersing individuals of all ages and sexes (often adult males) when moving between wetlands. At one monitored site, Smith and Dodd (1999) recorded a minimum of 26 red-bellied turtles killed by vehicles during one year along a stretch of highway crossing Payne's Prairie, a large marsh system in Alachua County.

Human-induced modifications of wetlands can lead to unnaturally high concentrations of turtle nests and correspondingly high levels of nest predation (e.g., Jackson, 1988; Jackson and Walker, 1997). Long-term effects of this on turtle populations are unknown. Additionally, natural events, particularly drought, may extirpate local populations of this and other turtles. Especially severe droughts in the late 1970s and again in the late 1990s through 2000 caused massive mortality of pond- and lake-dwelling turtles throughout much of Florida. Because of anthropogenic fragmentation of the native landscape, opportunities for natural recolonization after local extinction, as well as for gene flow among populations, may be reduced or lost.

STATUS

No federal or state agency formally lists the Florida red-bellied turtle as a protected species, and neither Georgia nor Florida specifically protects unlisted freshwater turtles. Developed in conjunction with haul seine fishery regulations, Florida Fish and Wildlife Conservation Commission (FFWCC) Rule 68A-23.012(2) restricts take of *P. nelsoni* from Lake Okeechobee and adjacent waters to turtles > 20.3 cm CL. Possession of red-bellied turtle eggs is restricted under a general FFWCC rule that prohibits possession of more than 50 turtle eggs collected from the wild without a permit (greater restrictions apply to some other species).

CONSERVATION OPTIONS AND SOLUTIONS

Neither state nor federal listing nor additional protective regulations are warranted for *P. nelsoni* at this time. The IUCN/SSC Tortoise and Freshwater Turtle Specialist Group (1989) Action Plan included the species in Category 4: species for which neither additional investigation nor conservation efforts appeared necessary at the time. However, because of its restricted distribution, periodic re-evaluation for possible inclusion in Category 2 (need for monitoring and conservation attention) was recommended as appropriate. Special attention should be paid to any populations in the Florida panhandle. As long as appropriate freshwater ecosystems throughout Florida are protected from pollution, drainage, and other unnatural disturbance, the survival prospects of this species appear to be good. Protection of complexes of wetlands within a fully functional, non-fragmented landscape is especially important.

Major steps could be taken to conserve Florida red-bellied turtles and other wetland wildlife in peninsular Florida if the effects of residential shoreline development were mitigated by better protection of littoral zone vegetation and natural upland buffers. This could be accomplished by passage and enforcement of more stringent state and local regulations. Where roads are developed around or bordering lakes and ponds, they should be situated such that they do not separate wetlands from the adjacent uplands used by turtles for nesting. At sites where established highways already cross wetlands, the installation of permanent wildlife barriers and underpasses can reduce the mortality of *P. nelsoni* and other reptiles that are prone to being killed while attempting to cross roads (Barichivich and Dodd, 2002).

In addition to protecting habitat within and surrounding individual wetlands, consideration should be given to preserving natural movement corridors between wetlands. When such connecting habitat is available, *P. nelsoni* has proven adept at recolonizing sites from which it had been extirpated by drought or other factors (J. Ward, *pers. comm.*).

Although drainage of wetlands for agriculture and urbanization was a common practice in Florida's recent history, the last three decades have seen a renewed public appreciation of the multiple values of wetlands. State regulations now offer protection to many, but not all, wetland habitats. Omitted from Florida's statewide wetland protective regulations are smaller, "isolated wetlands" that can be many acres in size. Although many of these tend to be ephemeral wetlands and hence unable to support permanent populations of red-bellied turtles, some are sufficiently large and deep to provide habitat for the species. The potential role of alligators in maintaining deeper microhabitats may be crucial to the survival of turtles in such situations. Conservation groups currently are seeking stronger measures from the state's five Water Management Districts, as well as the U.S. Army Corps of Engineers, to protect isolated wetlands.

Pseudemys nelsoni inhabits an undetermined number of protected areas, including Everglades National Park (but not throughout) and Payne's Prairie and Rock Springs Run state preserves in Florida, and Okefenokee National Wildlife Refuge in Georgia. Efforts to verify the presence of this species in other protected areas throughout its range would provide a valuable baseline for future conservation and land management activities.

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LITERATURE CITED

Allen, C. R., Forys, E. A., Rice, K. G., and Wojick, D. P. 2001. Effects of fire ants (Hymenoptera: Formicidae) on hatchling turtles and prevalence of fire ants on sea turtle nesting beaches in Florida. Florida Entomologist 84:250-253.

Allen, C. R., Rice, K. G., Wojick, D. P., and Percival, H. F. 1997. Effect of red imported fire ant envenomation on neonatal American alligators. Journal of Herpetology 31:318-321.

Bancroft, G. T., Godley, J. S., Gross, D. T., Rojas, N. N., Sutphen, D. A., and McDiarmid, R. W. 1983. Large-scale operations management test of use of the white amur for control of problem aquatic plants; the herpetofauna of Lake Conway, Florida: species accounts. Misc. Paper A-83-5, U. S. Army Engineer Waterways Experiment Station, CE, Vicksburg, Mississippi.

Barichivich, W. J., and Dodd, C. K., Jr. 2002. The effectiveness of wildlife barriers and underpasses on U.S. highway 441 across Paynes Prairie State Preserve, Alachua County, Florida, Phase II: post-construction, final report. Florida Caribbean Science Center, U.S. Geological Survey, report to Florida Dept. Transportation.

Bjorndal, K. A. 1986. Effects of solitary vs. group feeding on intake in *Pseudemys nelsoni*. Copeia 1986:234-235.

Bjorndal, K. A., Bolten, A. B., Lagueux, C. J., and Jackson, D. R. 1997. Dietary overlap in three sympatric congeneric freshwater turtles (*Pseudemys*) in Florida. Chelonian Conservation and Biology 2:430 433.

Blaney, R. M. 1971. An annotated checklist and biogeographic analysis of the insular herpetofauna of the Apalachicola region, Florida. Herpetologica 27:406-430.

Carr, A. F. 1938. *Pseudemys nelsoni*, a new turtle from Florida. Occasional Papersof the Boston Society of Natural History 8:305-310.

Carr, A. F. 1940. A contribution to the herpetology of Florida. University of Florida Publications, Biological Sciences Series 3(1):1-118.

Carr, A. F. 1952. Handbook of turtles: the turtles of the United States, Canada, and Baja California. Cornell Univ. Press, Ithaca, New York. 542 pp.

Carr, A. F., and Crenshaw, J. W. 1957. A taxonomic reappraisal of the turtle *Pseudemys* alabamensis Baur. Bulletin of the Florida State Museum BiologicalSciences 2:25-42.

Conant, R., and Collins, J. T. 1991. A field guide to reptiles and amphibians: eastern and central North America. Houghton Mifflin Co., Boston. 450 pp.

Crenshaw, J. W. 1955. The ecological geography of the *Pseudemys* floridana complex in the southeastern United States. Ph.D. dissertation, Univ. Florida. 204 pp.

Dalrymple, G. H. 1996. Growth of American alligators in the Shark Valley region of Everglades National Park. Copeia 1996:212-216.

Deitz, D. C., and Jackson, D. R. 1979. Use of American alligator nests by nesting turtles. Journal of Herpetology 13:510-512.

Delany, M. F., and Abercrombie, C. L. 1986. American alligator food habits in northcentral Florida. Journal of Wildlife Management 50:348-353.

Delany, M. F., Woodward, A. R., and Kochel, I. H. 1988. Nuisance alligator food habits in Florida. Florida Field Naturalist 16:86-90.

DeSola, C. R. 1935. Herpetological notes from southeastern Florida. Copeia 1955:44-45.

Dobie, J. L. 1985. Distribution and status of the Alabama red-bellied turtle, *Pseudemys alabamensis* Baur. Unpublished report submitted to U. S. Fish and Wildlife Service. 31 pp. + app.

Dobie, J. L., and Jackson, D. R. 1979. The first fossil record of the diamondback terrapin, *Malaclemys terrapin*, with comments on the fossil record of *Chrysemys nelsoni*. Herpetologica 35:139-145.

Duellman, W. E., and Schwartz, A. 1958. Amphibians and reptiles of southern Florida. Bulletin of the Florida State Museum Biological Sciences 3:181-324.

Dunson, W. A., and Mazzotti, F. J. 1989. Salinity as a limiting factor in the distribution of reptiles in Florida Bay: a theory for the estuarine origin of marine snakes and turtles. Bulletin of Marine Science 44:229-244.

Dunson, W. A., and Seidel, M. E. 1986. Salinity tolerance of estuarine and insular emydid turtles (*Pseudemys nelsoni* and *Trachemys decussata*). Journal of Herpetology 20:237-245.

Enge, K. M., Percival, H. F., Rice, K. G., Jennings, M. L., Masson, G. R., and Woodward, A. R. 2000. Summer nesting of turtles in alligator nests in Florida. Journal of Herpetology 34:497-503.

Ernst, C. H., and Barbour, R. W. 1972. Turtles of the United States. University Press of Kentucky, Lexington. x + 347 pp.

Ewert, M. A., Etchberger, C. R., and Nelson, C. E. 2004. Turtle sex-determining modes and TSD patterns, and some TSD pattern correlates. In: Valenzeula, N. and Lance, V. (Eds.). Temperature-dependent sex determination in vertebrates. Smithsonian Books. Washington, D.C., pp. 21-33.

Giovanetto, L. A. 1992. Population ecology and relative abundance of sympatric freshwater turtles in the headwaters of two spring fed rivers in western peninsular Florida. Ph.D. dissertation, Florida Institute of Technology, Melbourne.

Goodwin, T. M., and Marion, W. R. 1977. Occurrence of Florida red-bellied turtle eggs in north-central Florida alligator nests. Florida Scientist 40:237-238.

Hay, O. P. 1908. The fossil turtles of North America. Carnegie Institute of Washington Publication 75:1-568.

Hunt, R. H. 1987. Nest excavation and neonate transport in wild *Alligator mississippiensis*. Journal of Herpetology 21:348-350.

IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. 1989. Tortoises and freshwater turtles. An action plan for their conservation. IUCN/SSC. 47 pp.

Iverson, J. B. 1992. A revised checklist with distribution maps of turtles of the world. Richmond, Indiana. 363 pp.

Jackson, C. G. 1977. Courtship observations on *Chrysemys nelsoni* (Reptilia, Testudines, Testudinidae). Journal of Herpetology 11:221-222.

Jackson, C. G., and Davis, J. D. 1972. Courtship display behavior of *Chrysemys concinna suwanniensis*. Copeia 1972:385-387.

Jackson, D. R. 1978. *Chrysemys nelsoni*. Florida red-bellied turtle. Catalogue of American Amphibians and Reptiles 210:1-2.

Jackson, D. R. 1988. Reproductive strategies of sympatric freshwater emydid turtles in northern peninsular Florida. Bulletin of the Florida State Museum Biological Sciences 33:113-158.

Jackson, D. R. 2002. Survey of an important distributional gap in the Florida range of the river cooter and other freshwater turtles. Final report to Florida Fish and Wildlife Conservation Commission, Nongame Wildlife Program, Tallahassee.

Jackson, D. R., and Stearns, B. C. 2005. Geographic distribution: *Pseudemys nelsoni* (Florida red-bellied turtle). Herpetological Review 36:466.

Jackson, D. R., and Walker, R. N. 1997. Reproduction in the Suwannee cooter, *Pseudemys concinna suwanniensis.* Bulletin of the Florida Museum of Natural History 41:69-167.

Jacobsen, T., and Kushlan, J. A. 1989. Growth dynamics in the American alligator (*Alligator mississippiensis*). Journal of Zoology 219:309-328.

Kramer, M. 1984. Life history notes: *Pseudemys nelsoni* (Florida red-bellied turtle). Behavior. Herpetological Review 15:113-114.

Kramer, M. 1986. Field studies on a freshwater Florida turtle, *Pseudemys nelsoni*. In: Drickamer, L.C. (Ed.). Behavioral ecology and population biology. Privat, I.E.C., Toulouse, pp. 29-34.

Kramer, M. 1989. The behavior and natural history of the Florida red-bellied turtle, *Pseudemys nelsoni*: an ethological study. Ph.D. dissertation, Univ. Tennessee, Knoxville.

Kramer, M. 1995. Home range of the Florida red-bellied turtle (*Pseudemys nelsoni*) in a Florida spring run. Copeia 1995:883-890.

Kramer, M., and Fritz, U. 1989. Courtship of the turtle, *Pseudemys nelsoni*. Journal of Herpetology 23:84-86.

Kushlan, J.A., and Kushlan, M.J. 1980. Everglades alligator nests: nesting sites for marsh reptiles. Copeia 1980:930-932.

Leary, C.J., Dobie, J.L., Mann, T.M., and Floyd, P.S. 2003. Morphological variation in the endangered Alabama red-bellied cooter (*Pseudemys alabamensis*) and taxonomic status of a population in Mississippi. Chelonian Conservation and Biology 4(3):635-641.

Lewis, T.E., Irwin, L.K., and Irwin, K.J. 2001. Geographic distribution. *Pseudemys nelsoni*. Herpetological Review 32:117.

Loennberg, E. 1894. Notes on reptiles and batrachians collected in Florida in 1892 and 1893. Proc. U.S. Nat. Mus. 17:317-339.

Marchand, L.J. 1942. A contribution to a knowledge of the natural history of certain freshwater turtles. M.S. thesis, Univ. Florida, Gainesville.

McDiarmid, R.W., Bancroft, G.T., and Godley, J.S. 1983. Large-scale operations management test of use of the white amur for control of problem aquatic plants; the herpetofauna of Lake Conway, Florida: community analysis. Tech. Report A-78-2, U. S. Army Engineer Waterways Experiment Station, CE, Vicksburg, Mississippi.

Means, D.B. 1977. Aspects of the significance to terrestrial vertebrates of the Apalachicola River drainage basin, Florida. Florida Marine Research Publications (26):37-67.

Mertens, R. 1951. Zwischen Atlantik und Pazifik. Zoologische Reisekizzen aus Nordamerika. D. Gundert Verlag, Stuttgart. 160 pp.

Meshaka, W.E., Jr. 1988. *Pseudemys nelsoni* (Florida red-bellied slider). Mutualism. Herpetological Review 19:88.

Meshaka, W.E., Jr., and Deyrup, M. 1999. *Pseudemys floridana peninsularis* (peninsula cooter) and *P. nelsoni* (Florida redbelly turtle). Mutualism. Herpetological Review 30:95.

Meylan, P.A., Stevens, C.A., Barnwell, M.E., and Dohm, E.D. 1992. Observations on the turtle community of Rainbow Run, Marion Co., Florida. Florida Scientist 55:219-227.

Moll, E.O. 1979. Reproductive cycles and adaptations. In: Harless, M., and Morlock, H. (Eds.). Turtles: perspectives and research. John Wiley and Sons, New York, pp. 305-331.

Powers, A., and Smith, C.R. 1977. Geographic distribution: *Chrysemys nelsoni*. Herpetological Review 8:84.

Pritchard, P.C.H. 1980. Record size turtles from Florida and South America. Chelonologica 1:113-123.

Pritchard, P.C.H., and Greenwood, W. 1968. The sun and the turtle. International Turtle Tortoise Society Journal 2:20-25, 34.

Rose, F.L., Manning, R.W., Simpson, T.R., and Jenkins, S. 1998. A sustaining population of the Florida red-bellied turtle, *Pseudemys nelsoni* (Reptilia: Emydidae), in Spring Lake, Hays County, Texas. Texas Journal of Science 50:89-92.

Ross, D.A. 1989. Amphibians and reptiles in the diets of North American raptors. Wisconsin Endangered Resources Report no. 59. 33 pp.

Seidel, M.E. 1994. Morphometric analysis and taxonomy of cooter and red-bellied turtles in the North American genus *Pseudemys* (Emydidae). Chelonian Conservation and Biology 1:117-130.

Shoop, C.R., and Ruckdeschel, C. 1986. New herpetological records for Cumberland Island, Georgia. Herpetological Review 17:51.

Smith, L., and Dodd, C. K., Jr. 1999. Determination of the effectiveness of wildlife barriers and underpasses on U.S. highway 441 across Paynes Prairie State Preserve, Alachua County, Florida, Phase I, final report. Florida Caribbean Science Center, U.S. Geological Survey, report to Florida Department of Transportation.

Vitt, L.J., and Dunham, A.E. 1980. Geographic distribution: *Chrysemys nelsoni* (Florida redbelly turtle). Herpetological Review 11:80.

Ward, J.P. 1980. Comparative cranial morphology of the freshwater turtle subfamily Emydinae: an analysis of the feeding mechanisms and the systematics. Ph.D. dissertation, North Carolina State University, Raleigh.

Ward, J.P. 1984. Relationships of chrysemyd turtles of North America (Testudines: Emydidae). Special Publications of the Museum Texas Tech University 21:1-50.

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Pseudemys concinna – River Cooter

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Summary. – The river cooter, *Pseudemys concinna*, is a large, hard-shelled turtle widespread across the U.S., but restricted in Florida to rivers and associated lakes and impoundments that drain into the Gulf of Mexico. In Florida, two subspecies are found, one (*P. c. concinna*) from the western panhandle to the Apalachicola River, and the second (*P. c. suwanniensis*) from the Ochlockonee River east and south along the Gulf Coast to the Alafia River, which empties into Tampa Bay. This herbivore spends much of its day foraging on aquatic plants or basking on logs and stumps to raise its body temperature, presumably to increase digestive efficiency. The long nesting season in Florida extends from late March or early April into July and allows individual females to produce as many as five or more clutches of eggs at roughly 3-week intervals. Each clutch typically contains 12-25 relatively small eggs. Populations in some rivers may reach high densities which, combined with the turtle's large size (up to 10 kg for a large female), allows this species to achieve a very high biomass (e.g., 600 kg/river km) for a riverine reptile. Thus, the species may have a profound influence on aquatic ecosystems. Protection of the river cooter is largely dependent upon maintenance of high quality riverine systems free of pollution and human disturbance, as well as limitation on the number of cooters that can be harvested for human consumption or the pet trade. The Florida Fish and Wildlife Conservation Commission currently lists one subspecies, *P. c. suwanniensis*, as a Species of Special Concern, and restricts possession of any river cooter to two individuals or eggs per person, with the bulk of the nesting season closed to any possession.

Conservation Status. – FNAI Global - G5 (Demonstrably Secure), State - Species: S4 (Apparently Secure), *P. c. suwanniensis*: S3 (Rare, Local, or Vulnerable); ESA Federal - Not Listed; State - Species: Not Listed, *P. c. suwanniensis*: SSC (Species of Special Concern); CITES - Not Listed; IUCN Red List - Not Listed (LC-Least Concern).

Species Recognition. — Known by a broad array of local names (e.g., river turtle, Suwannee chicken, Suwannee cooter, Suwannee turtle, Mobile cooter, Mobilian, slider, streaky-head, streaky-legs, and streaky-neck), the river cooter, *Pseudemys concinna*, is a large (record carapace length, 43.7 cm) hard-shelled turtle with a mostly brown to black, relatively high domed shell (particularly in females) marked by a series of at least partially concentric yellow to orange lines on each of the scales of the shell (Figs. 23-1, 23-2). Most readily visible on the costal scutes, these lines vary geographically and locally in width (narrowest in *P. c. suwanniensis*, which appears completely black dorsally at a distance, Fig. 23-1; wider from the Apalachicola River westward, Fig. 23-2). The lines on the second, and often all, costal scutes usually open into a rearward-facing "C." The surface of the carapace is typically smooth in Florida specimens, especially compared to that of chicken turtles (*Deirochelys*), sliders (*Trachemys*), and other species of the genus *Pseudemys*, all of which may have extensive fine ridges and grooves or scale-like sculpturing on their upper shells. In contrast to map turtles (*Graptemys*), post-juvenile river cooters lack a mid-dorsal ridge with knobs or spines. The plastron is yellow-orange to orange in color and generally possesses a variable pattern of black pigment that runs along some or all of the scute seams (Fig. 23-3). Most Florida specimens also have a complete set of submarginal spots, which usually consist of concentric dark and light circles rather than solid smudges. The bridge often bears a dark bar. Head stripes are yellow to cream in color. Cusps on either side of the notch at the front of the upper jaw are normally absent or poorly developed (compared to *P. nelsoni*; see Fig. 22-7), although they do occur in some individuals in the Florida panhandle. Males reach sizes only slightly smaller than females and are characterized by much longer foreclaws, larger tails, and shells that typically are low in profile compared to females. Shell patterns of very young river cooters (Fig. 23-4) are similar to those of adults, although with the linear pattern somewhat bolder and with the carapacial background color greenish instead of black (Jackson and Jackson, 1968; Conant and Collins, 1991).

Taxonomic History. — The relationships among cooters have been and continue to be controversial. Although much of the literature of the 1960s and 1970s included all cooters as well as red-bellied turtles in an expanded genus *Chrysemys* that included sliders and painted turtles, following the arrangement of McDowell (1964), most current workers now reject that allocation and recognize them as the genus *Pseudemys* (see Ward, 1984, and Seidel and Smith, 1986). In the present account, I consider *Pseudemys concinna* and *P. floridana* (including *P. f. peninsularis*) as representing two

Figure 23-1. Adult female Suwannee cooter, *Pseudemys concinna suwanniensis,* from Wakulla River, Wakulla Co., Florida. Photo by Dale R. Jackson.

distinct species. This follows Le Conte's (1830) original recognition of these forms, which was resurrected by Crenshaw (1955) and has since been followed by most authors. In contrast, Carr (1952 and earlier papers) included the various forms of river cooter within an expanded *P. floridana*, and Seidel (1994) suggested the inclusion of *P. floridana* (exclusive of *peninsularis*) within *P. concinna*. Within these lineages many subspecies have been named; some of these at various times have been elevated to species. Most recent work (Jackson, 1995, 2002; Seidel and Dreslik, 1996) suggests that Florida currently supports two subspecies of river cooter, although their potential degree of intergradation has not been studied closely. These are the Suwannee cooter, *P. c. suwanniensis* from the Ochlockonee River eastward, and the eastern river cooter, *P. c. concinna* from the Apalachicola River westward (Jackson, 2002). Although Seidel (1994) suggested that *P. c. suwanniensis* was disjunct and morphometrically distinct from *P. c. concinna* and hence merited elevation to the level of full species, recent surveys have shown that populations of *P. c. suwanniensis* inhabit several of the intervening rivers where it previously was presumed to be absent, and hence is better retained as a subspecies at present (Jackson, 2002).

DISTRIBUTION

Geographic Distribution. — Pseudemys concinna is endemic to the southeastern coastal plain and piedmont of the United States, where it ranges northward to Virginia and Illinois, southward to west-central Florida, and westward to Texas. Traditionally, five subspecies have been recognized range-wide, but recently this has been the subject of considerable scientific disagreement. Closely related populations (*P. gorzugi* and *P. texana*), sometimes considered conspecific with the river cooter, extend the distribution of the river cooter lineage westward as far as New Mexico and northern Mexico.

In Florida, the species is restricted to Gulf coast drainages (Fig. 23-5). By most accounts, two subspecies are represented. Most authorities still recognize the Suwannee cooter (*P. c. suwanniensis*) as comprising those populations occurring from the Tampa Bay region (Alafia River) northwestward to approximately the Ochlockonee River just west

Figure 23-2. Adult female eastern river cooter, *Pseudemys concinna concinna*, from Spring Creek, Decatur Co., Georgia. Photo by Peter Meylan.

Figure 23-3. Plastral view of adult female Suwannee cooter, *Pseudemys concinna suwanniensis*, from Rainbow Run, Marion Co., Florida. Photo by George Heinrich.

Figure 23-4. Juvenile Suwannee cooter, *Pseudemys concinna suwanniensis,* from Rainbow Run, Marion Co., Florida. Photo by John Iverson.

of Tallahassee; this includes the Alafia, Weeki Wachee, Homosassa, Withlacoochee, Waccasassa, Suwannee, Steinhatchee, Fenholloway, Econfina, Aucilla, St. Marks, Sopchoppy, and Ochlockonee River drainages. Cooters from the westernmost of these drainages (especially the St. Marks, including the Wakulla) conform in most respects to Carr's description of *P. c. suwanniensis* (Jackson and Walker, 1997). River cooters in the remainder of the Florida panhandle (Apalachicola, Econfina Creek, Choctawhatchee, Yellow, Blackwater, Escambia, and Perdido drainages) are currently referred to the Eastern river cooter (*P. c. concinna*; see Seidel, 1994) or considered to be intergrades between the two subspecies. Although Auffenberg (1978) believed that river cooters were absent from a number of smaller rivers in Florida's "Big Bend" (principally Taylor County), this reflected inadequate sampling. The existence of *P. c. suwanniensis* in the Econfina, Fenholloway (at least formerly), and Steinhatchee rivers has recently been documented (Jackson 1997, 2002; Jackson and Ewert, 1998), thereby eliminating any substantial disjunction in the range of this species along Florida's Gulf coast. Additional surveys may confirm the species' presence in other poorly sampled rivers (e.g., East Bay, Chassahowitzka, Crystal). It is surprising and noteworthy that this species seems to be absent from the Hillsborough River. The species' occurrence in the Silver River, a tributary of the Atlantic coast-draining Ocklawaha/St. Johns River drainage, reflects the deliberate translocation (and subsequent escape) of many species of Florida turtles to the old Ross Allen Silver Springs Reptile Institute decades ago.

Ecological Distribution. — Throughout its range, this species is predominantly a turtle of rivers and river-associated habitats. Its adaptation to living in flowing waters is reflected in several structural specializations relative to its pond-dwelling kin: a smoother, thinner, and more streamlined shell; connection of skin nearer to the periphery of the shell (reducing turbulence); and very large, extensively webbed hind feet (Auffenberg, 1978; Jackson, 1992). Secondary habitats include oxbow lakes and impoundments, floodplain swamps and lakes, large ditches, and occasionally brackish tidal marshes (Carr, 1952; Ernst et al., 1994).

In Florida the river cooter is restricted to rivers (blackwater, alluvial, or spring-fed), spring runs, and associated backwaters and impoundments. Key habitat preferences seem to include moderate current, ample aquatic vegetation for feeding, and rocks, logs, or other sites for basking. The species uses a variety of microhabitats, including areas of floating, submerged, and emergent vegetation. Giovanetto (1992) found high numbers associated with maidencane (*Panicum hemitomon*) in the Rainbow River (Marion County). Although this turtle has been reported from estuaries, river mouths, and marine grass flats (Carr, 1952; P. Meylan, *pers. comm.*), the salinities at these sites have not been recorded. Nonetheless, the presence of living barnacles on a few cooters in the Wakulla River and elsewhere, coupled with capture of a few large individuals in salty water in the West Pass at the mouth of the Suwannee River (P. Meylan, *pers. comm.*), confirms that some turtles at least occasionally venture into brackish or saline habitats (Carr, 1952; Jackson and Walker, 1997). Salinity tolerance thus seems to be higher than it is for some other Florida freshwater turtles (e.g., softshell, mud, and musk turtles), perhaps similar to that of *P. nelsoni* (Dunson and Seidel, 1986).

Crenshaw (1955) noted two distinctly different optimal habitat types for *P. c. suwanniensis*: (1) rivers characterized by dark waters (from sediment and/or tannins), seasonally low temperatures, and frequent flooding, and (2) calcareous spring runs of remarkably clear water that emanate from the underlying aquifer and which are highly stable both in terms of temperature (range 19–23ºC, mean 21ºC in northern Florida) and water level, being relatively independent of the vagaries of rainfall (see also Rosenau et al., 1977; Giovanetto, 1992; Hubbs, 1995). Abundance of aquatic plants is distinctly seasonal in the former habitat and more stable in the latter. This is assuredly important ecologically to the exclusively herbivorous *P. c. suwanniensis.*

HABITAT RELATIONS

Activity. — River cooters are thoroughly aquatic and rarely venture onto land except to nest. Nonetheless, individuals of all ages spend considerable time basking on logs, rocks, and stumps, from which they may drop warily at the slightest approach. Most basking occurs on sunny days at air temperatures above 21ºC (Giovanetto, 1992). Where features of the habitat permit, adults typically bask on larger, mid-stream sites while juveniles favor smaller, nearshore sites (Jackson and Walker, 1997), a form of habitat partitioning noted for other riverine turtle populations (Pluto and Bellis, 1986). Even in northern Florida, basking and swimming continue year-round, although in winter such activities are restricted to warm, sunny days. In thermally stable habitats such as spring runs, river cooters may even continue to forage throughout the year (Jackson, 1964, 1970), although a limitation of the warm air temperatures needed to facilitate digestion must surely restrict the amount that is eaten in winter.

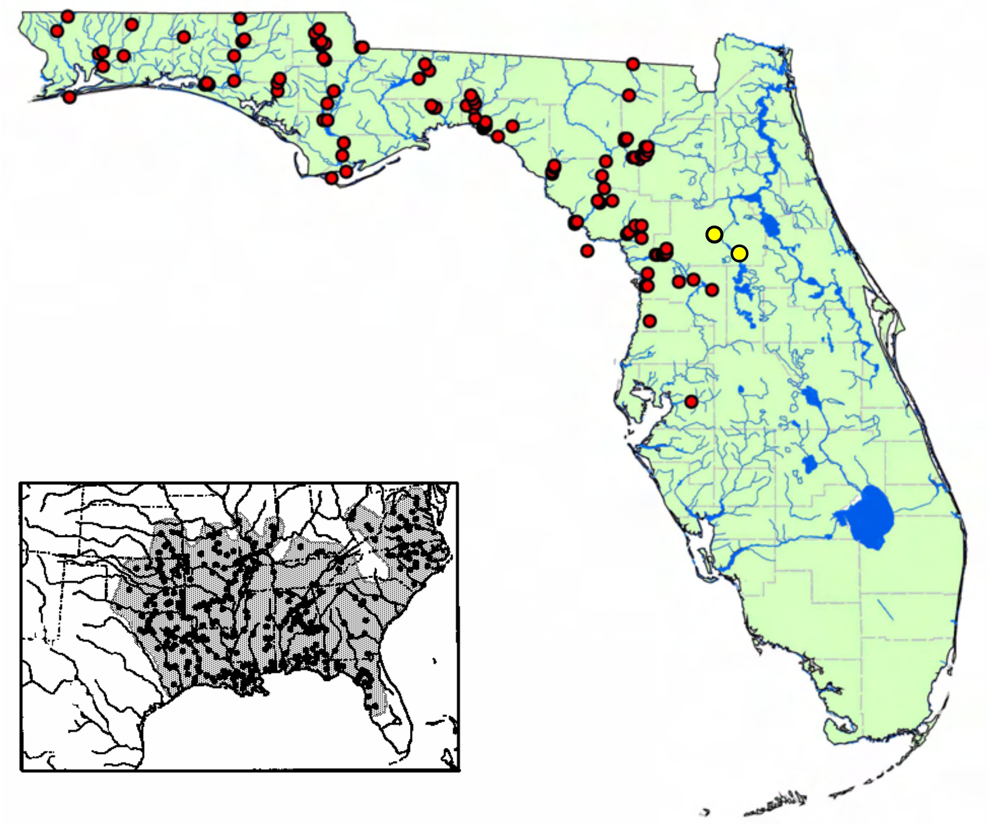

Figure 23-5. Available distribution records for the river cooter, *Pseudemys concinna,* from Florida. Inset: distribution records from entire range of *P. concinna* (adapted from Iverson, 1992; distribution in inset map not current for Florida as presented here). The records from Marion Co. (St. John's River drainage) (yellow dots) represent escaped individuals from Ross Allen's Reptile Institute (see text).

Home Range and Homing. — Individual river cooters seem to maintain distinct home ranges both within and across years. Because of the linear nature of riverine habitat, these ranges generally encompass a given stretch of river. By using radiotelemetry, Jackson and Walker (1997) determined the home ranges of four adult females in the Wakulla River (Wakulla County) to extend from 200–600 m. Home ranges appeared to overlap extensively with those of other turtles of all ages and sizes; in fact, up to 18 turtles shared the same basking log. Females generally nested inland from their aquatic home ranges. The same study revealed infrequent home range shifts of 3 km or more between years, the ability to home (return when displaced from a home range) at least 2 km, and evidence (barnacles on shells) of a few long-range movements.

GROWTH AND REPRODUCTION

Size, Growth, and Dimorphism. — River cooters, particularly the subspecies *P. c. suwanniensis*, are among the largest turtles in the family Emydidae. Females grow larger than males, reaching a maximum size of nearly 44 cm carapace length (CL), 39 cm plastron length (PL), and more than 10 kg (Pritchard, 1980; Jackson and Walker, 1997). A sample of 243 nesting females from the Wakulla River (Fig. 23-6) averaged 378 mm CL (328–427 mm), 341 mm PL (304–382 mm), and 6.5 kg post-nesting body mass (4.5–8.1 kg). Females at the same site matured at a minimum of 300 mm PL and 325 mm CL (ca. 4.5–5 kg), although most females grow another 35–50 mm prior to first reproduction (Jackson and Walker, 1997).

Males may grow to at least 290 mm PL (ca. 330 mm CL) and 3.4 kg, though relatively few seem to exceed 250 mm. The six largest males caught in a 1997–2003 study at Rainbow River, Marion County, averaged 242 mm PL, with most males measuring 171–230 mm PL (Huestis and Meylan, 2004). Eight large adult males captured in Florida's Withlacoochee (Citrus County) and Suwannee rivers from 1973–75 (D. Jackson, unpubl. data) averaged 269 mm CL (225–322 mm), 232 mm PL (201–272 mm), and 1.92 kg (1.21–2.97 kg). The same samples also included five juvenile males measuring 105–144 mm PL and 117–164 mm CL. Comparison with the sample of mature males yields an estimate of attainment of sexual maturity at 180–200 mm PL. This agrees well with Huestis and Meylan's (2004) Rainbow River data for males, which shows allometric elongation of the tail and foreclaws beginning at ca. 175 mm PL (Fig. 23-7).

Although females exceed males substantially in maximum size, the difference is less extreme than in some other freshwater turtles such as map turtles (*Graptemys*), softshells (*Apalone*), and perhaps even the Florida cooter (*P. floridana*: Jackson, 1988). Marchand (1942) and Jackson (1970) remarked on sexual size dimorphism of river cooters in penin-

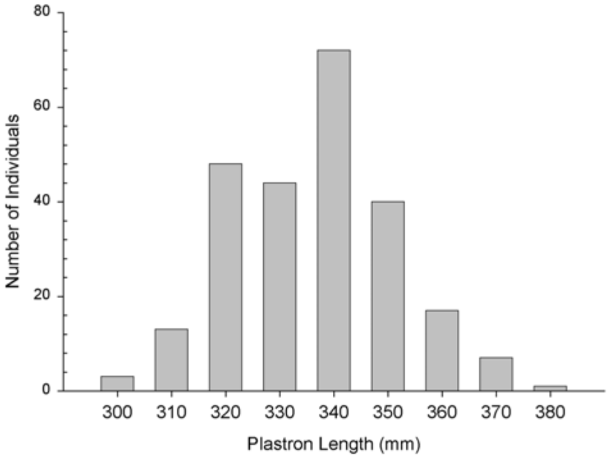

Figure 23-6. Plastron length at first measurement for 243 nesting *Pseudemys concinna suwanniensis* in the upper Wakulla River, Wakulla Co., Florida. Redrawn from Jackson and Walker (1997).

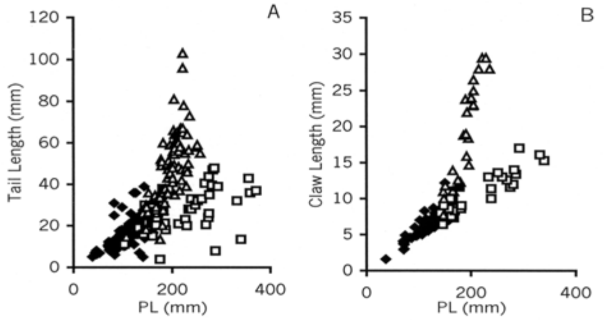

Figure 23-7. Basal (pre-cloacal) tail length (A) and longest foreclaw length (B), as a function of plastron length in *Pseudemys concinna suwanniensis* from the Rainbow River, Marion Co., Florida, 1997–2003. Triangles are males, squares females, and diamonds juveniles. From Huestis and Meylan (2004).

sular Florida, as did Fahey (1987) for a central Alabama population. The 10 largest females in a Suwannee River population (C. Jackson, unpubl. data) averaged 24% longer in CL than the 10 largest males; however, the sample may have included some immature turtles. Although quantitative measurements are lacking for Wakulla River males, casual observations of basking and swimming river cooters there suggest similar sexual size dimorphism (D. Jackson, *pers. obs.*). Based on the various samples above, female river cooters in Florida may average nearly half again as long and more than three times as heavy as males.

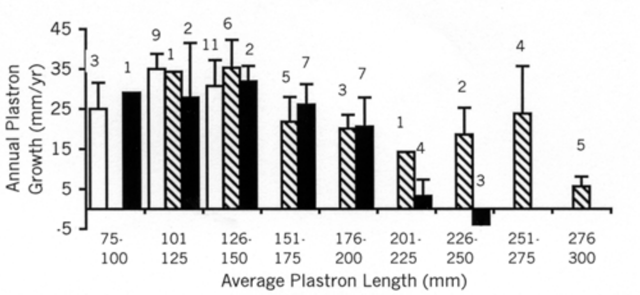

Figure 23-8. Annual plastron growth rate as a function of plastron length (PL) for *Pseudemys concinna suwanniensis* in the Rainbow River, Marion Co., Florida, 1997–2003. PL is an average of first capture and recapture. Open bars are unsexed juveniles, black bars males, hatched bars females. From Huestis and Meylan (2004).

Available data suggest that the relatively rapid rate of linear growth of juvenile turtles begins to slow substantially as turtles reach about 200 mm PL in males and about 300 mm PL in females (Fig. 23-8). Huestis and Meylan (2004) found the average annual growth for Rainbow River turtles to decline from a maximum of about 35 mm per year in individuals less than 150 mm PL, to about 20 mm per year for males less than 200 and females less than 275 mm PL. Growth appeared to be minimal (≤ 5mm/yr) in males over 200 mm PL and females over 275 mm PL. After reaching sexual maturity, the linear growth of females is almost imperceptible, averaging ca. 1 mm per year (Wakulla River; Jackson and Walker, 1997). Overall, the growth curve of river cooters reflects a shift from immature stages with rapid linear growth to later stages in which growth is dominated by increases in mass (Fig. 23-9).

Age at Maturity. — Data for determining the age at which each sex reaches maturity are limited, in part as a consequence of the general failure of these turtles to retain growth annuli beyond a few years. Based on a few females that did retain annuli, Jackson and Walker (1997) believed that Wakulla River females require at least 10–13 yrs to mature. Bancroft et al. (1983) re-analyzed the extensive growth data presented by Jackson (1964) for river cooters and subsequently suggested ages of maturity of only 5 yrs for males but 16 yrs for females. Although such age estimates seem reasonable, reservations about the presumed yearly formation of annuli in some turtles requires caution in their use (e.g., Brooks et al., 1997; Litzgus and Brooks, 1998; but see Germano and Fritts, 1994, and Aresco and Guyer, 1998).

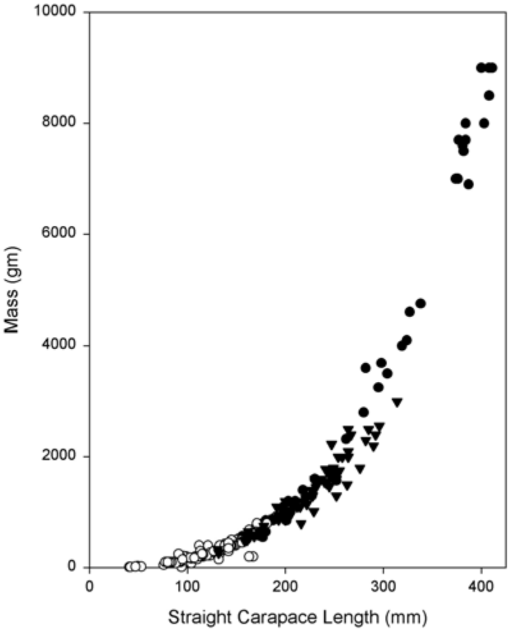

Figure 23-9. Mass as a function of plastron length for 249 *Pseudemys concinna suwanniensis* from the Rainbow River, Marion Co., Florida, 1997–2003 (first captures only). Juveniles indicated by open circles, females by closed circles, males by triangles. Data courtesy of P. Meylan and Eckerd College Rainbow Run Turtle Project.

Longevity. — Life span is unknown, but a minimum can be estimated at least for females. Of 239 nesting females originally marked from 1988–91 (Jackson and Walker, 1997), 11 were recaptured while nesting in the 1999–2002 nesting seasons. Because the number of years they had been nesting prior to first marking was unknown, I can only estimate that their reproductive lives extended at least 10–15 yrs beyond maturity, and probably considerably more; life span, therefore, must exceed 25 yrs (Jackson, 2003).

Male Reproductive Cycle. — The reproductive biology and cycle of male river cooters has received little attention. The epididymides of eight adult males from the Suwannee and Withlacoochee rivers (collected August, January, and March) contained mature sperm, but only those from January and March were swollen. Three early August males were characterized by low testicular mass (combined mass 1.20–1.74 g) and shortened foreclaws (possibly worn from courtship; see Jackson and Davis, 1972). In contrast, males from late August and January had elongate claws and heavy testes (combined mass 2.68–7.32 g); the sole March male had elongate claws but small testes (1.35 g). These data suggest peak spermiogenesis (sperm production) in late summer and early fall, with sperm being held over winter in the epididymides until spring or early summer mating. Such a pattern is characteristic of at least some other, if not most, North American turtles (Moll, 1979; Meylan et al., 2002).

Female Reproductive Cycle. — The female reproductive cycle presumably follows a pattern of oogenesis through ovulation and oviposition typical of most North American turtles (Moll, 1979), with the bulk of vitellogenesis (yolk buildup in the follicles) occurring during the spring prior to ovulation and egg-laying. Because river cooters produce multiple clutches in a single nesting season, follicles in the ovaries are usually in several stages of development simultaneously, with corpora lutea formed from the oviposition of early clutches co-occurring with vitellogenesis of subsequent clutches. A relatively quiescent period of unknown duration follows oviposition of the final clutch before the cycle starts anew for the following year.

Courtship and Mating Behavior. — Males and females have been observed courting during much of the year, but insufficient data are available to determine the timing and duration of the mating season. However, like most turtles, female river cooters presumably are able to store viable sperm for long periods, so the mating period does not set limits on nesting activity. Courtship (described by Jackson and Davis, 1972) takes place in water, with the male performing a series of stereotyped movements designed to gain a female's acceptance and cooperation in mating. Following a period of trailing and circling, the male positions himself over the female's back and reaches down with his front legs alongside her head. He then rapidly vibrates his greatly elongated foreclaws against or near her head, a process known as titillation. If courtship is successful, the pair may then sink to the bottom as they mate. Interestingly, neonates and juveniles also use foreclaw titillation, a practice of uncertain significance (see also *Trachemys* account in this volume).

Figure 23-10. Three-holed nest of *Pseudemys concinna suwanniensis* at Wakulla Springs State Park, Wakulla Co., Florida; fresh nest before covering, with eggs in each accessory hole but majority of clutch in central chamber. Photo by Dale R. Jackson.

Nesting. — Jackson and Walker (1997) conducted a detailed study of female river cooter reproductive and nesting biology along the Wakulla River, near Tallahassee, Florida, at the western edge of the range of *P. c. suwanniensis*. Their results probably typify river cooters statewide and are summarized here. Based on multi-year recaptures, most, if not all, mature females nest annually. Nesting begins in late March or early April and extends into early August, with the peak in May and June. During this extended nesting season, among the longest for North American turtles, females may lay 4 or more clutches at intervals of approximately 16–25 days. Nesting is diurnal and may occur at any time of day; it frequently coincides with rainfall, especially afternoon thunderstorms.

After leaving the river, female river cooters typically nest near the first open areas encountered. Within these areas, however, they search carefully before settling upon a precise location for excavating the nest. Selected sites must provide sufficient sunlight to warm the nest and well-drained, friable soil to permit digging and allow drainage to prevent drowning of eggs by heavy rains or flooding. Depending on height of banks and width of the river floodplain, nest sites may be situated from just above the river bank to more than 250 m inland. River cooters share with their close relative, *P. floridana* (Carr, 1952; Franz, 1986; Jackson, 1988), the unique and remarkable habit of digging nests with three holes instead of the usual single egg chamber (Fig. 23-10). Two shallow "accessory" or "satellite" holes, only a few cm deep, are dug to the left and right of the central egg chamber, which itself is flask-shaped and approximately 16 cm deep. Each lateral hole may contain zero to three eggs (zero and one being the most common), with the bulk of the clutch placed in the center hole. As is typical of North American emydids, the female uses her hind feet to back-fill the nest with soil, then returns immediately to the water. Jackson and Walker (1997) provided further details of nesting behavior.

Eggs, Clutch Size, and Reproductive Potential. — In the Wakulla River population studied by Jackson and Walker (1997), typical clutches contain 8–27 eggs (mean 17.5). Given that females may nest 4 or more times per season, average annual reproductive potential thus may approach 70 eggs, with a maximum for individuals of > 100. This is among the highest totals for any non-marine turtle in North America. Eggs are relatively small when compared to the large size of the female. Those of the Wakulla River population averaged 38.9 x 27.2 mm and 16.3 g. Each clutch of eggs represents an average of about 5% of female body mass.

Incubation and Hatchlings. — Incubation in the laboratory requires 58–122 days at temperatures ranging from 25–33ºC, with warmer temperatures accelerating development. In the wild, hatchlings may emerge from nests in the fall or may overwinter underground and delay emergence until the following spring. At the Wakulla River, hatchlings emerged in September, October, November, March, and April (Jackson, 1994). Sex determination of hatchlings is temperature-dependent, with a pivotal temperature at constant incubation temperatures of ca. 28.4ºC; eggs incubated at lower temperatures produce males, and higher temperatures females. Laboratory-incubated hatchlings from eggs collected along the Wakulla River averaged 34.2 mm PL, 38.1 mm CL, 37.3 mm carapace width, and 11.4 g. Hatchlings from natural nests were slightly heavier (13.1 g), possibly a result of greater water absorption.

POPULATION BIOLOGY

Population Density and Biomass. — Population densities of river cooters vary markedly among localities and habitat types. In seemingly optimal habitats, such as the Wakulla River and the Rainbow River in northern peninsular Florida, very high densities may typify non-exploited populations. Jackson and Walker (1997) estimated a population of about 305 adult females, with a collective biomass of 1967 kg, in ca. 5 km (41 hectares [ha] surface area) of the Wakulla River; inclusion of males and juveniles may have doubled the estimated biomass. It is probable that heavy predation both on eggs (by raccoons and fish crows) and juvenile turtles (by a dense alligator population) may be holding the Wakulla River cooter population below carrying capacity. Marchand's (1942) crude estimate of as many as 5000 Suwannee cooters (746 per km; half of all turtles) in a 6.7-km segment of the Rainbow River may even exceed that, but his sample included male and immature turtles (although also many large adult females based on Figs. 1 and 2 in Marchand, 1942). Nearly a half century later, Giovanetto (1992) estimated a population of 219 Suwannee cooters (all ages) in 0.7 km (5.42 ha) of the upper Rainbow River, for an estimated density of 40.4 per ha or 313 per km. The apparent population decline (including a marked decline in large adults) may be a result of human harvest (Giovanetto, 1992; Meylan et al., 1992). Elsewhere, Jackson (1970) collected 237 individuals in a small spring run (160 m x 20 m; equivalent to 1481 per km or 741 per ha) with a direct connection to a large river (Suwannee), but body size distribution indicates that his sample contained predominantly immature turtles. However, the habitat base from which he drew his sample may have been larger than his figures indicated, in which case actual population density may have been as much as 50% less.

Although not quantified, Carr (1952) commented on the former "extraordinary abundance attained by this turtle in the lower, brackish streams of the Gulf drainage." His quotation of Knight (1871) is revealing and worth repeating, at least for historical perspective: Suwannee cooters (as reassigned by Carr, 1952:299) "in the early summer congregated in great numbers in the warm and still bayous near the mouths of those streams [along the coast near Tallahassee] which empty into the Gulf. On one occasion the speaker, floating quietly down stream, came upon one of those gatherings where there seemed to be many thousands within the space of two or three acres, covering every log and stump and hummock almost as thickly as shingles lie upon a roof." In another instance, Carr (1940) counted 47 individuals basking on a single log in the Suwannee River in the 1930s. Nonetheless, Carr's later impression (*pers. comm.*) of the species' subsequent decline in that river system was integral to the turtle's eventual designation as a species of conservation concern both by the Florida Committee on Rare and Endangered Species and the state of Florida (see below).

Outside Florida, the densities of studied populations have been much lower. Buhlmann and Vaughan (1991) computed densities of only 0.7 to 2.3 adults (sexes combined) per ha in the New River, West Virginia, near the northern edge of the species' range. Lindeman (1997) estimated 1.58 river cooters per 100 m of shoreline in an impoundment in western Kentucky, and roughly similar densities in the Pearl and Pascagoula rivers in southern Mississippi and Louisiana.

Population Structure. — Population structure of river cooters may vary locally, with some rivers or localities being dominated by adults, and others by juveniles. This may reflect such factors as the type and density of predators (both of eggs and turtles), microhabitat representation, nesting success, food resources, or various forms of habitat disturbance (e.g., pollution, impoundment, exotic species, and adjacent upland management). In the Wakulla River, for example, observations of basking turtles suggest that adult and subadult turtles dominate the population; this may reflect the large numbers of alligators in the river, very high level of egg predation by raccoons and crows, and lack of suitable natural nesting areas as a result of fire exclusion from uplands adjacent to the floodplain. Even in a population dominated by larger animals, the range of sizes of mature animals can be substantial (Fig. 23-6). At least for females, this breadth is probably more attributable to differential size at maturity rather than to differential ages or growth rates among individuals.

At other localities, immature turtles may predominate. Such appears to be the case in the Suwannee River spring run population analyzed by Jackson (1964, 1970). In the Rainbow River population studied by Huestis and Meylan (2004), roughly 19% (8 females, 33 males) of 216 individuals were probably mature based on body sizes (Fig. 23-11). In both of these cases, turtles were captured by snorkelers. Low num-

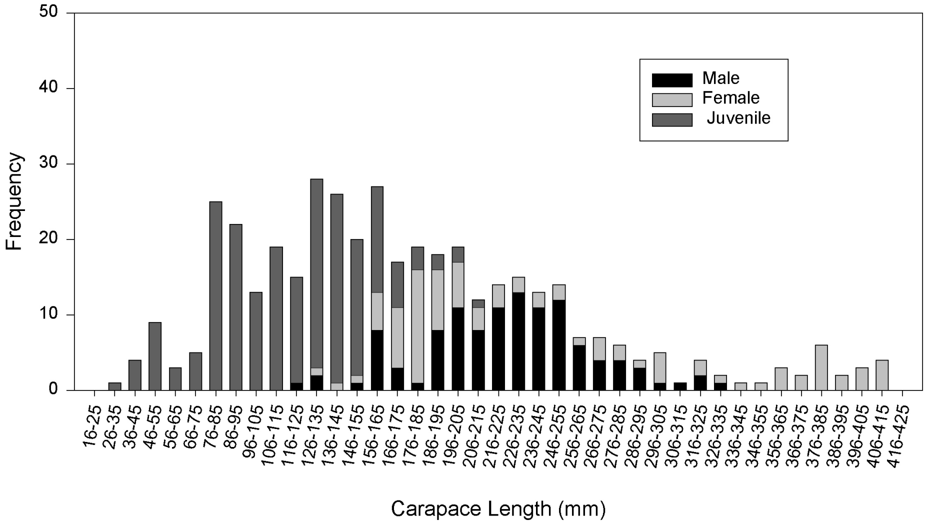

Figure 23-11. Size distribution (plastron length) by sex and age for *Pseudemys concinna suwanniensis* captured in the Rainbow River, Marion Co., Florida, 1997–2003. Females > 330 mm PL, and males > 190 mm, are presumed to be sexually mature. Sex determinations for individuals that were first captured at sizes below the minimum for sexual dimorphism were made during subsequent recaptures. Data courtesy of P. Meylan and Eckerd College Turtle Project.

bers of adult turtles may reflect their greater escapability or shyness, their use of less intensively sampled microhabitats, or true rarity due to factors such as human predation. In an earlier study of the Rainbow River, Marchand's (1942) sample of 240 females > 140 mm CL included at least 25% mature individuals as well as many large subadults (Fig. 23-12). His sample of 273 males > 150 mm CL included mostly turtles in the size range of adults (> 210 mm). However, based on his crude estimate of 5000 individuals in the study area, juveniles likely still predominated.

INTERSPECIFIC INTERACTIONS

Community Relations. — In various localities, river cooters coexist with most of the state's other freshwater emydid turtles, including *P. floridana*, *P. nelsoni*, *Trachemys scripta*, *Graptemys barbouri*, *G. ernsti*, and rarely *Deirochelys reticularia*. Non-emydids that share habitat with the river cooter include the softshells *Apalone ferox* and *A. spinifera* (and rarely *A. mutica*), both species of snapping turtles (*Macrochelys temminckii* and *Chelydra serpentina*), and all four of the state's mud and musk turtles (Kinosternidae) but especially *Sternotherus minor*. There may be minimal overlap with the diamondback terrapin (*Malaclemys terrapin*) at the interface of river mouths and estuaries along the Gulf coast.

Figure 23-12. Adult *Pseudemys concinna* and *Pseudemys floridana* captured during one sampling session at Rainbow Run, Marion Co., Florida, by Louis Marchand and R.F. Nunez in the early 1940s. Reproduced from Marchand (1942).

In rivers within its Florida range, *P. concinna* is often the dominant emydid turtle both numerically and by biomass. In the Wakulla River (Jackson and Walker, 1997; D. Jackson, unpubl. data), river cooters comprise > 95% of emydid turtles and > 99% of the biomass. In the Rainbow River population, *P. concinna* comprises more than half of all emydids, with estimates ranging from 53–65% (Marchand, 1942; Giovanetto, 1992; Meylan, 1992; Huestis and Meylan, 2004). In more sluggish rivers, such as the Withlacoochee in Citrus County, the percentage of emydids accounted for by *P. concinna* appears to decline as the habitat becomes more favorable for cooters with more lentic habits (*P. floridana* and *P. nelsoni*). In some rivers in the western half of the Florida panhandle, river cooters may be outnumbered by map turtles (*Graptemys* spp.).

Diet. — At least in Florida, post-juvenile (and perhaps all ages of) river cooters appear to be almost exclusively herbivorous (Loennberg, 1894; Allen, 1938; Marchand, 1942; Carr, 1952; Jackson, 1964; Ward, 1980; Lagueux et al., 1995; Bjorndal et al., 1997). Principal foods include rooted aquatic vegetation such as eelgrass (*Vallisneria americana*), strapleaf sagittaria (*Sagittaria kurziana*), coontail (*Ceratophyllum demersum*), water naiad (*Najas* spp.), and the exotic Brazilian elodea (*Egeria densa*), as well as filamentous algae (*Cladophora* sp.) (Marchand, 1942; Lagueux et al., 1995). Given the high population densities that this turtle can achieve, its role as a major herbivore and recycler of nutrients within aquatic ecosystems must be substantial.

Predation. — At many sites, even protected ones, the vast majority of river cooter nests are destroyed by predators, principally raccoons (*Procyon lotor*) and fish crows (*Corvus ossifragus*). As part of their study, Jackson and Walker (1997) monitored 114 freshly completed nests along the Wakulla River; 100% were depredated within 48 hrs by these two major egg predators. There, however, nest predation was facilitated by its virtual restriction to an artificial linear habitat (sand road and shoulders that, because of fire exclusion from adjacent uplands, represented the only non-canopied habitat available for nesting); this enabled predators to search systematically for nests and nesting females. The authors speculated that the observed presence of juvenile turtles in the river likely was attributable to the survival of some nests that were constructed during heavy rainstorms, which quickly dissipate both olfactory and visual signs of fresh nests.

Raccoons have been identified as major nest predators in most studies of North American turtles—including freshwater, marine, and terrestrial species—while fish crows are known to be important nest predators of other southeastern emydids (Shealy, 1976; Lahanas, 1982; U.S. Fish and Wildlife Service, 1989; Brauman and Seigel, 1995). Both species are anthrophilic (Harris and Silva-Lopez, 1990; Garrott et al., 1993), i.e., unusually large populations are supported in regions of human disturbance via increased food supplies and shelter, and decreased predation. Potential measures to limit the damage done by these two species are suggested below.

A third predatory species, the red imported fire ant (*Solenopsis invicta*), has the potential to become a major predator of river cooter nests, as well as those of most other egg-laying reptiles. Experimental evidence indicates the ability of this introduced and widespread species to attack and kill hatchling *P. nelsoni* (Allen et al., 2001); this almost certainly applies to *P. concinna* as well. The bones of hatchlings found in one river cooter nest at Wakulla Springs State Park strongly suggested fire ant predation (Jackson and Walker, 1997).

Predation on non-hatchling turtles is generally more difficult to confirm than it is for nests. However, Jackson and Walker (1997) documented the predation of nearly a dozen nesting female river cooters in a six-year period at Wakulla Springs State Park; raccoons were the likeliest culprits, although fish crows and vultures could not be dismissed. At the same site, park rangers reported several instances of cooters, some quite large, being consumed by alligators.

Parasites and Disease. — As with most freshwater turtles, river cooters commonly support a few minor parasites and commensals. River cooters emerging to nest from the Wakulla River frequently bore small loads of leeches (*Placobdella*) and algae (*Basicladia*). The latter was profuse on only a few individuals, and only one turtle, which was found trapped in a small sinkhole, bore a sufficient number of leeches to be of concern (Jackson and Walker, 1997). Basking and periodic shedding of scutes probably serve to reduce the loads of both leeches and algae.

Shell diseases of undetermined cause are known in at least two non-Florida populations of river cooters. A severe shell disease affects a large percentage of the river cooter population (as well as sliders) in one Georgia impoundment (Lake Blackshear, Flint River; Lovich et al., 1996; Garner et al., 1997). Although the impounded river eventually flows into Florida via the Apalachicola River, the disease has not yet been reported in this state. The river cooter is also one of six species of aquatic turtles recently reported to suffer from shell disease in a Virginia river (Ernst et al., 1999). Such occurrences suggest the possible role of pollutants in causing initial damage to turtles or their immune systems, which then allows invasion by microorganisms that may cause greater damage or even death.

THREATS

Although few quantitative data are available, many biologists and other long-time Florida residents believe that population densities of this species are considerably lower in most rivers than they once were. Large numbers of *P. c. suwanniensis* are known to have been taken in the past for human consumption (e.g., Carr, 1940, 1952), which prompted the former Florida Game and Fresh Water Fish Commission to establish legal harvest limits for the species (two per day per person, with a closed season from 15 April to 31 July). The habitual use of certain basking and nesting sites makes this turtle extremely vulnerable to collection or wanton destruction (including target practice, Fig. 23-13), particularly as its riverine habitats are almost completely accessible to anyone with a boat. The Commission's current regulations (see Protected Status) still allow harvest at a level that could easily exceed the species' ability to remain viable, but the agency believes that few or no people will harvest at that level. However, there have been several discoveries of evidence, in the form of large piles of shells of butchered river cooters (Fig. 23-14), that suggest at least periodic substantial illegal harvest in the Florida panhandle and

Figure 23-13. Carapace of adult female river cooter, *Pseudemys concinna concinna*, from Spring Creek, Decatur Co., Georgia (UF 132980). A bullet entered the shell in the 5th left costal bone and exited between the 5th and 6th right costals. Photo by Peter Meylan.

Figure 23-14. Butchered remains of river cooters, *Pseudemys concinna*, probably harvested illegally, found in a dump in Franklin Co., Florida, near the Apalachicola River in 1990. Photo by Dale R. Jackson.

peninsula. One explanation for the demographic structure of the Rainbow River population of Suwannee cooters cited earlier (Fig. 23-11), which seems to stand in such contrast to the adult-rich population of the Wakulla River (Jackson and Walker, 1997), is recurring (and documented) selective harvest of large turtles from the former. In such a case, further removal of even a few adult females might have potentially serious negative long-term effects on the population.

Predation on turtles and nests, as outlined above, can be high in some sites, although rarely at a level that might threaten a population's viability. Likewise, although I have witnessed adult females on nesting forays killed by vehicular traffic on three different Florida highways, the reticence of this species to wander overland minimizes this threat. A more serious problem in some areas is the loss or degradation of nesting sites. This can occur even in protected areas. For example, at Wakulla Springs State Park, continuing forest growth threatens to shade out much of the main nesting area and consequently to skew the sex ratios of hatchlings toward males. The park is now taking steps to restore naturally more open habitat through a program of prescribed burning.

Overall, most original river cooter habitat in Florida is still available and in reasonably good condition. However, several inhabited rivers, including sections of both the Suwannee and Apalachicola systems, have been degraded by dredging, impoundment, mining, and several forms of pollution, all of which can destroy the turtles' food supplies if not the turtles themselves. Residential and occasionally industrial development, as well as agricultural runoff, has led to various levels of decline in water quality in most Florida rivers. The worst example is the Fenholloway River (Taylor County), which has been poisoned by decades of industrial pulp mill effluent that may have extirpated the local population of Suwannee cooters; efforts are now underway to halt or reverse the problem and restore the river. Similar problems have been reported in the Escambia River (paper mill) and New River (Santa Fe drainage; sewage) and likely occur elsewhere. Fortunately, Florida has several active land and water protection programs that have been remarkably successful in preserving habitat along rivers, especially in the panhandle (Jackson, 2005). Still, more needs to be done.

No evidence to date has documented that river cooters in Florida suffer from epidemic diseases that might jeopardize populations. However, the occurrence of at least two instances of necrotic shell disease in the species elsewhere (above) suggests the need to monitor Florida populations regularly and to focus immediate attention on any suspicious observations.

STATUS

The river cooter receives partial state but no federal protection. The Florida Fish and Wildlife Conservation Commission formally designates only the subspecies *P. c. suwanniensis* as a Species of Special Concern, but its rules pertaining to harvest (closed season from 15 April –31 July, as well as bans on certain trapping methods) and possession (limit of two per person) apply to the entire species statewide. It is also illegal to buy or sell the species or its parts. These regulations may be adequate if fully enforced, but I have witnessed evidence (large piles of dumped, cleaned shells) of their almost certain violation. Greater efforts are needed to educate both the fishing public and law enforcement officers who then must rigorously enforce the regulations.

CONSERVATION OPTIONS AND SOLUTIONS

As for all Florida wildlife, present population densities and distribution should be established precisely so that baseline data will be available from which to determine future population changes. It should be realized, however, that current densities are not necessarily optimal and may, in fact, be far below historic levels. Although regulations exist regarding take (whether for food or as pets) of river cooters, it appears that increased efforts are needed to educate the public and to enforce these laws, as well as to monitor their effectiveness. Signs depicting the cooter and listing all pertinent regulations should be posted at boat ramps in view of all potential river users. Additionally, similar information should be included within the Florida Fish and Wildlife Conservation Commission's annual handbook on freshwater sport fishing regulations. Currently, such information is included only in the hunting handbook, but it is actually fishermen who are more likely to interact with the species. One option for better protecting river cooters is to eliminate all take of members of the genus *Pseudemys*. This would allow enforcement officers to protect river cooter populations without needing to be able to distinguish this species from its close relatives, the Florida cooter (*P. floridana*) and the red-bellied turtle (*P. nelsoni*).

All waterways inhabited by this species should be protected from habitat degradation resulting from impoundment, dredging, diversion, and development within floodplains, and all forms of pollution. Through programs such as Save Our Rivers (administered by the state's five water management districts), Conservation and Recreation Lands, Preservation 2000, and Florida Forever, the state of Florida has protected corridors of habitat along many of the rivers within the river cooter's range. Additional programs to protect water quality, particularly those administered by the Florida Department of Environmental Protection, U.S. Environmental Protection Agency, and the state's five water management districts, need to be further enhanced and supported with ample funding. In situations where river cooters (and probably other species) are known to have been extirpated by anthropogenic habitat degradation, such programs should focus on restoring not only water quality but also former faunal constituents to rivers. In the case of the Fenholloway River, if restoration efforts are successful, reintroduction of cooters, possibly from the nearby Econfina River, may be appropriate. However, monitoring efforts must first confirm that sufficient aquatic plants are supported by the river to provide a forage base for the turtles.

Resolving the problem of turtle and nest predation by such anthrophilic predators as raccoons and crows is difficult, in part because the public views those species as watchable (even attractive) wildlife rather than appreciating their potentially harmful ecological roles. Efforts to minimize the availability of human refuse to such opportunistic omnivores, by providing predator-proof waste receptacles, may assist in limiting local populations and thereby reducing predation of turtle eggs. Even then, however, periodic removal of these two predatory species, perhaps at 2- to 3-year intervals, may be necessary at some sites in order to protect rarer animals such as the Suwannee cooter. Such programs elsewhere (e.g., Christiansen and Gallaway, 1984) have boosted recruitment in freshwater turtle populations where nests had been subject to extensive predation. Alternatively, if predator control is infeasible at a site because of humane concerns, then an annual program using cages to protect nests (if they can be found in time) *in situ*, with sufficient numbers under conditions likely to produce females (full sun) and males (shade to sun-shade mixture), could be instituted, with resulting hatchlings transported manually to the river's edges. However, such a program would be time- and labor-intensive. More generally, I encourage funding for research to develop effective yet inexpensive methods of raccoon control.

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LITERATURE CITED

ALLEN, C.R., E.A. FORYS, K.G. RICE, AND D.P. WOJCIK. 2001. Effects of fire ants (Hymenoptera: Formicidae) on hatchling turtles and prevalence of fire ants on sea turtle nesting beaches in Florida. Florida Entomologist 84:250-253.

ALLEN, E.R. 1938. Notes on the feeding and egg-laying habits of the *Pseudemys*. Proceedings of the Florida Academy of Sciences 3:105-108.

ARESCO, M.J. AND C. GUYER, 1998. Efficacy of using scute annuli to determine growth histories and ages of *Gopherus polyphemus* in southern Alabama. Copeia 1998:1094-1100.

AUFFENBERG, W. 1978. Threatened: Suwannee cooter, *Chrysemys concinna suwanniensis* (Carr). In: R.W. McDiarmid (Ed.). Rare and Endangered Biota of Florida. Vol. 3: Amphibians and Reptiles. University Presses of Florida, pp. 32-33.

BANCROFT, G.T., J.S. GODLEY, D.T. GROSS, N.N. ROJAS, D.A. SUTPHEN, AND R.W. MCDIARMID. 1983. Large-scale operations management test of use of the white amur for control of problem aquatic plants; the herpetofauna of Lake Conway, Florida: species accounts. Miscellaneous Paper A-83-5, U. S. Army Engineer Waterways Experiment Station, CE, Vicksburg, Mississippi.

BJORNDAL, K.A., A.B. BOLTEN, C.J. LAGUEUX, AND D.R. JACKSON. 1997. Dietary overlap in three sympatric congeneric freshwater turtles (*Pseudemys*) in Florida. Chelonian Conservation and Biology 2:430-433.

BRAUMAN, R.J. AND R.A. SEIGEL. 1995. Nesting habits and nest temperatures of the yellow-blotched map turtle. Abstract, 38th Annual Meeting of the Society for the Study of Amphibians and Reptles, p. 27.

BROOKS, R.J., M.A. KRAWCHUCK, C. STEVENS, AND N. KOPER. 1997. Testing the precision and accuracy of age estimation using lines in scutes of *Chelydra serpentina* and *Chrysemys picta*. Journal of Herpetology 31:521-529.

BUHLMANN, K.A. AND M.R. VAUGHAN. 1991. Ecology of the turtle *Pseudemys concinna* in the New River, West Virginia. Journal of Herpetology 25:72-78.

CARR, A.F. 1940. A contribution to the herpetology of Florida. University of Florida Publications, Biological Sciences Series 3:1-118.

CARR, A.F. 1952. Handbook of Turtles: Turtles of the United States, Canada, and Baja California. Cornell University Press. 542 pp.

CHRISTIANSEN, J.L. AND B.J. GALLAWAY. 1984. Raccoon removal, nesting success, and hatchling emergence in Iowa turtles with special reference to *Kinosternon flavescens* (Kinosternidae). Southwestern Naturalist 29:343-348.

CONANT, R. AND J.T. COLLINS. 1991. A Field Guide to Reptiles and Amphibians: Eastern and Central North America. Houghton Mifflin Co., 450 pp.

CRENSHAW, J.W. 1955. The ecological geography of the *Pseudemys floridana* complex in the southeastern United States. Ph.D. dissertation, Univ. Florida.

Dunson, W.A. and M.E. Seidel. 1986. Salinity tolerance of estuarine and insular emydid turtles (*Pseudemys nelsoni* and *Trachemys decussata*). Journal of Herpetology 20:237-245.

Ernst, C.H., J.E. Lovich, and R.W. Barbour. 1994. Turtles of the United States and Canada. Smithsonian Institution, 578 pp.

Ernst, C.H., T.S.B. Akre, J.C. Wilgenbusch, T.P. Wilson, and K. Mills. 1999. Shell disease in the Rappahannock River, Virginia. Herpetological Review 30:214-215.

Fahey, K.M. 1987. Aspects of the life history of the river cooter, *Pseudemys concinna* (LeConte), in the Tallapoosa River, Tallapoosa County, Alabama. Ph.D. dissertation, Auburn University, Auburn, Alabama.

Franz, R. 1986. Life history notes: *Pseudemys floridana peninsularis* (peninsula cooter). Egg predation. Herpetological Review 17:64-65.

Garrott, R.A., P.J. White, and C.A. Vanderbilt White. 1993. Overabundance: an issue for conservation biologists? Conservation Biology 7:946-949.

Garner, M.M., R. Herrington, E.W. Howerth, B.L. Homer, V.F. Nettles, R. Isaza, E.B. Shotts, Jr., and E.R. Jacobson. 1997. Shell disease in river cooters (*Pseudemys concinna*) and yellow-bellied turtles (*Trachemys scripta*) in a Georgia (USA) lake. Journal of Wildlife Diseases 33:78-85.

Germano, D.J. and T.H. Fritts. 1994. Methods of age determination of the desert tortoise, *Gopherus agassizii*. Proceedings of the Desert Tortoise Council 1987-1991:93-100.

Giovanetto, L.A. 1992. Population ecology and relative abundance of sympatric freshwater turtles in the headwaters of two spring-fed rivers in western peninsular Florida. Ph.D. Dissertation, Florida Institute of Technology, Melbourne.

Harris, L.D. and G. Silva-Lopez. 1990. Forest fragmentation and the conservation of biological diversity. In: P. Fielder and S. Jain (Eds.). Conservation Biology: the Theory and Practice of Nature Conservation, Preservation and Management. Chapman and Hall, pp. 197-237.

Hubbs, C. 1995. Springs and spring runs as unique aquatic systems. Copeia 1995:989-991.

Huestis, D.L. and P.A. Meylan. 2004. The turtles of Rainbow Run (Marion County, Florida): observations on the genus *Pseudemys*. Southeastern Naturalist 3:595-612.

Iverson, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately printed, 363 pp.

Jackson, C.G., Jr. 1964. A biometrical study of form and growth in *Pseudemys concinna suwanniensis* Carr (Order Testudinata). Ph.D. Dissertation, Univ. Florida, Gainesville.

Jackson, C.G., Jr. 1970. A biometrical study of growth in *Pseudemys concinna suwanniensis*. I. Copeia 1970:528-534.

Jackson, C.G., Jr. and J. D. Davis. 1972. Courtship display behavior of *Chrysemys concinna suwanniensis*. Copeia 1972:385-387.

Jackson, C.G., Jr. and M.M. Jackson. 1968. The egg and hatchling of the Suwannee terrapin. Quarterly Journal of the Florida Academy of Sciences 31:199-204.

Jackson, D.R. 1988. Reproductive strategies of sympatric freshwater emydid turtles in northern peninsular Florida. Bulletin of the Florida State Museum, Biological Sciences 33:113-158.

Jackson, D.R. 1992. Species of special concern: river cooter, *Pseudemys concinna* (LeConte). In: P. E. Moler (Ed.). Rare and Endangered Biota of Florida, vol. 3: Amphibians and Reptiles. University Presses of Florida, Gainesville, pp. 166-170.

Jackson, D.R. 1994. Overwintering of hatchling turtles in northern Florida. Journal of Herpetology 28:401-402.

Jackson, D.R. 1995. Systematics of the *Pseudemys concinna-floridana* complex (Testudines: Emydidae): an alternative interpretation. Chelonian Conservation and Biology 1:329-333.

Jackson, D.R. 1997. Geographic distribution. *Pseudemys concinna suwanniensis*. Herpetological Review 28:94.

Jackson, D.R. 2002. Survey of an important distributional gap in the Florida range of the river cooter and other freshwater turtles. Final Report. Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida.

Jackson, D.R. 2003. *Pseudemys concinna suwanniensis* (Suwannee Cooter). Reproduction, life span. Herpetological Review 34:363.

Jackson, D.R. 2005. Florida rivers and turtles: an interdependence. In: W. Meshaka and K. Babbitt (Eds.). Amphibians and Reptiles: Status and Conservation in Florida. Krieger Press, Malabar, Florida, pp. 163-168.

Jackson, D.R. and M.A. Ewert. 1998. Geographic distribution. *Pseudemys concinna suwanniensis*. Herpetological Review 29:173-174.

Jackson, D.R. and R.N. Walker. 1997. Reproduction in the Suwannee cooter, *Pseudemys concinna suwanniensis*. Bulletin of the Florida State Museum, Biological Sciences 41:69-167.

Knight, C.F. 1871. [Remarks on Florida turtles]. Proceedings of the Boston Society of Natural History 14:16-18.

Lagueux, C.J., K.A. Bjorndal, A.B. Bolten, and C.L. Campbell. 1995. Food habits of *Pseudemys concinna suwanniensis* in a Florida spring. Journal of Herpetology 19:122-126.

Lahanas, P.N. 1982. Aspects of the life history of the southern black-nobbed sawback, *Graptemys nigrinoda delticola* Folkerts and Mount. M.S. thesis, Auburn University, Auburn, Alabama.

Le Conte, J. 1830. Description of the species of North American tortoises. Annals of the Lyceum of Natural History, New York 3:91-131.

Lindeman, P.V. 1997. A comparative spotting-scope study of the distribution and relative abundance of river cooters (*Pseudemys concinna*) in western Kentucky and southern Mississippi. Chelonian Conservation and Biology 2:378-383.

Litzgus, J.D. and R.J. Brooks. 1998. Testing the validity of counts of plastral scute rings in spotted turtles, *Clemmys guttata*. Copeia 1988:222-225.

Loennberg, E. 1894. Notes on reptiles and batrachians collected in Florida in 1892 and 1893. Proceedings of the U.S. National Museum 17:317-339.

Lovich, J.E., S.W. Gotte, C.H. Ernst, J.C. Harshbarger, A.F. Laemmerzahl, and J.W. Gibbons. 1996. Prevalence and histopathology of shell disease in turtles from Lake Blackshear, Georgia. Journal of Wildlife Diseases 32: 259-265.

Marchand, L.J. 1942. A contribution to a knowledge of the natural history of certain freshwater turtles. M. S. thesis, University of Florida, Gainesville.

McDowell, S.B. 1964. Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae. Proceedings Zoological Society of London 143:239-279.

Meylan, P.A., C.A. Stevens, M.E. Barnwell, and E.D. Dohm. 1992. Observations on the turtle community of Rainbow Run, Marion Co., Florida. Florida Scientist 55:219-227.

Meylan, P.A., R. Schuler, and P.E. Moler. 2002. Spermatogenic cycle of the Florida softshell turtle, *Apalone ferox*. Copeia 2002:779-786.

Moll, E.O. 1979. Reproductive cycles and adaptations. In: M. Harless and H. Morlock (Eds.). Turtles: Perspectives and Research. John Wiley and Sons, pp. 305-331.

Pluto, T.G. and E.D. Bellis. 1986. Habitat utilization by the turtle, *Graptemys geographica*, along a river. Journal of Herpetology

20:22-31.

Pritchard, P.C.H. 1980. Record size turtles from Florida and South America. Chelonologica 1:113-123.

Rosenau, J.C., G.L. Faulkner, C.W. Hendry, Jr., and R.W. Hull. 1977. Springs of Florida. Florida Bureau of Geology, Bulletin No. 31.

Seidel, M.E. 1994. Morphometric analysis and taxonomy of cooter and red-bellied turtles in the North American genus *Pseudemys* (Emydidae). Chelonian Conservation and Biology 1:117-130.

Seidel, M.E. and M.J. Dreslik. 1996. *Pseudemys concinna* (Le Conte), river cooter. Catalogue of American Amphibians and Reptiles 626.:1-12.

Seidel, M.E. and H.M. Smith. 1986. *Chrysemys*, *Pseudemys*, *Trachemys* (Testudines: Emydidae): did Agassiz have it right? Herpetologica 42:242-248.

Shealy, R.M. 1976. The natural history of the Alabama map turtle, *Graptemys pulchra* Baur, in Alabama. Bulletin of the Florida State Museum, Biological Sciences 21:47-111.

U.S. Fish and Wildlife Service. 1989. Alabama red-bellied turtle recovery plan. U.S. Fish and Wildlife Service, Jackson, Mississippi, 17 pp.

Ward, J.P. 1980. Comparative cranial morphology of the freshwater turtle subfamily Emydinae: an analysis of the feeding mechanisms and the systematics. Ph.D. Dissertation, North Carolina State University, Raleigh.

Ward, J.P. 1984. Relationships of chrysemyd turtles of North America (Testudines: Emydidae). Special Publications of the Museum, Texas Tech University 21:1-50.

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Pseudemys floridana – Florida Cooter

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Summary. – The Florida cooter, *Pseudemys floridana*, is a relatively large and abundant herbivorous freshwater turtle that is found throughout Florida. It is highly aquatic and resides in a variety of permanent and semi-permanent freshwater habitats. There are two subspecies native to the state, with *P. f. floridana* in the northern portion, and *P. f. peninsularis* mostly south of Alachua County. The species is mostly diurnal and is commonly seen basking on logs. Adult females are commonly encountered during their terrestrial nesting forays. Adult females are (on average) significantly larger than adult males. Titillation behavior is well known in this species but its exact function is not clearly understood. The nesting season appears to vary geographically across the state. Females usually nest in open, sandy areas with limited cover and often lay multiple clutches of eggs each year. They have the unusual behavior of digging a nest with satellite pockets on either side of a deeper central nest chamber and depositing eggs in all three chambers. The incubation period is variable, ranging from 60–150 days, and clutch size usually ranges from 11–16 eggs. Although generally abundant and widespread across Florida, some populations have shown significant declines. A wide variety of predators consume the eggs and hatchlings, while adults have few natural predators. Current threats include human consumption, habitat alteration, misinformed fishermen, busy roads, and heavy boat traffic. We discuss a variety of possible actions that might help decrease some of the mortality associated with these various threats.

Conservation Status. – FNAI Global - G5 (Demonstrably Secure), State - S5 (Demonstrably Secure); ESA Federal - Not Listed; State - Not Listed; CITES - Not Listed; IUCN Red List - Not Listed (LC-Least Concern).

Species Recognition. — The Florida cooter, *Pseudemys floridana*, is a relatively large freshwater turtle (ca. 24–35 cm plastron length [PL] and 25–40 cm carapace length [CL]) that has a moderately domed carapace that is typically dark with light yellow to orange parallel lines on the pleural scutes, the most conspicuous one being a bar forked at either or both ends (Mount, 1975) (Figs. 24-1, 24-2). Two subspecies occur in Florida: *P. f. floridana* and *P. f. peninsularis*. The unhinged plastron is typically yellow and without pattern (Fig. 24-3), but older males may develop a reddish-orange plastron with slight melanism (M. Aresco, *pers. comm.*). The skin is dark brown to black and the head and neck bear numerous longitudinal yellow stripes (Fig. 24-4) (Ernst et al., 1994). Although the paramedial and supratemporal head stripes of *P. f. peninsularis* often converge behind the eyes to form distinctive hairpins, these are sometimes incomplete and typically absent altogether in *P. f. floridana* (Seidel and Palmer, 1991; Ernst et al., 1994). The chin bears relatively wide yellow stripes with the medial chin stripe extending posteriorly and eventually dividing to form a Y-shaped mark (Ernst and Barbour, 1989). Hatchlings have a mid-dorsal keel, green rather than brown ground color, and tend to be more boldly patterned than adults (Figs. 24-4, 24-5) (Goff and Goff, 1932; Pope, 1949; Ernst et al, 1994). The plastron of hatchlings is colored like that of adults (Fig. 24-6). Denticulations are not present along the lateral jaw ridge and the upper jaw does not possess a medial notch or cusps (Fig. 24-6) (Conant and Collins, 1991; Ernst et al., 1994). Along with the presence of an unmarked plastron, *P. floridana* individuals often can be distinguished from other similar emydids by the absence of a notch in their upper jaw. Many common names have been used to refer to this species, including cooter, peninsula cooter, Florida cooter, hard-backed cooter, common cooter, Florida turtle, streaky-neck, streaky-legs, and coastal plain turtle.

Taxonomic History. — *Pseudemys floridana* was first described as *Testudo floridana* by LeConte (1830). Species taxonomy within *Pseudemys* is problematic and the status of *P. floridana* has been vigorously debated (e.g., Seidel, 1994, 1995; Jackson, 1995). We recognize that this issue is controversial and that more data are needed to resolve the systematics of the *P. floridana–P. concinna* group. However, in this account, we have chosen to view *P. floridana* as a species distinct from *P. concinna*, and we include within it both *P. f. floridana* and *P. f. peninsularis* (see Jackson, 1995).

DISTRIBUTION

Geographic Distribution. — *Pseudemys floridana* is primarily a southeastern coastal plain species, ranging from extreme southeastern Virginia, southward through Florida, and as far west as the Mobile Bay area of southern Alabama

Figure 24-1. Adult female peninsula cooter, *Pseudemys floridana peninsularis,* from Lee Co., Florida. Photo by Dick Bartlett.

(Conant and Collins, 1991; Ernst et al., 1994). The range of *P. floridana* is thought to extend throughout the entire state of Florida (Fig. 24-7), including the Florida Keys. One subspecies, *P. f. floridana,* is restricted to the northern portion of the state, while the other, *P. f. peninsularis,* is restricted to areas south of Alachua Co. (Carr, 1952; Conant and Collins, 1991; Ernst et al., 1994), although it is apparently rare in the Florida Everglades (Jackson, 1988). The two subspecies appear to intergrade over a broad area from near Ocala to Tallahassee (Giovanetto, 1992; M. Aresco, unpubl. data).

Ecological Distribution. — Pseudemys floridana inhabits slow moving or still waterways with abundant aquatic vegetation and available basking sites. Adult *P. floridana* in Alabama have been reported to spend considerable time in water lily shallows (Thomas, 1972), and the species is known to inhabit Carolina Bays (Jackson, 1995). In Florida, *P. floridana* primarily inhabits freshwater systems with abundant macrophytic communities, but the species may utilize bare bottom habitats as body size increases or if macrophytic communities are rare (Bancroft et al., 1983). Pope (1949) reported that *P. floridana* was extremely abundant in large swamps (e.g., Okefenokee) but could also be found in ponds, lakes, rivers, and streams. Marchand (1942) found the highest densities of *P. floridana* inhabiting Rainbow Run in areas away from the main current with heavy growths of *Naias* sp. and *Sagittaria lorata* and a fairly flat bottom. Pope (1949) also noted the attraction to dense stands of aquatic vegetation and quiet shallow water.

HABITAT RELATIONS

Activity. — Pseudemys floridana, and other sympatric *Pseudemys,* are thought to be most active during daylight hours when the water is not in direct sunlight (Marchand, 1942),

Figure 24-2. Nesting female Florida cooter, *Pseudemys floridana floridana,* from Okaloosa Co., Florida. Photo by John Jensen.

Figure 24-3. Plastral view of adult male Florida cooter, *Pseudemys floridana floridana* (left), and adult male river cooter, *Pseudemys concinna concinna* (right), both from Okaloosa Co., Florida. Photo by John Jensen.

Figure 24-4. Post-hatchling Florida cooter, *Pseudemys floridana floridana,* from Gilchrist Co., Florida. Photo by Dick Bartlett.

Figure 24-5. Hatchling Florida cooter, *Pseudemys floridana floridana,* from Sumter Co., Florida. Photo by David Dennis.

however, nocturnal activity has been reported (Marchand, 1942; Bancroft et al., 1983). *Pseudemys floridana* often inhabits open water during the early morning, zones of emergent vegetation during midday, and open water during late afternoon and evening (Marchand, 1942; Bancroft et al., 1983).

Home Range and Movements. — The average spatial distances among points of capture and recapture for *P. floridana* range from approximately 270 m (Crystal Springs, Pasco Co.) up to several km (Rainbow Run, Marion Co.; Marchand, 1945). Home range for the species may be influenced by local habitat characteristics (Marchand, 1945) and/or ontogenetic stage (Bancroft et al., 1983).

Terrestrial Activity. — *Pseudemys floridana* moves overland (Gibbons and Smith, 1968; Gibbons and Coker, 1977; Aresco, 2005a) and there are limited data indicating orientation ability (Gibbons and Smith, 1968). *Pseudemys f. floridana* on the Savannah River Site near Aiken, South Carolina, moved overland in response to falling water levels during a severe drought (Gibbons et al., 1983). However, there are many other factors that may influence overland movements and most of these factors have not been considered. For example, the potential for sexual, intrasexual, and/or ontogenetic differences in the amount, timing, and/or extent of overland movements are not known. In addition, recent data suggest that local population structure (e.g., sex ratio, size structure, density, etc.) might influence overland movements in closely related species (see Rose and Manning 1996; Thomas and Parker, 2000).

Figure 24-6. Plastral view of hatchling peninsula cooter, *Pseudemys floridana peninsularis,* from Alachua Co., Florida. Photo by Dick Bartlett.

GROWTH AND REPRODUCTON

Growth. — The growth pattern of *P. floridana* is characterized by a rapid juvenile growth rate with an abrupt decline at the onset of sexual maturity (Marchand, 1942; Gibbons and Coker, 1977). Size and age at sexual maturity vary, but typically range from 20–27 cm PL or ca. 24–30 cm CL (5–7 yrs) for females and from 12–14 cm PL or ca. 13–15 cm CL (3–4 yrs) for males (Gibbons and Coker, 1977; Jackson, 1988; Congdon and Gibbons, 1989). In contrast, Bancroft et al. (1983) estimated that it required 5–6 yrs for males to reach maturity and 15–16 yrs for females in the Lake Conway, Florida, system. They attributed these differences to depressed growth rates resulting from competition for food with the white amur (*Ctenopharyngodon idella*), a large fish introduced to control aquatic vegetation. Mean longevity has been estimated to be about 30 yrs (Congdon and Gibbons, 1989).

Size Dimorphism. — On average, adult females are larger in size (but see Marchand, 1942), attain higher domed carapaces, and have shorter tails and foreclaws than adult males (Marchand, 1942; Bancroft et al., 1983; Jackson, 1988). The plastron length (PL) of adult P. f. peninsularis usually ranges from about 12–30 cm (ca. 13–32 cm CL) for males and 25-36 cm (ca. 26–38 cm CL) for females (Fig. 24-8) (Marchand, 1942; Jackson, 1988). The maximum size of male *P. f. floridana* inhabiting Ellenton Bay on the Savannah River Site in South Carolina was 24 cm PL and 1888 g, while the largest female was 29.7 cm PL and 3775 g (Congdon and Gibbons, 1989). Bancroft et al. (1983) reported significant variation in body size among the various pools of the Lake Conway system (for males, females, and juveniles) and attributed these differences to variation in habitat quality.

Mating Behavior. — Behaviors leading to and clearly ending in copulation of *P. floridana* have not been described. It has commonly been assumed that titillation behaviors represent courtship (Goin and Goin, 1971; Ernst et al., 1994), but we are unaware of published data to support this assumption. Moreover, the communicative function(s) of

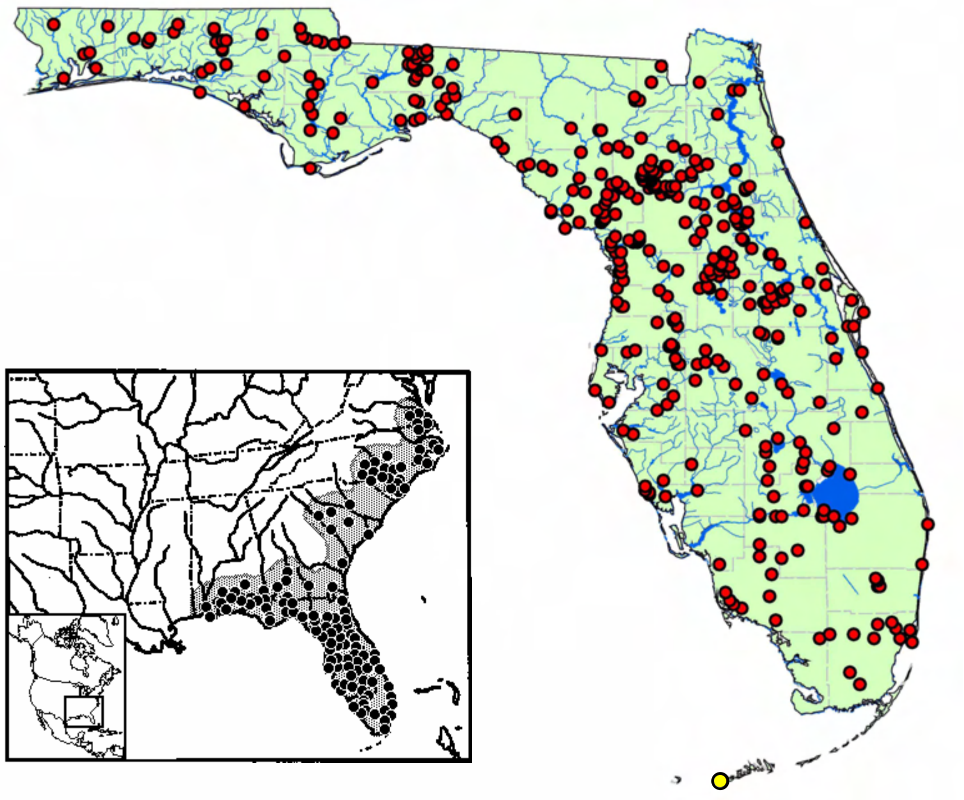

Figure 24-7. Available distribution records for the Florida cooter, *Pseudemys floridana*, from Florida. Inset: distribution records from entire range of *P. floridana* (adapted from Iverson, 1992; distribution in inset map not current for Florida as presented here). Record for Key West (yellow dot) may represent an escaped individual.

titillation behaviors are not well understood for any species of freshwater turtle (see Thomas, 1999, 2002; Thomas and Altig, 2006; Thomas et al., 1999). Titillation in the species usually occurs with the male and female facing in the same direction and the male maintaining a position just above the female. The male then extends his head downwards close to the female's head and turns his tail down and under the rear margin of her carapace. The two then sink to the bottom, where copulation is presumed to take place (Goin and Goin, 1971).

Most authors have suggested that the peak of courtship and mating for *P. floridana* occurs during spring (Thomas, 1972; Ernst et al., 1994). However, such assertions are based upon the observation of titillation and the assumption that courtship is the sole purpose for this behavior. We believe it is currently inappropriate to use titillation behaviors as the sole criteria for identification of the mating season. Indeed, Thomas (1972) noted that testes size in *P. floridana* increased throughout fall to a maximum in late winter. He also found sperm in the oviducts of several females during the fall and speculated that these might fertilize ova in the spring. In central Florida, Bancroft et al. (1983) found the greatest number of males with enlarged testes and epididymides in September. We suggest that the limited available data from peninsular Florida are consistent with a mating season that peaks during the fall and/or winter. Moreover, there is an increasing amount of data that are inconsistent with the traditional idea of a spring peak in courtship and mating for other species of emydid turtles (Gist et al., 1990; Thomas et al., 1999, 2002; Cash, 2000).

Nesting Season. — Pope (1949) reported that *P. f. floridana* eggs were laid in May and June but observed *P. f. peninsularis* nesting in February and March near Lake Griffin, Lake Co., Florida. Iverson (1977) categorized *P. floridana* as a continuous nester with a relatively large clutch size and estimated that annual reproductive potential may approach 100 eggs/individual. However, the term continuous nester may not be appropriate for *P. f. peninsularis* in northern peninsular Florida (Jackson, 1988). Northern peninsular populations have been observed nesting in late fall, winter, and early spring with a slight peak in November, and there is a period of time during July and August in which these populations do not nest. In contrast to such observations in peninsular Florida, *P. floridana* in northwestern Florida (Lake Jackson, Leon Co.) appears to nest only from mid-April to mid-July, with most nests observed in May (Aresco, 2004).

Nest Sites. — Nest site selection in *P. floridana* seems to be relatively consistent throughout its range, with a preference for open, sandy areas possibly containing some ground cover (e.g., grasses) but with limited canopy cover. For example, populations from the Okefenokee Swamp in Georgia, Lake Griffin, Lake Co., Florida, and central Florida all utilized cleared sandy areas with sparse grasses and direct sunlight (Wright and Funkhouser, 1915; Goff and Goff, 1932; Marchand, 1942; Pope, 1949; Thomas, 1972; Franz, 1986; Bodie et al., 1996). Distances from the nest to the

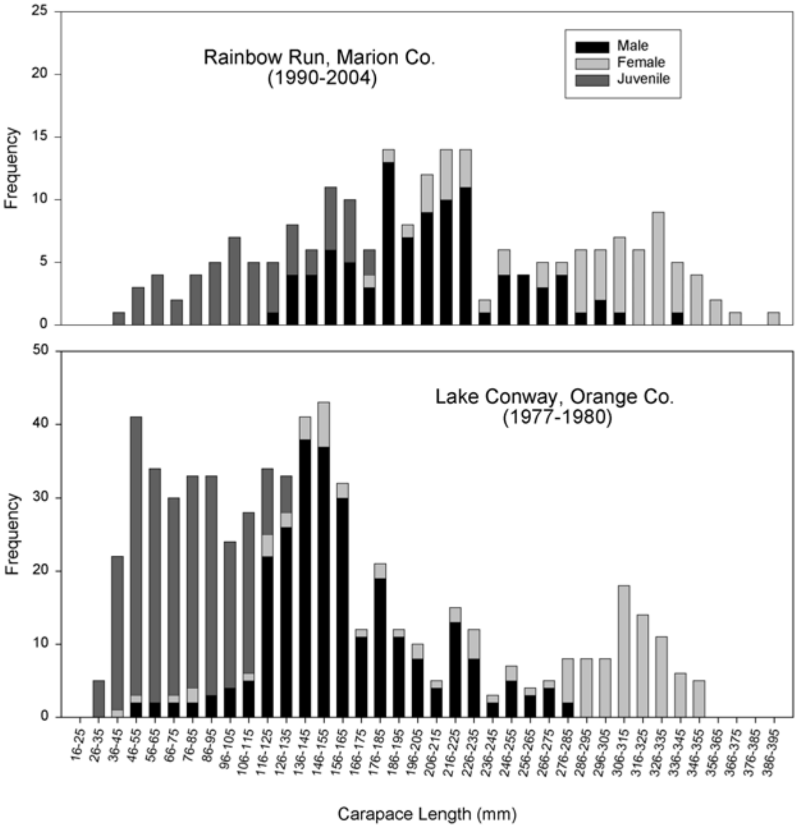

Figure 24-8. Population structure of *Pseudemys floridana* at two sites in Florida. The Rainbow Run data are from a clear spring run near Dunnellon (Huestis and Meylan, 2004), the Lake Conway data are from a series of interconnected lakes near Orlando (Bancroft et al., 1983).

nearest water ranged from the shoreline (Pope, 1949) to 200 m (Franz, 1986). Thomas (1972) described typical nesting habitat for the species as areas with dark-colored, sandy, well-drained soil. The nests were usually exposed to direct sunlight most of the day and the distance to the nests from the shoreline varied from 6–90 m. A fairly dense layer of grasses covered the nesting area, primarily broom sedge (*Andropogon* sp.), wiregrass (*Aristida*), and Bahia grass (*Paspalum notatum*), with sparsely distributed small saplings (e.g., sassafras [*Sassafras albidum*], sweet gum [*Liquidambar styraciflua*], and wax myrtle [*Myrica cerifera*]). Specific habitat types in Florida documented to be nesting habitat for the species include recently burned high pine, xeric live oak forests, longleaf pine-scrub oak forests, and sparsely vegetated open fields (Marchand, 1942; Franz, 1986; Bodie et al., 1996).

Nesting Behavior. — *Pseudemys floridana* constructs nests in a manner similar to that described by Ross (1938) and Carr (1952). Each nest usually has a deep central chamber (mean depth = 12.5 cm) with two shallow satellite pockets (mean depth = 6.0 cm) (Fig. 24-9). The satellite pockets typically contain fewer eggs than the deeper central chamber. This method of nest construction might represent an antipredator strategy that reduces egg mortality by drawing the attention of a nest predator toward the shallow satellite pockets and away from the eggs in the deeper central chamber (see Carr, 1952; Franz, 1986; Cople and Pilgrim, 1993). Bodie et al. (1996) studied six *P. f. floridana* nests in South Carolina and examined nest temperatures and nest site selection. They reported the following environmental characteristics: mean nest depth = 7.54 cm; time of maximum nest temperature = ca. 1500 hrs; mean percent soil moisture = 5.3%.

Pseudemys floridana typically lays its eggs diurnally (Jackson, 1988; but see Marchand, 1942, for evidence of nocturnal nesting) and nesting activities often coincide with rainfall (Thomas, 1972; but see Aresco, 2004). Females often nest on warmer days during the winter months that may produce periodic nesting synchrony (Ross, 1938; Jackson, 1988). The nesting period of *P. f. floridana* outside of Florida is similar to that of many other sympatric emydids (e.g., *Trachemys scripta*, *Chrysemys picta*) and is restricted to a few months with peaks in May, June, or July (Carr, 1952; Thomas, 1972). Some authors have speculated that the winter-nesting peak exhibited by *P. f. peninsularis* may be related to the fact that they live sympatrically with the ecologically similar *P. nelsoni* (Jackson, 1988). Winter nesting may allow rapid hatchling growth, reduce the risk of nest predation, and provide an interspecific competitive advantage (Jackson, 1988).

Incubation. — The freshly laid eggs of *P. floridana* can tolerate continuous exposure to 20ºC for periods > 30 days (Ewert, 1991). This ability (i.e., cold torpor) may be necessary for a species that participates in winter nesting activities, because eggs laid in the winter probably endure long periods of exposure to temperatures less than 20ºC. Thomas

Figure 24-9. Three-holed nest of Florida cooter, *Pseudemys floridana floridana,* abandoned by female before eggs were laid, Leon Co., Florida. Photo by Matt Aresco.

(1972) noted that females can produce multiple clutches (at least 3/yr), large females produce more clutches than smaller females, and the largest females nest earlier and later than smaller females. Similarly, Jackson (1988) found that most adult females in northern Florida laid 3–6 clutches/yr and suggested smaller females may produce only one or two clutches during their first year of reproduction.

Eggs are retained in the oviducts for less than two weeks in nature but captives may retain the eggs in the oviducts from 30–60 days, with embryogenesis apparently suspended at the late gastrula stage until the eggs are laid (Ewert, 1979; Jackson, 1988). Thomas (1972) noted that the incubation time was 72 days at 30ºC. Jackson (1988) reported the time of oviposition to pipping under constant laboratory temperatures of 22.5 to 30.0ºC to range from 60 to 122 days. Ewert (1991) reported that laboratory incubation of *P. floridana* eggs at 22.5ºC allowed eggs to hatch in 118–122 days. However, eggs in natural nests may remain viable for periods exceeding 150 days (Goff and Goff, 1932; Jackson, 1988). Temperature-dependent sex determination is known to exist in this species, with cool temperatures producing males and warm temperatures producing females (Ewert and Nelson, 1991). In addition, rate of development is influenced by temperature, and hatching occurs almost synchronously within a single clutch, with all viable eggs usually hatching within a period ± 3 days (Jackson, 1988).

Clutch Size and Egg Size. — Clutch size averages 11 to 16 (Pope, 1949; Bancroft et al., 1983; Congdon and Gibbons, 1985; Jackson, 1988; Aresco, 2004). A positive relationship between clutch size and body size has been observed in *P. floridana* (Thomas, 1972; Iverson, 1977; Congdon and Gibbons, 1985; Jackson, 1988; Aresco, 2004), as is common among turtles (Moll, 1979). Egg length averages 34.1 to 37.9 mm (Wright and Funkhouser, 1915; Pope, 1949; Thomas, 1972; Congdon and Gibbons, 1985; Jackson, 1988), and egg width averages 23.2 to 24.8 mm (Congdon and Gibbons, 1985; Jackson, 1988. Clutch and egg parameters are similar across the range of *P. floridana*. Although environmental conditions can alter individual reproductive output (e.g., drought, Gibbons et al., 1983; Jackson, 1988), there are no data to suggest differences in size among successive clutches of *P. f. peninsularis* under normal conditions (Jackson, 1988).

Hatching. — The process of hatching is similar to the process described for *Trachemys scripta* (Cagle, 1950; Thomas, 1972). Across the range of *P. floridana*, hatchlings may emerge in late summer, fall, or overwinter in nests (or underground away from the nest) and emerge in early spring (Thomas, 1972; Gibbons and Coker, 1977). Jackson (1994) and Aresco (2004) documented that at least some Florida hatchlings overwinter in nests northeast of Tallahassee, Leon County. It has been suggested that egg lipid proportions are related to the length of time that hatchlings are able to delay emergence from the nest (Congdon et al., 1983), and the egg lipid proportions reported for *P. f. floridana* were consistent with this hypothesis (Congdon and Gibbons, 1985). Hatchling size ranges from 18–30 mm PL (or ca. 19–35 mm CL) and 7.0–10.0 g (Goff and Goff, 1932; Marchand, 1942; Thomas, 1972; Jackson, 1988).

POPULATON BIOLOGY

Density. — In general, most turtle biologists agree that *P. floridana* currently is common across its range. *Pseudemys floridana* was documented as the most common species around the islands of the Okefenokee Swamp in the early 1900s (Wright and Funkhouser, 1915), and Giovanetto (1992) reported that *P. f. peninsularis* was the most abundant species in the Homosassa River comprising 61.9% of all turtles collected. However, *P. f. peninsularis* represented only 18.8% of all turtles collected in Rainbow River and was the third most abundant species. The estimated density of *P. f. peninsularis* in Homosassa River was 48.4 individuals/ha and 44.6 individuals/ha in Rainbow River (Giovanetto, 1992). However, the density of *P. floridana* inhabiting Ellenton Bay, South Carolina, has been estimated at only 7 individuals/ha (Congdon and Gibbons, 1989).

Population Structure. — Both male- and female-biased sex ratios have been reported (Marchand, 1942; Bancroft et al., 1983; Giovanetto, 1992; Aresco, 2005a), but numerous factors may influence estimates of sex ratio (e.g., trapping method, trapping effort, and time of year; Ream and Ream, 1966; Bancroft et al., 1983; Thomas et al., 1999). Indeed, accurate estimates of population sex ratios are lacking for many turtle species, a deficiency that will become increasingly important with the need to develop population viability models for individual species.

INTERSPECIFIC INTERACTIONS

Diet and Feeding. — *Pseudemys floridana* is strongly herbivorous throughout its range (Ross, 1938; Marchand, 1942; Pope, 1949; Thomas, 1972; McDiarmid et al., 1983). One group of captive animals readily consumed a variety of plant items (e.g., *Sagittaria* sp.) but never consumed live fish (Allen, 1938). Marchand (1942) observed hundreds of *Pseudemys* (many of which were *P. floridana*) feeding on aquatic vegetation, but never observed carnivory or scavenging. Common food items reported include *Naias* sp., *Sagittaria lorata*, *Lemna* sp., filamentous algae, *Ceratophyllum* sp., *Vallisneria americana*, *Potamogeton illinoisensis*, *Hydrilla verticillata*, *Nitella megacarpa*, *Mayaca* sp., *Panicum hemitomon*, *Egeria densa*, and *Nymphoides aquatica* (Marchand, 1942; Thomas, 1972, Bancroft et al., 1983; McDiarmid et al., 1983; Bjorndal et al., 1997). The diet of *P. floridana* exhibits seasonal and geographic variations (Thomas, 1972) as well as ontogenetic variations (Bancroft et al., 1983).

Bjorndal et al. (1997) revealed almost complete overlap in the diets of *P. floridana* and *P. nelsoni* and substantial overlap between *P. floridana* and *P. concinna* inhabiting the Withlacoochee River, Citrus Co., Florida. However, their results were based on a small number of animals collected during only one month in an area where food items were plentiful.

Predation. — Many species prey upon the eggs and/or hatchlings of *P. floridana*. These include feral hogs (*Sus scrofa*), opossums (*Didelphis virginianus*), raccoons (*Procyon lotor*), dogs (*Canis familiaris*), black bears (*Ursus americanus*), king snakes (*Lampropeltis getulus*), skunks (*Mephitis mephitis*), alligators (*Alligator mississippiensis*), red fire ants (*Solenopsis invicta*), fish, herons, egrets, predaceous turtles, and frogs (Wright and Funkhouser, 1915; Ross, 1938; Marchand, 1942; Thomas, 1972; Franz, 1986; Jackson, 1988; Aresco, 2004). Adult *P. floridana* have few natural predators, although otters (*Lutra canadensis*) and large alligators do consume them (Bancroft et al., 1983; Delaney and Abercrombie, 1986). Delany and Abercrombie (1986) reported that *P. f. peninsularis* occurred in 5.7% of the alligator stomachs examined (*n* = 350) and comprised 3.9% of the total volume.

Turtle populations are most sensitive to the loss of adults (Brooks et al., 1991; Congdon et al., 1993); therefore, predation by alligators may pose a more serious threat than predators of nests and/or neonates. However, turtles and alligators have coexisted for tens of millions of years, so alligators alone are unlikely to be the sole factor responsible for reported population declines (see below). It is more likely that turtles cannot withstand the unnatural pressures of invasive species, habitat loss, degradation of remaining habitat, and mortality resulting from numerous anthropogenic factors (e.g., road-kills, shooting, etc.).

Parasites. — Thomas (1972) reported that *P. f. floridana* in Alabama were parasitized by leeches (*Placobdella* sp.), acanthocephalans (possibly *Neoechinorhynchus*), and unidentified pinworms (Oxyuridae). However, the dearth of information on the parasites of *P. floridana* prevents knowledgeable commentary on their relationship to survival.

THREATS

Cooters have endured exploitation by human populations for thousands of years (Neill et al., 1956; Holman and Clausen, 1984) and this exploitation continues today (Enge, 1992). Although *P. floridana* is generally considered to be a common species, population declines have been reported and significant reasons for concern do exist. Meylan et al. (1992) compared the turtle community of the Rainbow River, Marion Co., Florida, during 1990 to the findings of Marchand (1942). The total density of turtles in the study site did not change, but the relative abundance and density of *P. f. peninsularis* significantly declined between the 1940s and 1990 collections. The methods of collection in the two studies were only slightly different; therefore, it is likely that populations of *P. f. peninsularis* had declined during that 50-year interval. In addition, most of the *P. f. peninsularis* captured in 1990 were immature individuals while most were large adults in the 1940s, suggesting that whatever caused the decline probably most affected the adults. Meylan et al. (1992) speculated that the decline might have resulted from: (1) human consumption, (2) high mortality from boat collisions, and/or (3) an insufficient number of basking sites. Giovanetto (1992) studied the turtle communities in two Florida locations: (1) Homosassa River, Citrus Co., and (2) Rainbow River, Marion County; the work on Rainbow River was conducted upstream from the sites studied by Marchand (1942) and Meylan et al. (1992). Giovanetto (1992) also suggested that the relative abundance of *P. f. peninsularis* had decreased (at least when compared to Marchand, 1942) and road-kills and human consumption were listed as likely causes for the decline. The results of this study were consistent with the assertion that the Rainbow River population was comprised largely of smaller individuals. This is especially troubling given that the loss of adults, particularly females, is likely to be most detrimental to long-term population survival (see Brooks et al., 1991; Congdon et al., 1993).

McDiarmid et al. (1983) and Bancroft et al. (1983) studied the Lake Conway System in Orange Co., Florida. Their goal was to assess the impact of the introduced white amur (*Ctenopharyngodon idella*) on biodiversity of the lake system, but the effect of human development confounded their results. The density of *P. floridana* decreased over the course of their study and yearly decreases in the recruitment of juveniles into the adult population were noted. *Pseudemys floridana* shifted its habitat use from the littoral zone and *Potamogeton* beds to beds of *Nitella megacarpa*, *Vallisneria americana*, and over bare bottoms as white amur feeding activity altered the aquatic macrophyte community. However, juvenile cooters did not shift their preference for littoral zone habitats even though the amount of this habitat decreased during the study. Juveniles and small males were more dependent on littoral zone habitats than were larger adults, thus, an intact littoral zone may be necessary for hatchling survival. These authors attributed the decline of turtle species to the following factors: (1) destruction of littoral zone habitats, (2) loss of suitable nesting sites, (3) heavy boat traffic, (4) direct competition for food with the white amur, (5) human predation, and (6) water fluctuations. Boat-propeller injuries were responsible for 46.4% of the deaths (*n* = 28) of known cause in Lake Conway and 21.1% of the 819 turtles examined had scars from boat propellers (Bancroft et al., 1983). Similarly, boat propeller injuries were found on

5.4% (n = 1173) of *P. floridana* at Lake Jackson, Leon Co., Florida (M. Aresco, unpubl. data).

A decline of *P. floridana* in Raleigh, North Carolina, was noted subsequent to pollution of local waters by sewage and dye-works refuse (Pope, 1949), and pollution is known to negatively influence other freshwater turtle species (e.g., Shelby and Mendonca, 2001; Bell et al., 2006). Therefore, the potential impacts of pollution on *P. floridana* populations warrant concern. In addition, the potential problems with xenoestrogens should be of concern given that the application of estrogen to turtle eggs during certain periods of development influences the sex ratio of the offspring regardless of incubation temperature (Pieau, 1985). Importantly, the effects of such chemicals on the behavior and social dynamics of turtle populations are unknown. Given the threatened status of many species of turtles and the fact that animals cannot reproduce without communication (Bradbury and Vehrencamp, 1998), we suggest that communication in turtles, and the effect of environmental pollutants on that communication, deserves further attention.

Collisions with automobiles may be a large source of mortality for cooters during their overland movements in urban areas and/or areas with high recreational usage. For example, 276 *P. floridana* were killed from 22 February 2000 through 1 November 2003 by vehicles along a short stretch of U.S. 27N that bisects Lake Jackson, Leon Co., Florida (Aresco, 2005b) (Fig. 24-10). Roadsides may provide attractive nesting sites for females, but crossing roads to reach such habitats may lead to significantly greater female mortality risk and a male biased sex ratio (Aresco, 2005a), a troubling finding given the relative importance of large females in maintaining a viable population (see Congdon et al., 1993). We assume that the risk of mortality increases with terrestrial activity in areas with high road densities and, consequently, represents a significant threat for some populations (see Forman and Alexander, 1998, for review). However, the use of drift fences to safely direct turtle movements can reduce vehicular-related turtle mortality (Aresco, 2005b).

Figure 24-10. Remains of 90 road-killed Florida cooters (*Pseudemys floridana floridana*) and yellow-bellied sliders (*Trachemys scripta scripta*), that were part of a sample of 343 turtles killed on U.S. 27 in a 40-day period (March–April 2000) during a significant drying event at Lake Jackson, Leon Co., Florida. Photo by Matt Aresco.

Many people will shoot basking turtles and/or kill aquatic turtles for a variety of reasons. For example, some people consider basking turtles as inexpensive targets for shooting practice. In addition, the myth that these herbivorous emydids consume large quantities of gamefish motivates many fishermen to kill them. Large adults are often found with bullet holes in their shells (Marchand, 1942). Indeed, Thomas (1972) mentioned an individual who lived on the shores of Lake Cassidy who killed approximately 50 cooters as they left the shores of the lake to nest.

STATUS

Pseudemys floridana is not currently listed as species about which there should be conservation concern in Florida.

CONSERVATION OPTIONS AND SOLUTIONS

By virtue of its size and abundance, *P. floridana* is an important, integral component of many Florida ecosystems, but its functional role is not well understood (McDiarmid et al., 1983). *Pseudemys floridana* is not currently listed as a protected species; at present, it is thought to be quite common. However, populations in certain areas have declined (e.g., Bancroft et al., 1983; Meylan et al., 1992). Therefore, steps should be taken to insure that common species such as *P. floridana* remain common.

Urbanization negatively impacts many aspects of the habitat of *P. floridana*. Water quality often declines because of landscape management practices (see Bjorndal et al., 1997) and general surface runoff (see Boyd and Gardiner, 1990). The direct alteration of habitats often reduces the amount of the specific habitats that are necessary for the survival of the smaller size classes (Bancroft et al., 1983) and critical nesting areas may be lost altogether. Increasing demands for water may lead to lower water tables, which may drain vital wetland habitats. Falling water tables should be of concern given the negative effects on reproductive output that have been associated with drought (Gibbons et al., 1983; Jackson, 1988). Additionally, the construction of new roads increases the risk of mortality during overland movements.

Giovanetto (1992) suggested stricter regulation of the development of waterfront property and a commitment to maintaining high water quality throughout the range of the species. Following these suggestions would likely have positive effects on populations of *P. floridana*. However, the development of waterfront property and the conversion of existing habitat continue. We suggest that the following steps may assist in minimizing the effects of such development on *P. floridana* populations: (1) the potential impact(s) on aquatic turtles should be considered prior to further development, (2) specific efforts should be made to preserve nesting areas and the preferred habitat (i.e. littoral zones) of the smaller size classes, and (3) the construction of new roads in areas that *P. floridana* is likely to frequent during overland treks (e.g., nesting forays) should be avoided, or the road should be designed such that *P. floridana* is able to migrate safely (i.e., drift fences directed to culverts; Aresco, 2005b).

The loss of adults from injuries associated with boat propellers could be minimized by stricter regulation of boat traffic in areas inhabited by high densities of the larger size classes. Identifying those areas, and then restricting motorboat access to them, would assist in minimizing propeller mortality. Another option would be to place strict regulations on the speed that motorboats are allowed to travel through habitats that hold large numbers of adults.

Sadly, the practice of shooting basking turtles is still quite common and laws to prevent such senseless acts are usually quite difficult to enforce. We suggest that the most effective method of minimizing these activities is public education. Fishermen who learn that *P. floridana* is strictly herbivorous are not likely to be motivated to destroy these animals. And although it may be difficult to alter the views of those who equate basking turtles with skeet, we believe individuals that possess a certain amount of factual knowledge of their natural surroundings are more likely to appreciate the complex biological world in which they live. For example, people aware of the fact that *P. floridana* may live > 30 years are less likely to senselessly destroy this animal. These are not the only benefits that public education may offer. In general, people with a greater appreciation of the living world around them are more likely to support measures to conserve and/or preserve the natural world. Therefore, public education may be one of the most important tasks in conserving freshwater turtles.

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LITERATURE CITED

ALLEN, E.R. 1938. Notes on the feeding and egg-laying habits of the *Pseudemys*. Proceedings of the Florida Academy of Sciences 3:105-113.

ARESCO, M.J. 2004. Reproductive ecology of *Pseudemys floridana* and *Trachemys scripta* (Testudines: Emydidae) in northwestern Florida. Journal of Herpetology 38:249-256.

ARESCO, M.J. 2005a. The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. Biological Conservation 123:37-44.

ARESCO, M.J. 2005b. Mitigation measures to reduce highway mortality of turtles and other herpetofauna at a north Florida lake. Journal of Wildlife Management 69:549-560.

BANCROFT, G.T., J.S. GODLEY, D.T. GROSS, N.N. ROJAS, D.A. SUTPHEN, AND R.W. MCDIARMID. 1983. Large-scale operations management test of use of the white amur for control of problem aquatic plants; the herpetofauna of Lake Conway, Florida: Species Accounts, Misc. Pap. A-83-5, U.S. Army Eng. Waterways Exp. Stn., CE, Vicksburg, Miss, 304 pp.

BELL, B., J. R. SPOTILA, AND J. CONGDON. 2006. High incidence of deformity in aquatic turtles in the John Heinz National Wildlife Refuge. Environmental Pollution 142:457-465.

BJORNDAL, K. A., A. B. BOLTEN, C. J. LAGUEUX, AND D. R. JACKSON. 1997. Dietary overlap in three sympatric congeneric freshwater turtles (*Pseudemys*) in Florida. Chelonian Conservation and Biology 2:430-433.

BODIE, J. R., K. R. SMITH, AND V. J. BURKE. 1996. A comparison of diel nest temperature and nest site selection for two sympatric species of freshwater turtles. American Midland Naturalist 136:181-186.

BOYD, G. AND N. GARDINER. 1990. Urban storm water: an overview for municipalities. Public Works 121:39-42.

BRADBURY, J. W., AND S. L. VEHRENCAMP. 1998. Principles of Animal Communication. Sinauer Associates, Inc., Sunderland, Massachusetts, 882 pp.

BROOKS, R. J., G. P. BROWN, AND D. A. GALBRAITH. 1991. Effects of a sudden increase in natural mortality of adults on a population of the common snapping turtle (*Chelydra serpentina*). Canadian Journal of Zoology 69:1314-1320.

CAGLE, F. R. 1950. The life history of the slider turtle, *Pseudemys scripta troostii* (Holbrook). Ecological Monographs 20:31-54.

CARR, A. F. 1952. Handbook of turtles: turtles of the United States, Canada, and Baja California. Cornell Univ. Press, Ithaca, NY, 542 pp.

CASH, W. B. 2000. Behavioral and physiological ecology of the slider turtle: laboratory and field studies integrating hormonal and behavioral aspects. Ph.D. Dissertation, Univ. Mississippi, Oxford.

CONANT, R., AND J. T. COLLINS. 1991. A field guide to reptiles and amphibians: eastern and central North America. Houghton Mifflin Co., Boston, 450 pp.

CONGDON, J. D., AND J. W. GIBBONS. 1985. Egg components and reproductive characteristics of turtles: relationships to body size. Herpetologica 41:194-205.

CONGDON, J. D., AND J. W. GIBBONS. 1989. Biomass productivity of turtles in freshwater wetlands: a geographic comparison. In: Sharitz, R. R., and J. W. Gibbons (Eds.), Freshwater Wetlands and Wildlife. Oak Ridge, Tennessee: U.S. Dept. of Energy Technical Information Center, pp. 583-591.

CONGDON, J.D., D. W. TINKLE, AND P. C. ROSEN. 1983. Egg components and utilization during development in aquatic turtles. Copeia 1983:265-268.

CONGDON, J. D., A. E. DUNHAM, AND R. C. VAN LOBEN SELS. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. Conservation Biology 7:826-833.

COPLE, P.E. AND M. A. PILGRIM. 1993. The effects of satellite nests on predation in artificial nests of *Pseudemys floridana peninsularis.* Florida Scientist 56(Supplement):32.

DELANY, M. F. AND C. L. ABERCROMBIE. 1986. American alligator food habits in northcentral Florida. Journal of Wildlife Management 50:348-353.

ENGE, K.M. 1992. Herptile exploitation. Florida Game and Fresh Water Fish Commission, Nongame Wildlife Section Annual Report, 55 pp.

ERNST, C.H., AND R.W. BARBOUR. 1989. Turtles of the World. Smithsonian Institution Press, 313 pp.

ERNST, C.H., R.W. BARBOUR, AND J. E. LOVICH. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, 578 pp.

EWERT, M. A. 1979. The embryo and its egg: development and natural history. In: Harless, M. and H. Morlock (Eds.), Turtles: Perspectives and Research. New York: John Wiley and Sons, pp. 333-413.

Ewert, M. A. 1991. Cold torpor, diapause, delayed hatching and aestivation in reptiles and birds. In: Deeming, D. C., and M. W. J. Ferguson (Eds.) Egg Incubation: its Effects on Embryonic Development in Birds and Reptiles. New York: Cambridge University Press, pp. 173-191.

Ewert, M. A., and C. E. Nelson. 1991. Sex determination in turtles: diverse patterns and some possible adaptive values. Copeia 1991:50-69.

Forman, R. T. T. and L. E. Alexander. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207-231.

Franz, R. 1986. Life history notes: *Pseudemys floridana peninsularis* (peninsula cooter). Egg predation. Herpetolical Reveiw 17:64-65.

Gibbons, J. W., and J. W. Coker. 1977. Ecological and life history aspects of the cooter, *Chrysemys floridana* (Le Conte). Herpetologica 33:29-33.

Gibbons, J. W., and M. H. Smith. 1968. Evidence of orientation by turtles. Herpetologica 24:331-334.

Gibbons, J. W., J. L. Greene, and J. D. Congdon. 1983. Drought-related responses of aquatic turtle populations. Journal of Herpetology 17:242-246.

Giovanetto, L. A. 1992. Population ecology and relative abundance of sympatric freshwater turtles in the headwaters of two spring-fed rivers in western peninsular Florida. Ph.D. Dissertation, Florida Inst. Tech., Melbourne.

Gist, D. H., J. A. Michaelson, and J. M. Jones. 1990. Autumn mating in the painted turtle, *Chrysemys picta*. Herpetologica 46:331-336.

Goff, C. C., and D. S. Goff. 1932. Egg laying and incubation of *Pseudemys floridana*. Copeia 1932:92-94.

Goin, C. J., and O. B. Goin. 1971. Introduction to Herpetology, second edition. W. H. Freeman and Co., San Francisco, 353 pp.

Holman, J. A. and C. Clausen. 1984. Fossil vertebrates associated with Paleo-Indian artifact at Little Salt Spring, Florida. Journal of Vertebrate Paleontology 4:146-154.

Huestis, D.L. and P.A. Meylan. 2004. The turtles of Rainbow Run (Marion Co., Florida): Observations on the genus *Pseudemys*. Southeastern Naturalist 3:595-612.

Iverson, J. B. 1977. Reproduction in freshwater and terrestrial turtles of north Florida. Herpetologica 33:205-212.

Iverson, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately printed, 363 pp.

Jackson, D. R. 1988. Reproductive strategies of sympatric freshwater Emydid turtles in northern peninsular Florida. Bulletin of the Florida State Museum, Biological Sciences 33:113-158.

Jackson, D. R. 1994. Overwintering of hatchling turtles in northern Florida. Journal of Herpetology 28:401-402.

Jackson, D. R. 1995. Systematics of the *Pseudemys concinna-floridana* complex (Testudines: Emydidae): an alternative explanation. Chelonian Conservation and Biology 1:329-333.

LeConte, J. 1830. Description of the species of North American tortoises. Ann. Lyceum Nat. Hist. New York 3:91-131.

Marchand, L. J. 1942. A contribution to the knowledge of the natural history of certain freshwater turtles. M.S. Thesis, Univ. Florida, Gainesville.

Marchand, L. J. 1945. The individual range of some Florida turtles. Copeia 1945:75-77.

McDiarmid, R. W., G. T. Bancroft, and J. S. Godley. 1983. Large-scale operations management test of use of the white amur for control of problem aquatic plants; the herpetofauna of Lake Conway, Florida: Species Accounts. Technical Report A-78-2, U.S. Army Corp of Engineers, Waterways Experiment Station, CE, Vicksburg, Miss, 167 pp.

Meylan, P. A., C. A. Stevens, M. E. Barnwell, and E. D. Dohm. 1992. Observations on the turtle community of Rainbow Run, Marion Co., Florida. Florida Scientist 55:219-228.

Moll, E. O. 1979. Reproductive cycles and adaptations. In: Harless, M., and H. Morlock (Eds.). Turtles: Perspectives and Research. New York: John Wiley and Sons, pp. 305-331.

Mount, R. H. 1975. The Reptiles and Amphibians of Alabama. Auburn University Agricultural Experiment Station, Auburn, AL, 347 pp.

Neill, W. T., H. J. Gut, and P. Brodkorb. 1956. Animal remains from four preceramic sites in Florida. American Antiquity 21:383-395.

Pieau, R. A. 1985. Embryonic development of the genital system. In: Gans, C., and F. Billet (Eds.). Biology of the Reptilia, volume 15. New York: Wiley, pp. 149-300.

Pope, C. H. 1949. Turtles of the United States and Canada. Alfred A. Knopf, Inc., 343 pp.

Ream, C., and R. Ream. 1966. The influence of sampling methods on the estimation of population structure in painted turtles. American Midland Naturalist 75:325-338.

Rose, F. L., and R. W. Manning. 1996. Notes on the biology of the slider, *Trachemys scripta elegans* (Reptilia: Emydidae), inhabiting man-made cattle ponds in west Texas. Texas Journal of Science 48:191-206.

Ross, E.R. 1938. Notes on the feeding and egg-laying habits of the *Pseudemys*. Proceedings of the Florida Academy of Science 3:105-113.

Seidel, M. E. 1994. Morphometric analysis and taxonomy of cooter and red-bellied turtles in the North American genus *Pseudemys* (Emydidae). Chelonian Conservation and Biology 1:117-130.

Seidel, M. E. 1995. How many species of cooter turtles and where is the scientific evidence? A reply to Dale Jackson. Chelonian Conservation and Biology 1:333-336.

Seidel, M. E., and W. M. Palmer. 1991. Morphological variation in turtles of the genus *Pseudemys* (Testudines: Emydidae) from central Atlantic drainages. Brimleyana 17:105-135.

Shelby, J.A., and M.T. Mendonca. 2001. Comparison of reproductive parameters in male yellow-blotched map turtles (*Graptemys flavimaculata*) from a historically contaminated site and a reference site. Comparative Biochemistry and Physiology 129C:233-242.

Thomas, K. 1972. The annual cycle of reproduction of the emydine turtle, *Pseudemys floridana floridana* (Testudinata, Testudinidae) with observations on its ecology. M.S. Thesis, Auburn University, Auburn, Alabama.

Thomas, R.B. 1999. Intraspecific variation in the behavior of adult slider turtles (*Trachemys scripta*). Ph.D. Dissertation, Mississippi State University, Mississippi State.

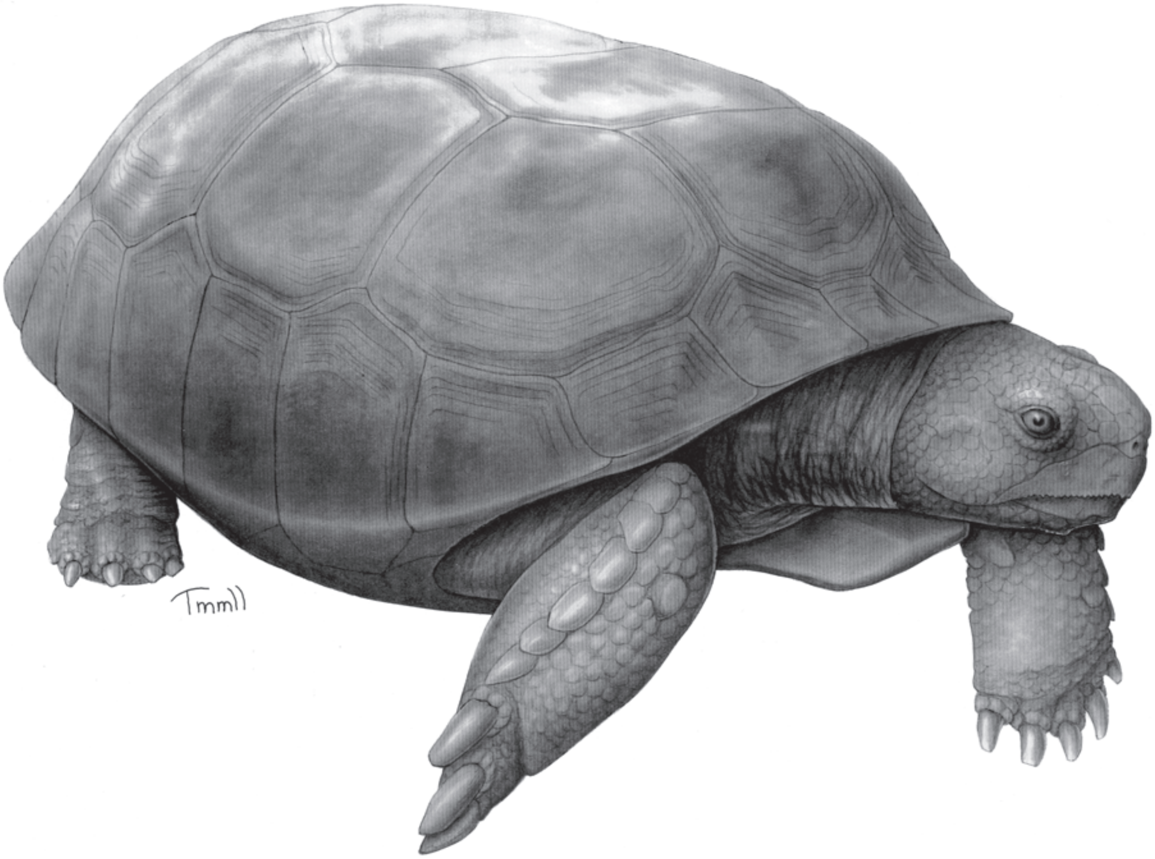
Thomas, R.B. 2002. Conditional mating strategy in a long-lived vertebrate: ontogenetic shifts in the mating tactics of male slider turtles (*Trachemys scripta*). Copeia 2002:456-461.

Thomas, R.B., and R. Altig. 2006. Characteristics of the foreclaw display behaviors of female slider turtles (*Trachemys scripta*). Southeastern Naturalist 5:227-234.

Thomas, R.B., and W.S. Parker. 2000. Intrasexual variations in overland movements of slider turtles (*Trachemys scripta*). Journal of Herpetology 34:469-472.

Thomas, R.B., N. Vogrin, and R. Altig. 1999. Sexual and seasonal differences in behavior of *Trachemys scripta* (Testudines: Emydidae). Journal of Herpetology 33:511-515.

Wright, A. H., and W. D. Funkhouser. 1915. A biological reconnaissance of the Okefinokee Swamp in Georgia. The reptiles. Proceedings of the Academy of Natural Sciences, Philadelphia 67:107-192.



Gopher Tortoise, *Gopherus polyphemus* (Testudinidae).
Drawing by Susan Trammell.

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Introduction to the Land Tortoises: Family Testudinidae

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The land tortoises are represented in Florida by a single species, the gopher tortoise, *Gopherus polyphemus*. There are three other gopher tortoise species—all live in North America: the desert tortoise (*G. agassizii*) occurs in the Sonoran and Mojave deserts, the Texas tortoise (*G. berlandieri*) occurs in south Texas and northeast Mexico, and the Bolson tortoise (*G. flavomarginata*) is restricted to the Mexican Plateau where the states of Chihuahua, Coahuila, and Durango meet. Land tortoises have suffered serious extinction as human populations have expanded and a significant proportion of living species are currently under threat, including all four of the North American gopher tortoises.

Content. — The taxonomy of the land tortoise family is in flux. A conservative estimate of the number of genera and species would be about 11 genera and 40 species (Iverson, 1992). If the genera *Geochelone* and *Testudo* are each divided into multiple genera and additional species in such genera as *Testudo* and *Aldabrachelys* are recognized, this family might be considered to include as many as 16 or 17 genera and perhaps as many as 65 species.

Relationships. — Land tortoises have always been considered closely related to the pond turtles and together these families have been treated as a superfamily, the Testudinoidea. Only recently has it been pointed out that pond turtles should be split into two families, the Geoemydidae (= Bataguridae of some authors) and the Emydidae. Furthermore, it is clear that land tortoises are more closely related to the former than to the latter (Hirayama, 1985; Gaffney and Meylan, 1988; Shaffer et al., 1997; Honda et al., 2002).

The North American genus *Gopherus* appears to be the single surviving genus in an old lineage of tortoises that split off from other living tortoises in the Eocene. Their closest relatives appear to be the extinct genus *Hesperotestudo* (Meylan and Sterrer, 2000).

Geologic Distribution. — The fossil record of the superfamily Testudinoidea goes back to the end of the age of dinosaurs. But land tortoises themselves appear to be younger. Although we can now be certain that the Cretaceous turtles, *Mongolemys* and *Lindholmemys* are tesudinoids (Shaffer et al., 1997; Sukanov, 2000), they do not appear to fit within the Emydidae or Geoemydidae, but rather may constitute the sister group of the living members of the three testudinoid families. The earliest dates for the divergence among the living families of the Testudinoidea depend on fossils whose relationships lie within one of those three families. These include two representatives of testudinoid families that have been reported from the lower Eocene (± 52 million years ago) of Wyoming. The geoemydid, *Echmatemys testudinea,* and the testudinid, *Hadrianus majusculus*, are the earliest representatives of their families (Benton, 1993).

It is clear that *Hadrianus* is a land tortoise and can be used to provide a minimum age for the family. *Hadrianus* is reported from the Willwood Formation of Wyoming (Hutchison, 1980), providing a minimum age of 52 million years for the split between the land tortoises and other kinds of turtles.

Geographic Distribution. — Land tortoises are found on all continents except Australia and Antarctica. They are most diverse in Africa and Madagascar where about half of the living species in this family are found. Other continents have six or fewer species. Members of this group are well known for reaching oceanic islands and survive on two island groups today, the Galapagos and Seychelles.

Status. — Giant tortoises in many continental and island regions have gone extinct in the last 10,000 years, with many of those lost in relatively recent historical times, and nearly all living species of tortoise are threatened with extinction.

LITERATURE CITED

Benton, M.J. 1993. Reptilia. In: Benton, M.J. (Ed.). The Fossil Record 2. Chapman & Hall, London, pp. 681-715.

Gaffney, E.S. and Meylan, P.A. 1988. A phylogeny of turtles. In: Benton, M.J. (Ed.). The Phylogeny and Classification of the Tetrapods, Volume1: Amphibians, Reptiles, Birds. Clarendon Press, Oxford, pp. 157-219.

Hirayama, R. 1985. Cladistic analysis of batagurine turtles (Batagurinae: Emydidae: Testudinoidea): a preliminary result. Studia Geologica Salmanticensia, Studia Palaeocheloniologica 1:141-157.

Honda, M., Yasukawa, Y., Hirayama, R., and Ota, H. 2002. Phylogenetic relationships of the Asian box turtles of the genus *Cuora* sensu lato (Reptilia: Bataguridae) inferred from mitochondrial DNA sequences. Zoological Science 19:1305-1312.

Hutchison, J.H. 1980. Turtle stratigraphy of the Willwood Formation, Wyoming: preliminary results. University of Michigan Museum of Paleontology Papers in Paleontology 24:115-118.

Iverson, J.B. 1992. A revised checklist with distribution maps of the turtles of the world. Privately published. Richmond IN, 363 pp.

Meylan, P.A. and Sterrer, W. 2000. *Hesperotestudo* (Testudines: Testudinidae) from the Pleistocene of Bermuda, with comments on the phylogenetic position of the genus. Zoological Journal of the Linnean Society 128:51-76.

Shaffer, H.B., Meylan, P.A., and McKnight, M. 1997. Tests of turtle phylogeny: molecular, morphological and combined approaches. Systematic Biology 46(2):235-268.

Sukanov, V.B. 2000. Mesozoic turtles of Middle and Central Asia. In: Benton, M.J., Shishkin, M.A., Unwin, D.M., and Kurochkin, E.N. (Eds.). The Age of Dinosaurs in Russia and Mongolia. Cambridge University Press, pp. 309-367.

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Gopherus polyphemus – Gopher Tortoise

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Summary. – The gopher tortoise, *Gopherus polyphemus*, is the only North American land tortoise found east of the Mississippi River, where it occurs in portions of six states in the southeastern coastal plain. The gopher tortoise is a medium-sized terrestrial turtle that constructs and inhabits a distinctive burrow. Adults grow to 38.7 cm (15 in) carapace length. Distinguishing external features include short elephantine hindlimbs and shovel-like forelimbs covered with relatively thick scales. The gopher tortoise is most commonly found in upland habitats that are characterized by a deep, well-drained, sandy soil suitable for construction of their extensive burrows. The gopher tortoise digs its burrow in a relatively open site that provides sunlit areas for nesting and thermoregulation, and ample herbaceous ground vegetation for forage. Burrows of adult gopher tortoises average approximately 4.5 m in length and about 2 m in depth. A gopher tortoise may use several burrows during a year, and the number of burrows at a given site is almost always greater than the number of tortoises at that site. Sexual maturity is associated with size, not age, and individuals may become mature in 10 to 20 or more years, depending on location and habitat quality. Mating and nesting activities occur primarily from May through mid-June. Eggs are often laid just outside the burrow and hatchlings emerge from eggs between late August and October. Human activities pose the greatest threats to the survival of gopher tortoise populations. Loss of habitat to human activities can take three forms: reduction in area of suitable habitat (true displacement), degeneration of suitable habitat (abandonment of habitat), and increased fragmentation of habitat (increased isolation of populations). During the past decade or so, Upper Respiratory Tract Disease (URTD) also has been identified as a potential threat to the survival of the gopher tortoise. The State of Florida currently lists the gopher tortoise as Threatened. We consider it endangered. We propose a three-part approach to ensure a healthy future for the gopher tortoise. First, outright purchase of land known to support populations of gopher tortoises by individuals or agencies willing to conserve the species. Second, education of private land owners and public land managers about the value of active management of habitats known to support tortoise populations. Third, re-introduction of the gopher tortoise to suitable habitats on protected lands from which it has been extirpated or lands that have been restored to suitable habitat.

Conservation Status. – FNAI Global - G3 (Rare, Local, or Vulnerable), State - S3 (Rare, Local, or Vulnerable); ESA Federal - LT (Threatened): populations west of Mobile and Tombigbee Rivers in Alabama, Mississippi, and Louisiana, Not Listed: populations in rest of range; State - T (Threatened); CITES - Appendix II; IUCN Red List - VU (Vulnerable).

Species Recognition. — The gopher tortoise, *Gopherus polyphemus*, is a medium-sized terrestrial turtle that constructs and inhabits a distinctive burrow (Fig. 25-1). Adults grow to 38.7 cm (15 in) carapace length (CL) (Timmerman and Roberts, 1994). External features that distinguish it from other turtles include short elephantine hindlimbs, shovel-like forelimbs covered with relatively thick scales, and an anterior gular projection of the plastron (Figs. 25-2, 25-3). Often, the surface of the shell is quite smooth, reflecting the abrasion it receives as the tortoise enters and exits the burrow. The carapace is oblong with the greatest width near the posterior margin of the well-developed bridge, and the greatest height is in the pelvic region. The carapace drops off abruptly posterior to the pelvic region (Ernst and Barbour, 1972). The carapace of adults varies from dark-brown to tan to grayish-black in color. In Florida, individuals from populations in coastal areas generally are darker than those from populations in central areas of the peninsula. The gular scutes of the plastron project anteriorly from below the chin. Males often have longer gular projections than females;

Figure 25-1. Two adult gopher tortoises, *Gopherus polyphemus,* in front of the mouth of a gopher tortoise burrow, Duval Co., Florida. Photo by Barry Mansell.

however; because both sexes use their projections during agonistic encounters, the gular projections are often broken and may not accurately reflect the sex of an individual (Mushinsky et al., 1994). Unlike the relatively smooth scutes on the carapace, plastral scutes in most individuals show concentric growth rings.

Hatchling gopher tortoises emerge from eggs at a CL of about 5 cm. Coloration of the carapace of hatchlings is yellow to yellowish-orange, but each scute has a brownish border (Fig. 25-4; Allen and Neill, 1953). The skin on the head and limbs is likewise bright yellow to yellowish-orange. The bright coloration of hatchlings darkens somewhat during the first year or two of life, but individuals less than five or six years of age typically are lighter in coloration than older individuals. Young gopher tortoises spend a considerable amount of time basking at the mouths of their burrows, and their colors blend well with the shadows on the orange-yellow sandhill soils. The gular scutes of young tortoises are less prominent than those of adults and the claws of young tortoises are relatively longer and sharper (Allen and Neill, 1953).

Figure 25-2. Young adult gopher tortoise, *Gopherus polyphemus*, from Alachua Co., Florida. Photo by Dick Bartlett.

Figure 25-3. Plastral view of adult male gopher tortoise, *Gopherus polyphemus*, from Florida, Photo by David Dennis.

Figure 25-4. Hatchling gopher tortoise, *Gopherus polyphemus*, from Liberty Co., Florida. Photo by Dick Bartlett.

Taxonomic History. — The gopher tortoise was originally named *Testudo polyphemus*, in 1802, by Daudin. In 1815, Rafinesque introduced the genus *Gopherus*, to which this species has been attributed regularly since 1893 (Smith and Smith, 1980). The extensive burrowing habits of the gopher tortoise are reflected in its common name.

DISTRIBUTION

Geographic Distribution. — The gopher tortoise is the only North American tortoise found east of the Mississippi River, where it occurs in portions of six states in the southeastern coastal plain (Auffenberg and Franz, 1982). In Louisiana, populations occur in upland pine ridges in the extreme eastern Parishes of St. Tammany, Washington, and Tangipahoa. In Mississippi, populations occur in a 14-county region in the southern portion of the state. Populations exist throughout most of southern Alabama. In South Carolina, populations are restricted to river ridges in Jasper and Hampton counties. In Georgia, populations occur in a series of disjunct locations south and east of the Fall Line on the coastal plain. The state with the largest numbers of the gopher tortoise is Florida.

Gopher tortoise populations occur in all 67 Florida counties (Fig. 25-5). Throughout the state, however, many populations have become isolated and their numbers reduced greatly to small fractions of their former abundances. In the southern portion of the state, south of Lake Okeechobee, the gopher tortoise probably always occurred in relatively small isolated populations, mostly along the coastline. Scattered populations of tortoises occur in the relatively high elevation hammock islands within the northern Everglades.

Ecological Distribution. — The gopher tortoise is most commonly found in upland habitats that are characterized by deep, well-drained, sandy soil suitable for construction of their extensive burrows. All gopher tortoises live in burrows, usually one individual per burrow. Occasionally, two individuals may occur temporarily in one burrow, but double occupancy is rare. Individuals require open, sunny patches of habitat for feeding, nesting, and thermoregulation. The gopher tortoise is most abundant in upland habitats that are burned frequently. The notion that gopher tortoises occur in colonies, implying a social cohesion, may have been falsely created by their strong need to live in open patches. For example, high concentrations of gopher tortoises exist on many power line rights-of-way that have become surrounded by overgrown uplands that once supported the gopher tortoise. Nevertheless, the gopher tortoise is a social animal and we have only a poor understanding of its social structure.

Spatial distribution and social structuring of populations of organisms are frequently influenced by their reproductive systems. Our understanding of the ecological distribution and social structure of the gopher tortoise has changed during the past few decades. A "colony" of gopher tortoises was described as several adult females living in close proximity with one or two males, who excluded other males from interacting with the resident females (McRae et al., 1981b). The notion that a "loose or incipient harem" mating system influenced the ecological distribution and colony structure of the gopher tortoise was introduced by Douglass (1986). A colony was presumed to be occupied by a large, dominant male who was more or less surrounded by females, and those females nearest to the male experienced a greater number of courtships than females more distant from the central male. Recently, Boglioli et al. (2003) tested the ideas put forth by McRae et al. (1981b) and Douglass (1986). The setting for their research was large, contiguous populations of gopher tortoises. They concluded that distance from neighboring tortoises did not influence mating opportunities, nor did the degree of isolation of females influence the frequency of courtship or mounting by males, nor the size of the males doing the courting. The general pattern of reproduction closely resembled scramble-competition polygyny rather than harem defense polygyny. Based on our current understanding of the distribution and behavior of the gopher tortoise, there appears to be no reason to use the term "colony" to describe a local population of tortoises.

Using the broad descriptions for upland habitats found in Myers and Ewel (1990), the habitat types most often occupied by the gopher tortoise in Florida include sandhill (pine-turkey oak), sand pine scrub, xeric hammock, pine flatwoods, dry prairie, coastal grasslands and dunes, and mixed hardwood-pine communities (Landers and Speake, 1980; Auffenberg and Franz, 1982; Kushlan and Mazzotti, 1984; Diemer 1986, 1992a). The gopher tortoise is known to occupy other types of habitats occasionally, especially on islands. At some locations, for example, Sanibel Island, and Cape Sable, gopher tortoises have constructed their burrows in the shell-laden substrate. On Egmont Key, gopher tortoise burrows primarily are located around the periphery of the island among open sandy areas between the shoreline and the island interior forests.

The gopher tortoise prefers open habitats that support a wide variety of herbaceous ground cover vegetation for forage. It usually abandons densely canopied areas that lack the preferred herbaceous ground cover and frequently is forced to occupy disturbed habitats such as roadsides, fence-

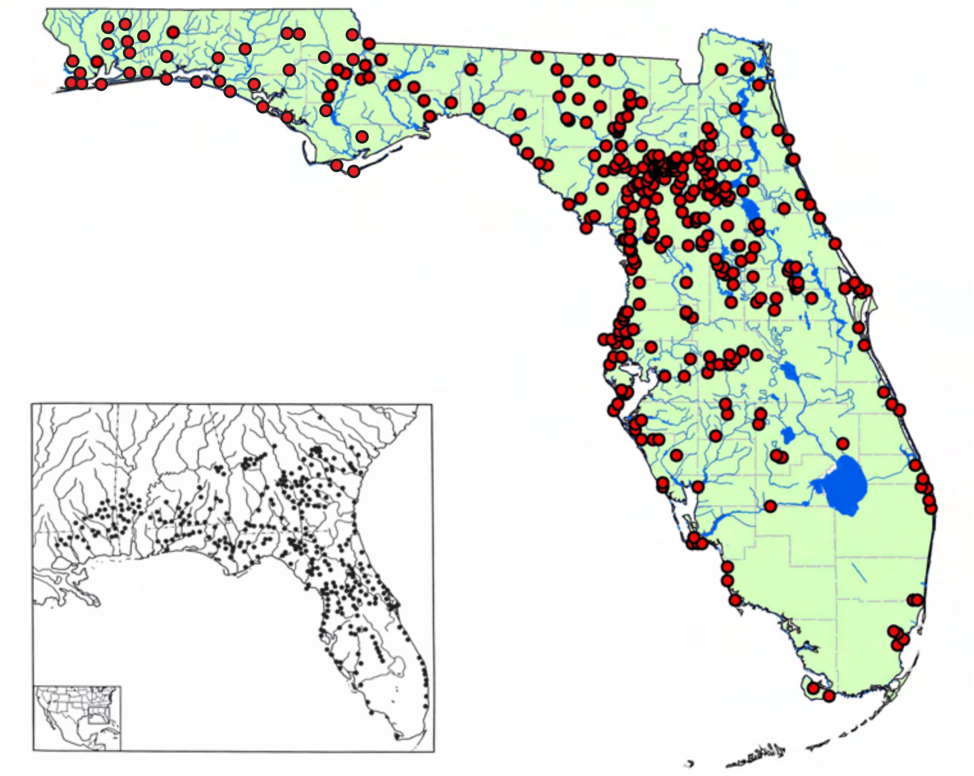

Figure 25-5. Available distribution records for the gopher tortoise, *Gopherus polyphemus*, from Florida. Inset: distribution records from entire range of *G. polyphemus* (from Iverson, 1992; distribution in inset map not current for Florida as presented here). Localities for the Florida panhandle were supplemented with data from the Florida Natural Areas Inventory data base for this species on 21 September 2006.

rows, old fields, and the edges of overgrown (unburned) uplands (see Diemer, 1989; Stewart et al., 1993; Breininger et al., 1994). Overgrown habitats may inhibit gopher tortoises from reaching their minimum thermal requirements for normal development and reproduction (Mushinsky and McCoy, 1994). The gopher tortoise can co-exist with resident cows in grazed pastures (Ashton, unpubl. data).

Since the first general survey across the full range of the gopher tortoise by Auffenberg and Franz (1982), there has been a growing understanding of the ecological factors that influence the distribution of the gopher tortoise. For more than 20 years, biologists at the University of South Florida (USF) have studied the effects of fire periodicity on plants and animals that reside in the sandhill habitat at the University Ecological Research Area (Mushinsky and Gibson, 1991). By burning small (1–2 ha) plots of land on different frequencies, the biologists have created a mosaic of plots of land with different vegetation profiles among which the resident tortoises can choose when digging their burrows. Repeated surveys have revealed that when individuals are free to move among fragments, their movements are highly directional, and the density of tortoises increases within the most suitable patches. After 25+ years of prescribed burning, the percent of the ground surface covered by living non-woody vegetation (mostly grasses and herbaceous plants) increased among burn plots in the following order (from least to most): (1) unburned plots, (2) 7-yr plots (i.e., plots burned at 7-yr intervals), (3) 1-yr plots, (4) 5-yr plots, and (5) 2-yr plots (McCoy and Mushinsky, unpubl. data). The abundances of gopher tortoises increased in precisely the same order, as did the evenness of the size distribution of individuals (McCoy and Mushinsky, unpubl. data). In other words, gopher tortoises were least abundant in the unburned plots, where canopy coverage was high and grass and herbaceous vegetation was least common, and they were most abundant in the plots burned every two years, where canopy coverage was low and the grass and herbaceous plants were most common. In general, these results from the experimental burn plots confirmed the observations of Auffenberg and Franz (1982).

HABITAT RELATIONS

The Burrow. — Regardless of the specific type of habitat, the gopher tortoise digs its burrow in a relatively open site that provides sunlit areas for nesting and thermoregulation, and ample herbaceous ground vegetation for forage (Macdonald and Mushinsky, 1988). Dimension of burrows of adult gopher tortoises average approximately 4.5 m in length and about 2 m in depth (Hansen, 1963; Diemer, 1989). Burrows have been found to be significantly shorter in clayey soils than sandy soils, which may be a result of respiratory limitations of the gopher tortoise. Decrease in O_2 and increase in CO_2 are greatest in burrows in clayey soils and are positively correlated with burrow length (Ultsch and Anderson, 1986). The high humidity within the burrow may offer the tortoise protection from desiccation (Auffenberg and Weaver, 1969; Means, 1982). Typically, a gopher tortoise burrow terminates with an end chamber at or near the level of the water table, just above the clay hardpan. Measurements of soil temperatures within burrows, taken as burrows were excavated, documented temperature gradients from the mouth of the burrow to the end chamber (Ashton, unpubl. data). From April to November, in north Florida, the end chamber temperatures were 16 to 22ºC, and from December to March the end chamber had temperatures of 5 to 12ºC. At the mouth of each burrow is a mound of subsoil. These soil mounds undergo micro-succession and contribute increased plant species diversity in the surrounding habitat (Kaczor and Hartnett, 1990). Female gopher tortoises often deposit their eggs in these deep sandy mounds immediately outside the burrow.

A gopher tortoise may use several burrows during a year, and the number of burrows at a given site is almost always greater than the number of tortoises at that site. In an attempt to estimate burrow occupancy, burrows have been classified as active, inactive, or abandoned based on their physical appearance (Auffenberg and Franz, 1982; Cox et al., 1987). "Active" burrows show signs of tortoise activity within the previous 24-hr period, such as footprints, or scrape marks in the sand at the mouth made by the plastron as the tortoises entered or exited the burrow. "Inactive" burrows show no signs of recent activity and may harbor small amounts of debris, such as leaves or grasses that have been blown into the mouth of the burrow. The roof of an inactive burrow has a distinct half-moon shape. Following heavy rains, inactive burrows may show signs of erosion. "Abandoned" burrows are those that harbor considerable vegetation near the mouth of the burrow, and in which the roof of the burrow has lost the half-moon shape. Vertically oval-shaped burrow openings typically indicate occupancy by an armadillo. Eventually, abandoned burrows fill-in with sand and debris, collapse, and disappear from the landscape.

The time of the year when assessment of burrow occupancy is made will influence the classification of a burrow. Best assessments are made during the warm summer months, when tortoises typically leave their burrow daily to forage. Estimates of burrow occupancy based on activity classes of burrows are not perfect. Of 1019 burrows classified and excavated by Witz et al. (1991), 454 active burrows yielded 341 individuals (75% occupancy), 449 inactive burrows yielded 53 individuals (12% occupancy), and 116 abandoned burrows yielded 6 individuals (5% occupancy). In another study, Ashton (unpubl. data) excavated what appeared to be abandoned burrows of adult tortoises and found that 27% of the burrows contained individuals between one and about eight years of age. Wide discrepancies in the numbers of individuals in "abandoned burrows" might suggest a need for more rigorous definitions and implementation of standards by researchers. Reliable criteria to be used to distinguish among categories of burrows have been proposed (McCoy and Mushinsky, 1992a).

The width of a burrow is related to the size (CL) of the resident tortoise (Alford, 1980; Martin and Layne, 1987; Wilson et al., 1991; Doonan and Stout, 1994; Smith, 1995). A gopher tortoise digs a burrow by alternately scooping sand from the burrow with its front legs. As it alternates the power stroke from forelimb to forelimb, it pivots from side to side to form a burrow that is wider than the width of the tortoise, but about the length of the carapace. Wilson et al. (1991) concluded that burrow width is a reliable indicator of carapace length because of the morphological components and the digging behavior used in burrow construction. It appears that the ability of a gopher tortoise to turn around in any portion of its burrow is a fortuitous by-product of its morphology and digging behavior. To assess the size of the occupant, burrow width typically is measured at a depth of 50 cm because the mouth of the burrow is frequently enlarged or eroded (Martin and Layne, 1987). Burrow widths can be used to construct a size class profile for a population study (Alford, 1980).

Most hatchlings dig their own burrows, often just a few meters away from the nest from which they emerged (Mushinsky and McCoy, unpubl. data). In fact, it is not uncommon to find groups of three to six burrows of hatchlings within a few square meters. Not all young or juvenile gopher tortoises dig their own burrows, however. Some neonates will dig a small burrow directly into the wall of a large burrow and reside in it until the following spring. Although most juvenile gopher tortoises excavate their own burrow, occasionally they can be found in an abandoned burrow of a larger individual (Ashton and Ashton, 2001).

From a human perspective, it seems an enormous task to dig a burrow that penetrates several meters into the ground, yet the gopher tortoise can dig one in a day or so in most habitats. Adult gopher tortoises may dig at a rate of 3 m per day in sandhill habitats (Ashton, unpubl. data). Perhaps it is the speed with which a gopher tortoise can dig a burrow, coupled with its strong need to reside in open sunny habitats that causes individuals to abandon existing burrows to construct new ones. For example, at a site in Alabama, Aresco and Guyer (1999a) reported that of 124 active burrows marked in 1991, only 31 (25%) were active five years later. Active burrows were abandoned at the rate of 22% per year. Surprisingly, abandoned gopher tortoise burrows seem to have about the same longevity in the clay-based soils of southern Georgia as they do in sandy soils of south Alabama (Guyer and Herman, 1997). Not surprisingly, these researchers demonstrated that the larger the burrows the longer they persist over time.

Individuals typically frequent more than one burrow as they move about their home ranges. For adult gopher tortoises, the calculated mean distance moved between burrows is 37.0 ± 37.0 m by females and 79.0 ± 69.0 m by males (Diemer, 1992c). For juvenile tortoises, the calculated mean distance moved is 16.0 ± 17.0 m in a north Florida population (Diemer, 1992c) and 15.2 ± 22.8 m in a central Florida population (Wilson et al., 1994).

Excluding moves between burrows, movements away from the burrow have been considered to be a tortoise's feeding radius. McRae et al. (1981b) reported a mean feeding radius of 7.8 ± 4.4 m for juvenile tortoises and 13.0 ± 8.6 m for adult tortoises in a Georgia population. Adults may move up to 200 m in 30 min in search of broadleaf plants (Ashton and Ashton, unpubl. data). In central Florida, Wilson et al. (1994) reported a mean feeding radius of 7.9 ± 8.6 m for juveniles. Also in central Florida, Mushinsky et al. (2003) reported that juvenile foraging forays averaged 19.4 (± 10.3) min and individuals traveled an average of 26.8 (± 41.5) m round trip from their burrows during that time.

In north Florida, Diemer (1992c) documented that, on average, adult male tortoises used 5.5 burrows and adult female tortoises used 2.7 burrows per activity season (April–December). In Georgia, tortoises were reported to use 7 and 4 burrows for males and females, respectively (McRae et al., 1981b). Average annual burrow use by juvenile tortoises ranged from 1.1 by 0–1 yrs old, 2.2 by 2 yrs old, 1.7 by 4–5 yrs old tortoises in a southern Georgia population (McRae et al., 1981b) to 4.4 burrows (1–4 yrs old) in a central Florida population (Wilson et al., 1994). Suggested reasons for differences in burrow use among populations include variation in habitat quality (i.e., canopy and ground cover), soil composition, temperature extremes at different latitudes, and number of disturbances to burrows. Although juvenile tortoises use several burrows, they reside in a primary burrow, where they may spend 75% of their time (Wilson et al., 1994). No data exist in support of a primary burrow (one in which an individual spends more than 50% of its time) for adult gopher tortoises, at least not for an extended time period. Gopher tortoises use shallow depressions, possibly as temporary resting sites, when traveling far from their burrows (Fucigna and Nickerson, 1989; Godley, 1989; Stout et al., 1989; Diemer, 1992c) and windrows, possibly for protection from cattle and machinery (Diemer, 1992c).

In north Florida, Diemer (1992b) found that the number of burrows showing signs of recent activity increased in April, peaked in July, and remained high through October. The burrow surveys showed a continuous cycle of burrow creation and abandonment. The ratio of number of captured tortoises to burrows (active and inactive) varied among sites and years; the ratio of tortoises to burrows ranged from 0.45 to 0.69. Percentages of adult individuals in the three populations studied ranged from 40–62%.

The orientation of gopher tortoise burrow often reflects man-made and natural topographic features that result in burrows being oriented in the four primary compass directions (McCoy et al., 1993). Among other things, the direction of topographic relief, the amount of tree shading, and the orientation of man-made structures such as roads, rights-of-way, and railroads all exert an influence on the orientation of the burrow.

Activity and Home Range. — Generally, the gopher tortoise confines its daily activities to the area immediately surrounding its burrow. The area used for routine activities by a species is the home, or activity range. Many publications provide estimates of home range size based on data collected during a small fraction of the life of a gopher tortoise. Because the gopher tortoise is a long-lived organism, and habitats change quality during the course of a life time, most individuals change the home range many times during their lives. Estimates of home range sizes will increase over time for most individuals. Home range sizes for adult female gopher tortoises range from 0.08 ha (McRae et al., 1981b) to 0.56 ha (Doonan, 1986) and adult males from 0.45 ha (McRae et al., 1981b) to 1.27 ha (Diemer, 1992c). In north Florida, Smith (1995) followed female tortoises for up to 500 days and reported home ranges that varied from 0.002 to 1.435 ha. Male home ranges have been reported to be larger than those of females in some populations (Auffenberg and Iverson, 1979; McRae et al., 1981b), but not in others (Diemer, 1992c). The home range for juveniles (1–4 yrs) varied from 0.0095 ha to 0.3576 ha in a central Florida population (Wilson et al., 1994) and from 40 m^2 to 0.2502 ha in a north Florida population (Diemer, 1992c). Wilson et al. (1994) found that home ranges of juveniles were largest in summer months, a pattern that is similar to that observed in adults. Home range size is a function of the quality of the habitat (Diemer, 1992c; Mushinsky and McCoy, 1994) and it decreases with an increase in the amount of herbaceous ground cover (Auffenberg and Iverson, 1979; Mushinsky and Gibson, 1991). Management of gopher tortoise habitat by controlled burning during the warm season increases the amount of herbaceous ground cover, and thus tortoises do not have to travel far from their burrows to find ample food.

Long Distance Movements. — Gopher tortoises make long distance movements. Using radiotelemetry, Diemer (1992c) found that among her radio-tagged animals, the longest movement made was 0.74 km by an emigrating subadult. An adult female tortoise observed by Ashton (unpubl. data) resided in two adjacent burrows for 11 months, then moved 2.1 km to a new location, where it resided for at least 9 months. Juveniles also will make relatively long distance movements, usually following some type of disturbance to the resident burrow (Diemer, 1992c; Wilson et al., 1994).

The daily and periodic movements of a gopher tortoise enable it to become very familiar with its home range, and, over the course of several decades, an individual may become familiar with a portion of its environment that is much greater than the home range it may occupy at a given point in time. It should come as no great surprise, therefore, that an individual intentionally displaced some distance from its burrow can find its way back to its home burrow. Connor (1996) observed that upon release, gopher tortoises displaced 40 to 200 m from their home burrows moved toward their home range, but several individuals displaced 200 m from their burrows demonstrated a reluctance to pass through highly overgrown habitat on their return trip, although they clearly were moving toward their home range.

Temperature Relations. — Gopher tortoises spend a limited amount of time above ground outside of their burrows, perhaps in response to physiological limitations. The gopher tortoise has been found to desiccate more rapidly when deprived of a burrow than any other member of the genus *Gopherus* (Auffenberg and Weaver, 1969). The gopher tortoise can withstand high body temperatures (Bogert and Cowles, 1947), although when heat-stressed, it will froth at the mouth and breathe rapidly. Critical thermal maximum for the gopher tortoise is 43.9ºC (Hutchinson et al., 1966). With a device positioned at the mouth of the burrow that automatically recorded activity, Auffenberg and Iverson (1979) calculated that an adult tortoise was active 9.2% of its time. An "active" tortoise is one that minimally comes to the mouth of the burrow. Juveniles have been reported to spend 90% of their time underground inside their burrows (Wilson et al., 1994). Activity away from the burrow tends to peak in the late spring and summer. For juveniles, Wilson et al. (1994) found that 80% of observed activity in fall, winter, and spring consisted of basking on the burrow mound; juveniles moved away from their burrows significantly more during the summer months. During the winter months, tortoises bask at the mouths of their burrows on warm days throughout their range (Douglass and Layne, 1978; McRae et al., 1981b; Diemer, 1992c; Wilson et al., 1994). Thus, the activities of gopher tortoises away from their burrows are limited in the winter months and increase as seasonal temperatures increase. Daily activity has been reported as unimodal in the spring and bimodal in the summer in a Georgia population (McRae et al., 1981b), and in a north Florida population (Ashton, unpubl. data). Adult tortoises may be active in the late morning and late afternoon in summer to avoid the hottest part of the day (McRae et al., 1981b). In contrast, Douglass and Layne (1978) and Wilson et al. (1994) found that juvenile tortoises were more active in the mid-afternoon and did not display a bimodal activity pattern in the summer. Activity patterns of juvenile tortoises may be influenced by the risk of predation and thermoregulatory behavior (see Wilson, 1991; Wilson et al., 1994). Mushinsky (unpubl. data) observed an adult gopher tortoise a few hours after sunset in mid-summer, but generally gopher tortoises are diurnal.

GROWTH AND REPRODUCTION

Growth and Maturation. — In Georgia, Landers et al. (1982) reported rapid growth through the age of 11 yrs after which growth rates gradually decreased. In central Florida, Mushinsky et al. (1994) reported an average increase of 18.9 mm/yr for ages 1–11, after which growth slowed to approximately 3%/yr until age 20. Female gopher tortoises became sexually mature at a CL of 230–240 mm. Body size, rather than age, seems to determine sexual maturity in gopher tortoises. In southern Georgia, it may take from 19–21 yrs for females to become sexually mature (Landers et al., 1982), while in central Florida females may mature in as few as 9–11 yrs (Mushinsky et al., 1994). In part, this variation reflects the long activity season available to tortoises in central Florida. In addition to geographic location, however, local conditions also influence the number of years required to achieve sexual maturity. For example, one study of gopher tortoises in central Florida (Godley 1989) found that females attained sexual maturity in 14–16 yrs, while results of another study from the same county found that females attained sexual maturity in 9–11 yrs (Mushinsky et al., 1994). The study area occupied by the faster maturing females was a frequently burned sandhill habitat (the University of South Florida Ecological Research Area), whereas the study area with slower growth rates was a mosaic of less favorable habitats, including pine flatwoods and mixed mesic forests. Males likely mature at a smaller size than females. In both north (Diemer and Moore, 1994) and central Florida (Mushinsky et al., 1994) males apparently mature at a CL of about 180 mm. Another report (Aresco and Guyer, 1999b) underscored the relationship between body size, growth, and attainment of sexual maturity. The authors reported that the slow growth of tortoises at Conecuh National Forest in south Alabama was a response to a managed pine plantation with little ground vegetation and poor forage. Gopher tortoises at this site took about 20 yrs to become sexually mature. Gopher tortoises translocated to reclaimed phosphate mined lands in central Florida were found to be gravid at CL less than 200 mm (Small and Macdonald, 2001).

Counts of growth rings have been used to age individuals (Mushinsky et al., 1994; Aresco and Guyer, 1999b). The use of the growth rings to age individuals must be done with caution, however, because the production of "false" rings is known to occur throughout the range of the species (Ernst and Barbour, 1989). In other words, individuals may produce several rings within a single growing season, and, therefore, a ring is not necessarily an annual growth ring. Without independent methods to calibrate the production of growth rings, counts of growth rings should not be considered a reliable method to age gopher tortoises (Wilson et al., 2003). Under the best circumstances, it seems that aging gopher tortoises by counting growth rings on the plastral scutes produces reliable results on tortoises up to 12 (Mushinsky et al., 1994) or 15 (Aresco and Guyer, 1999b) yrs old. Examination of thin sections of scutes has been investigated as a means to determine the age of adult desert tortoises, *G. agassizii* (Germano and Bury, 1994).

Sexual Dimorphism. — The best indicator of the gender of an adult gopher tortoise is the depth of the plastral concavity (Mushinsky et al., 1994). Mature males have a distinct depression in the posterior, central portion of the plastron that facilitates mounting a female for copulation. Some mature females have a shallow plastral concavity (2–4 mm) compared to that of mature males (5–8 mm). Males often have larger integumentary glands under the chin than females (Ernst and Barbour, 1989), but the size of these glands varies seasonally. Based on numerous anatomical measurements, McRae et al. (1981a) developed a discriminate function that accurately identified the sex of adult individuals. In a similar effort, Burke et al. (1994) used a stepwise multiple regression of numerous morphological measurements to develop a non-invasive technique to determine the sex of hatchling and juvenile gopher tortoises.

Female Reproductive Cycle. — The ovarian cycle of female tortoises is described by Iverson (1980) and Palmer and Guillette (1988).

Mating. — The mating patterns of the gopher tortoise are reasonably well known. Male tortoises seek females for mating primarily from May to July, although one might observe a male following a female at any time during the summer or fall. Some observational data suggest that dominant males breed with several females (Douglass, 1976, 1986). When seeking a female, a male positions himself at the mouth of a burrow occupied by a female and displays a head bobbing behavior (Auffenberg, 1966; Wright, 1982). If the female exits her burrow, the courting male walks in a circle around her, periodically stopping and performing the head bobbing behavior. When the female approaches the courting male, he bobs his head violently, and bites her on the forelegs, head, anterior edge of the carapace and gular projection. The female then backs in a semicircle, with the male following. Eventually, the female stops and extends her rear legs. Thereafter, she rotates her body about 180 degrees, so that her posterior end is near the head of the male. The courting male will attempt to mount the female, and if unsuccessful, he will repeat the courting behavior (Auffenberg, 1966; Ernst and Barbour, 1972). The significant amount of direct head to head contact between courting adults unfortunately may serve to facilitate the spread of respiratory diseases.

A recent study examined the mating system and reproductive behaviors of a population of gopher tortoises in central Florida. Using microsatellite makers, Colson-Moon (2003) was able to determine the fathers of the offspring in clutches of eggs oviposited and incubated in the lab and determined that multiple fathers were present in 28.6% of the examined clutches. By assessing patterns of paternity, she was able to determine that the study population exhibited promiscuous mating. Paternity patterns in the study population also suggested that female size may affect the presence of multiply-sired clutches, while male size may affect the ability of a male to gain fertilizations (Moon et al., 2006).

Nesting. — Nesting occurs primarily from May through mid-June (Iverson, 1980; Landers et al., 1980; Wright, 1982). Females deposit white, nearly spherical, brittle-shelled eggs in a typically flask-shaped nest cavity. The cavity is excavated with the hindlimbs to a depth of about 10–15 cm. Iverson (1980) reported an average maximum egg diameter of 42–43 mm and an average wet mass of 40.9 g (also see Arata, 1958; Landers et al., 1980; Linley and Mushinsky, 1992). Note that measurements of eggs taken from radiographs of gravid females should be considered rough estimates (Linley and Mushinsky, 1994). Nests may be located in any open sunny area near the burrow of the female, but most often, nests are placed in the spoil mound (apron) immediately outside the female's burrow (e.g., Hallinan, 1923; Allen and Neill, 1951; Arata, 1958; Mount, 1975; Landers et al., 1980). In one study, 21 of 25 located nests were positioned in the apron (Butler and Hull, 1996). In contrast, during a period of three years, Smith (1995) found that fewer than 2% of the 2008 burrow aprons examined contained nests and she observed that only 2 of 18 females deposited their eggs in the apron.

Clutch Size. — Female tortoises lay a single annual clutch of 5 to 9 eggs (see Diemer and Moore, 1994; Butler and Hull, 1996, for summaries); however, a large female that had been translocated to reclaimed phosphate mined land in central Florida produced an exceptionally large clutch of 25 eggs (Godley, 1989). Clutch size of female gopher tortoises has been shown to increase with CL in north Florida (Diemer and Moore, 1994) and in southern Georgia (Landers et al., 1980). In a study that was conducted on gopher tortoises translocated to reclaimed phosphate-mined land in central Florida, Macdonald (1996) reported that mean clutch size of translocated individuals increased from 8.6 to 12.6 in four years. Six female tortoises that established burrows on reclaimed land (these individuals were not translocated) had clutches containing more than 13 eggs. Virtually all of the adult tortoises translocated to the reclaimed land exhibited an atypical growth spurt and were large individuals (Small and Macdonald, 2001).

Incubation and Hatching. — The incubation period of eggs varies latitudinally from about 80 days near the southern edge of the gopher tortoises range to 106 days farther north (Iverson, 1980; Landers et al., 1980; Butler and Hull, 1996). Most clutches of eggs hatch during August and September, but in northern Florida some may hatch as late as early October (Butler and Hull, 1996). At hatching, and from 24 to 48 hrs prior to emergence, hatchlings may exhibit a large external yolk sac (Linley and Mushinsky, 1994). The external yolk sac is absorbed as the hatchlings remain in the nest cavity prior to emergence. Just after emergence, a deep transverse groove across the plastron is visible, but it disappears two to three days after emergence as the anterior-posterior axis of the body becomes straight and the plastron flattens (Ernst and Barbour, 1972).

POPULATION BIOLOGY

Density. — Densities of gopher tortoises are known to be relatively high in sandhill habitats, especially those that are frequently burned. These densities are typically based on counts of numbers of burrows per ha (see below). However, relatively high densities of gopher tortoise burrows, per se, can be misleading in areas where land is being cleared for human development. Individuals in harm's way may be forced to reside in smaller and smaller parcels of undisturbed land. The result is that one observes a relatively dense population of gopher tortoises and an illusion of a "healthy" population, based on a large number of gopher tortoise burrows per unit area. Under some circumstances, high densities of gopher tortoises have been viewed as a sign of a healthy productive population. Under current conditions, however, where human development has encroached into land occupied by the gopher tortoise or the upland habitats have become overgrown, high densities of individuals must be viewed more carefully. For example, Mushinsky and McCoy (1994) reported that apparent high densities of some gopher tortoise populations may be the result of individuals confined to either a true island or a "habitat" island. Habitat islands are patches of good quality habitat for the gopher tortoise surrounded by poor quality habitat, such as agricultural lands or urban development, and are a product of habitat fragmentation. Gopher tortoises in habitat islands are unable to move freely to new locations as the quality of the habitat degenerates. Gopher tortoises confined to these habitat fragments tend to dig many burrows creating the illusion of a large healthy population. In reality, however, the ratio of burrows to tortoises is high because individuals move and dig new burrows frequently as they search for good quality habitat. More research is needed on the effects of habitat fragmentation on the demography and social interactions of the gopher tortoise.

One significant difficulty in studying the health of populations of the gopher tortoise involves the methods used to estimate the number of individuals within a given area. Without a reliable, repeatable method to use when estimating numbers of gopher tortoises, any attempts to monitor changes in populations will be fraught with doubt. Some creative methods of directly counting individuals have been used (Cox et al., 1987), but determining population size directly by use of underground cameras or bucket trapping of burrows can be expensive and time consuming. More commonly, estimates of the number of tortoises in a population have been made on the basis of tortoise burrow surveys (Carr, 1952; Alford, 1980; Cox et al., 1987). Some years ago, researchers realized that if they could use the number of burrows to estimate the number of tortoises, then the difficulty in estimating population sizes would be greatly reduced. Auffenberg and Franz (1982) presented data on more than 100 gopher tortoise burrows in northern Florida, observed for as long as 15 years each, which indicated that an average of 38.6% of the burrows were unoccupied. Based on this relationship, a "correction factor" was suggested:

Number of Tortoises = 0.614 * *Number of Active Burrows*.

It is important to note that abandoned tortoise burrows (i.e., burrows that cannot be used again by tortoises without extensive excavation), which are often quite common, were not included in this calculation. Although Auffenberg and Franz (1982) did not suggest that their correction factor had any general application, and despite the fact that their correction factor could be shown to be unreliable in some cases (Burke, 1989; Godley, 1989; Stout et al., 1989; Breininger et al., 1991; Diemer, 1992b), the Auffenberg and Franz (1982) estimate became the standard correction for converting numbers of burrows to numbers of gopher tortoises. McCoy and Mushinsky (1992a) rigorously examined the use of this technique. They found that the "standard" correction factor overestimated the number of tortoises in 22 of the 26 populations they examined. Furthermore, they showed that environmental variables, such as habitat type, could influence the tortoise-to-burrow ratio. If the "standard" correction factor often yields estimates of numbers of tortoises that are too high, then a false complacency about the well-being of gopher tortoises could be fostered. That is, if most populations are thought to be larger than they really are, then protective measures may be implemented more slowly than needed.

Surveys for gopher tortoises on Federal protected areas in Florida during the late 1980s yielded estimates of populations greater than 1000 individuals on Egmont Key National Wildlife Refuge (NWR), Merritt Island NWR (including Canaveral National Seashore), St. Marks NWR, and Ocala National Forest (McCoy and Mushinsky, 1988, 1991). Using Landsat Thematic Mapper imagery and Geographic Information System (GIS) technology, Cox et al. (1994) estimated that 93 conservation areas in Florida had sufficient habitat to support gopher tortoise populations greater than 200 individuals. Their estimates assumed densities of 3 tortoises/ha, which may be high for some sites. McCoy et al. (2002) provided a detailed comparative analysis of GIS and transect-survey estimates of the amount of gopher tortoise habitat and number of individuals at 44 conservation areas in Florida. Two estimates of total amount of habitat on conservation areas ≥ 20 ha in size differed by about 11%, with survey estimates larger than GIS estimates. The elimination of marginal habitats in the GIS estimates accounted for most of this difference. Two estimates of the total number of individuals on conservation areas ≥ 20 ha in size differed by about 25%. Different assumptions and methods were used to calculate numbers of individuals from GIS and survey data. The GIS method produced reasonable estimates of gopher tortoise habitat assumed to be of high quality. The authors cautioned, however, that results from GIS methods are best considered only a good first estimate. Without supporting information from transect surveys, results from GIS methods must be viewed conservatively.

INTERSPECIFIC INTERACTIONS

The Burrow. — The gopher tortoise burrow provides shelter for many other upland habitat residents and provides the basis for the suggestion that the gopher tortoise is a keystone species (Eisenberg, 1983). The research needed to demonstrate that the gopher tortoise is a keystone species has yet to be done, however. Gopher tortoises excavate deep burrows which provide shelter from environmental conditions and refuge from predation for the tortoises as well as other vertebrate and invertebrate species (Hansen, 1963; Jackson and Milstrey, 1989; Lips, 1991; Witz et al., 1991). An enlarged area at the bottom of the burrow usually contains fecal matter and other organic debris, which serves as an important food source for a suite of other species (Milstrey, 1986). Many vertebrate and invertebrate species have been recorded from gopher tortoise burrows (Young and Goff, 1939; Brode, 1959; Franz, 1986), including protected species, such as the eastern indigo snake (*Drymarchon corais couperi*) and the gopher frog (*Rana capito*) (Auffenberg, 1969, 1978; Diemer, 1986). Some burrow associates have been shown to prefer burrows occupied by a gopher tortoise while others seem to prefer less active burrows (Lips, 1991). In particular, Eisenberg (1983) found that 73.7% of gopher frogs censused were found in active tortoise burrows. Witz et al. (1991) excavated 1019 burrows and found that of the vertebrate symbionts captured, only lizards were found significantly more often in active rather than in either inactive or abandoned burrows. Snakes and other potential symbionts did not seem to distinguish among active, inactive, or abandoned burrows.

As a gopher tortoise excavates its burrow, it produces a habitat disturbance by creating a mound of sand outside the mouth of the burrow that is composed of soils with a relatively low nutrient and organic content. The temperatures at the surface of the soil mounds exhibit greater diurnal fluctuations than adjacent undisturbed areas and the soil mounds are relatively cool during the periodic summer fires (Kaczor and Hartnett, 1990). Soils on the burrow mounds undergo micro-succession that contributes to increased plant species diversity in the habitat surrounding a tortoise burrow. Seedlings that emerge on the burrow mound often are consumed by the resident gopher tortoise.

Diet and Feeding. — As an herbivore, the gopher tortoise interacts with the plants in its environment. Gopher tortoises feed primarily on grasses and other herbaceous plants (Fig. 25-6) (Carr, 1952; Garner and Landers, 1981). Using scat analysis and foraging observations, researchers in central Florida identified 26 families of plants in 68 genera in the diet. The most common families of plants ingested were the Poaceae, Asteraceae, Fabaceae, Pinaceae, and Fagaceae (Macdonald and Mushinsky, 1988). The most common species ingested was wire grass (*Aristida beyrichiana*) (see also Wright, 1982). Young tortoises tend to ingest fewer plants of the family Poaceae and fewer plants with external defense mechanisms and more forbs, such as legumes, than adults (Garner and Landers, 1981; Macdonald and Mushinsky, 1988). The gopher tortoise tends to fall somewhere between a generalist and a specialist forager. While it does prefer some plants over others with respect to their availability in the habitat, it also tends to avoid some fairly common species (Macdonald and Mushinsky, 1988).

Juvenile gopher tortoises show dietary preferences, avoidances, and seasonal differences. At the same site where Macdonald and Mushinsky (1988) studied the foraging habits of mixed age individuals, Mushinsky et al. (2003) studied the diets of juveniles. In all, they observed individuals to ingest 26 genera of plants, of which 16 were ingested positively with respect to their availability in the environment. These 16 genera of plants were ingested more often than one would expect if plants available to gopher tortoises were ingested at random. The most abundant plant genus along the foraging pathways, *Aristida beyrichiana* (wiregrass), was selected negatively (avoided). Grasses (Poaceae) were consumed more during the cooler months than the warm weather months when many herbaceous plants were available. The rank order of plants eaten by juvenile individuals was not different from the rank order of plants eaten by mixed age gopher tortoises.

Figure 25-6. A gopher tortoise, *Gopherus polyphemus,* from Pinellas Co., Florida feeding on non-native grasses. Photo by Marius Moore.

Some items ingested by the gopher tortoise are unexpected. Rocks, for example, may be intentionally ingested as a source of minerals. During a study on gopher tortoise reproduction in central Florida, radiography of adult female gopher tortoises revealed that a large proportion contained rocks in their digestive tracts (Mushinsky and Wilson, unpubl. data). Insects were found in 75% of scats examined and charcoal in 67%, suggesting intentional ingestion of these items (Macdonald and Mushinsky, 1988). Details about the digestive efficiencies of the gopher tortoise have been studied by Bjorndal (1987).

In addition to obtaining water from the plants they consume, gopher tortoises drink water, at least occasionally. Similar to many other savanna-dwelling species, gopher tortoises display a specialized behavior for drinking water (Ashton and Ashton, 1991). The edge of the burrow entrance and the surrounding burrow apron functions as a collecting area for subsurface sheet flow during rain events. A gopher tortoise may respond to rainfall by positioning itself to drink water at the corner of a burrow. A gopher tortoise will drink water by projecting its nose and mouth into the surface of the sand. Individuals were observed drinking for an average of 18 seconds (Ashton and Ashton, 1991).

Predation. — Gopher tortoises are prey for many carnivorous species. The level of predation on gopher tortoise eggs and young individuals is high. For example, over a 2-yr period in South Carolina, 17 of 24 nests (74%) were destroyed (Wright, 1982). In Georgia, an average female is estimated to produce a successful clutch of eggs (i.e., eggs are not destroyed prior to hatching) once a decade (Landers et al., 1980). Common predators of eggs are raccoons *(Procyon lotor*), gray foxes (*Urocyon cinereoargenteus*), striped skunks (*Mephitis mephitis*), and opossums (*Didelphis virginianus*) (Hallinan, 1923; Ernst and Barbour, 1972; Douglass and Winegarner, 1977; Landers et al., 1980). Armadillos (*Dasypus novemcinctus*) dig up and destroy eggs as well. Hatchlings and juveniles, up to an age of 5–7 yrs, have relatively soft shells and are highly vulnerable to predation (Douglass, 1978; Wilson, 1991). From egg laying to one year of age, gopher tortoises in northern Florida were estimated to have a mortality rate of 94.2% (Alford, 1980). Results from a study in central Florida, which also combined mortality of eggs and hatchlings, suggested an annual mor-

Figure 25-7. A selection of carcasses of hatchling gopher tortoises, *Gopherus polyphemus*, observed on a single day in August 1994 on Egmont Key, Hillsborough Co., Florida. A total of 15 were observed. There are no mammalian predators on this island so it is suspected that crows were the major predators. Photo by George Heinrich.

tality rate of 92.3% (Witz et al., 1992). Wilson (1991) found that predation of juvenile tortoises, aged 1–4 yrs, was higher in October–November and April–May than any other two month interval of the year. Juvenile tortoises are known to bask at the mouths of their burrows more often in the spring and fall of the year than during the summer or winter months (Wilson et al., 1994). It appears that a juvenile tortoise, when positioned at the mouth of the burrow to thermoregulate during the cool months of the year, may be quite vulnerable to predation by avian and mammalian predators (Wilson, 1991; Fitzpatrick and Woolfenden, 1978). On Egmont Key, at the mouth of Tampa Bay, where there are no mammalian predators, crows appear to be the most important predators of hatchlings (Fig. 25-7). The shell of a dead tortoise decomposes gradually, but at a fairly predictable rate (Dodd, 1995).

Parasites. — The gopher tortoise and its burrow provide food and shelter for numerous parasites, some of which may be harmful to organisms other than tortoises (see Lavender and Oliver, 1996). One common external parasite of the gopher tortoise is the gopher tortoise tick, *Amblyomma tuberculatum*, which embeds into tortoise skin where it obtains a blood meal. Often, this hard tick can be found by sifting through the soils at the mouth of the gopher tortoise burrow. The gopher tortoise tick is of minor medical or economic importance, with its main host being the gopher tortoise (Milstrey, 1986). A soft tick that parasitizes the gopher tortoise, *Ornithodorus turicata americanus*, is a potential vector of African swine fever, which is a highly contagious and lethal virus of the swine, *Sus scrofa*. The swine disease has yet to be reported in the USA, but the risk of introduction is high (Milstrey, 1986).

Some concern has developed recently about a disease called heartwater. This disease, caused by the rickettsial agent *Cowdria ruminantium,* has devastated hoofed livestock in parts of Africa and has invaded into the Carribean (Deem, 1998). The disease attacks domestic livestock, such as cattle, sheep, and goats, as well as a variety of non-domestic hoofed animals. The African tortoise tick, *Amblyomma marmoreum*, is known to feed on mammals and reptiles when immature, and is known to acquire and transmit *Cowdria ruminantium* under experimental conditions (Peter et al., 2000). The tick has the potential to spread the deadly heartwater disease to domestic livestock (Allan et al., 1998). With the tremendous increase in the popularity of reptiles as pets, and the increase in international trade of reptiles, many of which are infected with ticks, there is growing concern among importing countries that a deadly disease such as heartwater could invade North America through the reptile pet trade (Burridge, 2001). Should the disease invade the southeastern U.S. and infect the gopher tortoise, it could pose another major threat to this species. One would predict a wholesale sacrifice of infected tortoises to protect livestock.

THREATS

Documented Threats. — Although the gopher tortoise is taken illegally for food, the heyday of harvesting gophers for human consumption is long past. The gopher tortoise was a food source for many families during the 1930s and 1940s (Hutt, 1967; Taylor, 1982; Mickler, 1986). Its importance during the Depression was reflected in names like "Hoover Chicken" (Hutt, 1967). Recent reports of illegal harvest are sporadic and localized, but some populations may still be depleted by sustained human predation (Figs. 25-8, 25-9). The increasing proximity of human residences to gopher tortoise populations has resulted in increased predation by dogs and cats. Gopher tortoises less than about 20 cm in CL have relatively soft shells which afford them only limited protection from potential predators, such as domestic dogs. Causey and Cude (1978) described feral dog predation on tortoises in Alabama, and Hawkins and Burke (1989) described dog predation on relocated gopher tortoises in north-central Florida. In Alachua, Sumter, and Marion counties, Ashton (unpubl. data) has observed predation by coyotes (*Canis latrans*). Coyotes were observed waiting behind a

Figure 25-8. Pick-up truck-load of gopher tortoises, *Gopherus polyphemus*, collected illegally for the food trade. Seizure made by Florida Fish and Wildlife Conservation Commission during the early 1980s, at the truck weigh-in station on I-10 between I-75 and Tallahassee. The pullers reported that they were bringing tortoises from the peninsula to the panhandle because they had about wiped out the tortoises in a 50-mile radius from their home base in Calhoun Co., Florida. Photo from FFWC archives.

Figure 25-9. Recently butchered shells of the gopher tortoise, *Gopherus polyphemus*, from Sumter Co., Florida, June 1981. Separation of the carapace from the plastron along the bridge is typical of tortoises that have been butchered for human use. Photo by George Heinrich.

burrow opening for the gopher tortoise to emerge, flipping the tortoise over to prevent its retreat into the burrow, and then eating it.

Human activities pose the greatest threats to the long-term survival of the gopher tortoise in Florida. Humans and the gopher tortoise are in direct competition for limited high, dry ground. The loss of habitat to human activities can take three forms: reduction in area of suitable habitat (true displacement), degeneration of suitable habitat (abandonment of habitat), and increased fragmentation of habitat (increased isolation of populations). The direct influences of humans on the gopher tortoise are manifested through development of upland habitats for urban, agricultural, or mineral recovery uses. The gopher tortoise cannot live in most subdivisions, mall parking lots, agriculturally developed land, and most reclaimed phosphate-mined land. As significant as the direct influences of humans on the gopher tortoise may be, the indirect influences also are great. Suppression of natural fires and the reluctance of the general public to support controlled fires have contributed greatly to a general decline in the quality of most gopher tortoise habitat. The upland habitats occupied by the gopher tortoise are normally dynamic. If fire is excluded from sandhill habitat for just a few decades the quality of the habitat for the gopher tortoise and other members of upland ecosystems decline dramatically. Frequent warm-season burns promote healthy sand hill habitats (Mushinsky and Gibson, 1991).

Conversion of native upland habitats to housing developments, commercial centers, landfills, citrus groves, thickly planted pine monocultures, phosphate and heavy metals mines, and sand extraction pits constitutes the most significant threat to gopher tortoise populations (Landers and Garner, 1981; Auffenberg and Franz, 1982; Diemer, 1986, 1987a; Mushinsky and McCoy, 1996). Suppression of natural fires and limitations of controlled fires, however, cause a rapid decline in habitat quality even in protected areas. Many areas that appear to be suitable gopher tortoise habitat, for example, longleaf pine (*Pinus palustris*)— turkey oak (*Quercus laevis*) sand ridges, actually support low tortoise densities because of increased canopy closure, shrub density, and accumulated ground litter which results from a lack of fire (Diemer, 1987a). Prescribed burning in such areas would reduce the woody component, increase herbaceous ground cover, and foster nutritious tortoise forage plants such as legumes (Landers, 1980; Landers and Speake, 1980; Mushinsky and Gibson, 1991). If all of the publicly owned lands that could support populations of the gopher tortoise were burned frequently and routinely, then we would be increasing greatly the opportunity to expand existing and already protected gopher tortoise populations. Generally, managers of Florida State Parks and other protected lands have insufficient funds and lack the personnel to implement the rigorous burn program necessary to maintain or grow the resident gopher tortoise population.

A comprehensive study of about 50 Florida populations of gopher tortoises (McCoy and Mushinsky, 1988) found several trends resulting from the loss of habitat for the species. Populations residing on sites that had experienced severe area reduction (greater than 25% reduction over the past 20 years), or occurred on sites with greater than 50% tree canopy, or occurred on sites of small size (< 2 ha), tended to have demographic profiles that suggest little recruitment of individuals into the population and abandonment of the site by larger, mature individuals. In contrast, tortoise populations on sites where area reduction was limited or absent, or sites with less than 50% tree canopy, or relatively large sites (> 2 ha), tended to have a high proportion of large, mature individuals and evidence of recruitment of young into the population (McCoy and Mushinsky, 1988).

Comparisons of tortoise populations on true islands and in habitat fragments on the mainland suggested that tortoises are affected similarly by the small size and isolation of the two kinds of areas (McCoy and Mushinsky, 1988; Mushinsky and McCoy, 1994). Both island and mainland tortoise populations show a direct correlation between the number of active and inactive burrows and the area of habitat. Density of burrows, however, decreased as area increased on the mainland, but density of burrows was not related to area on the islands. Also, on the mainland, the ratio of inactive to active burrows (a measure of the tendency of individuals to construct new burrows) increased with area of habitat, and burrow density increased with increasing herbaceous vegetation, but neither of these relations could be demonstrated on islands. Collectively, these findings suggest that tortoises have a greater choice of habitats on the mainland than on islands. Gopher tortoises on islands are confined and may be forced to live in less than ideal conditions. The implications of these findings are profound for tortoises living in small, fragmented “habitat islands” on the mainland. In time, perhaps a few decades, as the quality of their habitat island is degraded, mature adults may be forced to abandon a site in search of better habitat quality. Individuals that may be forced to abandon isolated patches of habitat in areas surrounded by human dwellings seem doomed to perish. Prior the work of Mushinsky and McCoy (1994), the observation of large numbers of active and inactive gopher tortoise burrows in a confined area would likely have been viewed as indicators of a "healthy" population; however, these findings suggest just the opposite. Rather than a signal of a healthy population, large numbers of active and inactive gopher tortoise burrows, relative to the actual number of tortoises, may signal a stressed population (see also Stewart et al., 1993).

Fragmentation of upland habitats by roads and highways increases the opportunity for gopher tortoises to be killed by automobiles. Mortality on highways affects gopher tortoise populations (Landers and Garner, 1981; Lohoefener, 1982; Diemer, 1987a). Landers and Buckner (1981) cited vehicular traffic as the greatest mortality factor on their study area in rural Georgia. Diemer (1987a) observed seven road killed gopher tortoises on a single July day along the southbound lane of the Florida Turnpike; three of the dead tortoises occurred in a 5-km stretch near Orlando. During a 21-month examination of road-killed wildlife, the gopher tortoise was the third most frequently killed species along 19.3 km of highway north of Orlando; the number of tortoises killed (18) was exceeded only by the numbers of opossums (65) and raccoons (47) (J. Roof, unpubl. data). One can only wonder just how many gopher tortoises are killed by automobiles annually in Florida, although some quick calculations suggests that the number could reach into the thousands. The rate at which gopher tortoises are killed on highways is greater in urban than rural areas for two reasons. The heavy automobile traffic in urban areas increases the likelihood of death for any tortoise on a highway, and the more or less continuous sprawl of urban areas increases the likelihood of displacing tortoises which causes them to venture onto highways in search of new habitat.

To appreciate fully the consequences of habitat loss, we need to review some facts about the upland habitats that may support gopher tortoises. Gopher tortoises are most frequently associated with xeric uplands, especially sandhill and scrub habitats (Auffenberg and Franz, 1982; Garner and Landers, 1981; Diemer, 1986). Because these habitats have been (and still are) in high demand for urban development and other human activities, their rate of destruction is alarming. In the 1960s, scrub habitat covered approximately 1.03 million acres of Florida (Davis, 1967). But only 422,000 acres remained by 1990 (Kautz, 1993; Kautz et al., 1993), and much of that has been developed or cleared for agriculture during the 1990s. In the 1960s, sandhill habitat occupied about 6.9 million acres in Florida (Davis, 1967), but less than 851,000 acres remained by 1990 (Kautz et al., 1993), and it also has undergone further reduction during the past decade. A conservative estimate is that less than 20% of the xeric upland habitat that existed in the 1960s remained in 2000. If the rate of loss of gopher tortoise habitat is indicative of the rate of loss of the gopher tortoise, then we estimate at least an 80% decline in the gopher tortoise in Florida since the 1960s. The decline is likely greater, however, because as humans have developed the xeric lands, they also have altered the burn cycles of the surrounding undeveloped uplands, which translates into habitat degradation for the gopher tortoise.

No other southeastern state rivals Florida in the magnitude of urban development (Diemer, 1987b). According to the Florida Chamber of Commerce, the population of Florida is expected to grow at a minimal rate of 2% per year through the year 2010. Continuous urbanization is predicted on both coastal ridges and along Interstate Highway 4 between Tampa and Daytona Beach (Fernald, 1981). Remaining unprotected scrub and flatwoods habitats on the extreme southeastern and southwestern coasts will disappear unless they are protected from development in the immediate future. Similarly, very rapid habitat loss and tortoise population fragmentation are occurring near Orlando and on the Brooksville Ridge. Even opportunities for habitat restoration and subsequent re-introduction of gopher tortoises will diminish as former orange groves in central and south Florida are converted to housing developments. In summary, the future of the gopher tortoise is threatened by tremendous growth of the human population, which causes expanded use of upland habitats, increases fragmentation of existing parcels of land, increases the likelihood of road kills, and decreases the opportunity for the proper management of the fire-dependent habitats (McCoy et al., 2006).

During the past decade or so, upper respiratory tract disease (URTD) has also been identified as a potential threat to the gopher tortoise (Brown et al., 2002). We may never know if humans had any role, direct or indirect, in causing and/or spreading the disease in the gopher tortoise. Many biologists suspect that URTD has a long history as a gopher tortoise disease and that we have recently discovered the disease because more biologists are now studying the species. It is possible that URTD was introduced to the gopher tortoise by humans through the pet trade, although the widespread nature of the disease does not support this notion. Furthermore, one of the organisms known to cause URTD is the same organism that causes the disease in the desert tortoise (Brown et al., 1994, 1999), suggesting that the disease has a long evolutionary history. Perhaps the tremendous amount of development of uplands and fragmentation of formerly large populations of gopher tortoises during the past several decades have increased levels of stress and thereby lowered the resistance of the gopher tortoise to the pathogens that cause URTD. Perhaps a more virulent form of the pathogen has evolved. Although we may never know the origin of URTD, we can investigate how humans today may be affecting the spread and severity of this disease.

Although much attention and research have been directed toward increasing our understanding of clinical aspects of URTD, virtually nothing is known about the ecology of the disease. In particular, fragmenting formerly large populations of the gopher tortoise into numerous small isolated ones may exacerbate the effects of the disease. Gopher tortoises in small isolated populations likely have increased contact with their neighbors, thereby increasing the potential to spread the disease and the probability that many individuals within the small isolated population will be exposed to the disease. In effect, the detrimental aspects of the disease may be intensified in small populations simply because of the small numbers of individuals that may survive the disease. A small population, especially a population of long-lived organisms with a slow rate of reproduction, is less likely to recover from a population crash than a large population. Additionally, prescribed burning often becomes more difficult in habitats surrounded by development, and the resulting habitat degradation may also be a source of physiological stress because food resources are depleted. Disturbance from humans and dogs can also increase in fragmented habitats. Unfortunately, our ability to determine what role these "stresses" might play in URTD transmission and spread currently suffers from an inadequate understanding of exactly how such factors negatively affect gopher tortoise populations (Berish et al., 2000; McCoy et al., 2005).

Upper respiratory tract disease has been observed in both captive and wild gopher tortoises in Florida (Beyer, 1993; Epperson, 1997; McLaughlin, 1997; Smith et al., 1998; Berish et al., 2000; McLaughlin et al., 2000; Gates et al., 2002; Seigel et al., 2003). *Mycoplasma agassizii* is known to be a causal agent of URTD in both the gopher tortoise (Brown et al., 1999) and the desert tortoise (Schumacher et al., 1993; Brown et al., 1994). Recently, other *Mycoplasma* species and possible strains have been isolated from the nasal passages of wild gopher tortoises (Berish et al., 2000; Brown et al., 2001, 2003). Early in the disease cycle, clinical signs may be difficult to ascertain (e.g., a slight swelling of the eyelids). Later in the disease cycle, clinical signs of URTD can include nasal discharge, ocular discharge, swollen eyelids, conjunctivitis, eyes recessed into the orbits, and dullness to the skin and scutes (Fig. 25- 10) (Jacobson et al., 1991; Schumacher et al., 1993; Brown et al., 1994; McLaughlin, 1997); however, some infected individuals may remain asymptomatic (McLaughlin et al., 2000). This disease is highly contagious and is transmitted by close contact between tortoises (McLaughlin, 1997), as during courtship or male combat. Clinical signs may appear within 1–2 wks post-exposure, but it takes 6–8 wks for an exposed gopher tortoise to develop a detectable immune response (McLaughlin, 1997). Because mycoplasmas (bacteria lacking cell walls) can be difficult to culture, a blood test has been developed to detect antibodies to *M. agassizii* in desert tortoises (Schumacher et al., 1993) and has been refined for use in gopher tortoises. This test is currently the most effective, rapid, and inexpensive way to detect exposure to this pathogen (Schumacher et al., 1997). However, the test indicates only whether a gopher tortoise has been exposed to the pathogen and cannot distinguish between asymptomatic carriers (which may pose a threat to healthy animals) and tortoises which have cleared the pathogen and are no longer infected (Brown et al., 1994; Schumacher et al., 1997). Consequently, a polymerase chain reaction (PCR) test was developed to detect actual presence of *Mycoplasma* in gopher tortoise nasal secretions (Brown et al., 1995).

Figure 25-10. Close-up of head of gopher tortoise, *Gopherus polyphemus*, from Duval Co., Florida, showing nasal discharge and palpebral edema (swollen eyelids), common symptoms of Upper Respiratory Tract Disease (URTD). Photo by Lori Wendland.

Exposure to URTD may not necessarily confer immunity on an individual; in fact, some data suggest gopher tortoises exposed a second time may become ill more quickly than when initially exposed (McLaughlin, 1997). The studies regarding second exposure were conducted under laboratory conditions, however, and more field research is needed to determine if post-exposure immunity occurs in wild tortoise populations. Based upon some recent findings from captive tortoises in zoos, seropositive individuals may be able to lead apparently healthy lives for many years. In captivity, transfer of antibodies from females to their offspring has been documented in both gopher tortoises (McLaughlin, 1997) and desert tortoises (Schumacher et al., 1999).

Mortality correlated with URTD has been high in some desert tortoise populations (Jacobson et al., 1991, 1995; Berry, 1997), but little is known about the effect of the disease on gopher tortoise populations (Berish et al., 2000; McLaughlin et al., 2000; Brown et al., 2003). Symptomatic gopher tortoises have been found with some regularity on Sanibel Island in Lee County (McLaughlin, 1990; Beyer, 1993), and at least one Sanibel Island population appears to have experienced a 25–50% reduction in breeding age adults (McLaughlin, 1997; McLaughlin et al., 2000). This barrier island has a history of gopher tortoise releases, primarily animals used in tortoise races during the 1970s (Dietlein and Smith, 1979). Numerous dead gopher tortoises have been found at a state preserve, a water management district landholding, a federal facility, and two mitigation parks (Gates et al., 2002; Seigel et al., 2003; M. Allen, *pers. comm.*; B. Blihovde, *pers. comm.*; M. Barnwell, *pers. comm.*). We cannot assume that gopher tortoises residing on public lands are safe from diseases or other threats.

Blood samples have been collected at various sites around the Southeast to determine exposure to the *Mycoplasma* that causes this disease. Seropositive (i.e., exposed), wild gopher tortoises have been found in several locations in Georgia and Mississippi (Smith et al., 1998; R. Birkhead, *pers. comm.*; D. Rostal, unpubl. data; D. Epperson, unpubl. data), and in more than a third of Florida's 67 counties (Beyer, 1993; Epperson, 1997; McLaughlin, 1997; Smith et al., 1998; Berish et al., 2000; McLaughlin et al., 2000; Seigel et al., 2003). On Sanibel Island, 85% of tortoises tested were seropositive for exposure to the pathogen. Exposure to the disease has been detected on numerous public lands in Florida (Epperson, 1997; Smith et al., 1998; Berish et al., 2000; Seigel et al., 2003; McCoy et al., 2005). As available habitat on private lands is converted to development, the health of tortoise populations on public lands becomes more important. Data are needed regarding URTD-related effects on mortality in tortoise populations. Although seropositive tortoises have been found at the previously noted sites with tortoise die-offs, the mortality has not yet been linked directly to URTD. Several recent (McCoy et al., 2005) and ongoing studies are investigating the effects of URTD on gopher tortoise populations; results of these studies should help elucidate anthropogenic and habitat-related influences.

Many areas of uncertainty remain regarding URTD. The disease, like many other diseases, has the potential to influence survival and reproduction of individual tortoises but definitive data are lacking (Brown et al., 2003). More research is warranted to rule out transmission between female and offspring, and transmission from contact with burrows of infected tortoises; current thought is that these types of transmission are either minimal or unlikely (Brown et al., 2003).

A tendency exists for humans to use resources to combat diseases in sick individuals that might be better used to protect healthy ones. We already know that upland habitats available to the gopher tortoise in Florida have long been under siege and the threat imposed by loss of habitat is going to increase in the future. We know also that land managers in Florida are strapped for funds to manage public lands properly, yet we know that lack of management of gopher tortoise habitat for just a few decades can have a strong negative effect on the population that may take centuries to overcome. A wise use of all resources aimed at protecting and increasing current gopher tortoise populations for future generations seems prudent. The purchase, protection, and proper management of upland habitats for the gopher tortoise are the most direct means to insure the future of the species.

Potential Threats. — A great deal of uncertainty exists regarding the future of the gopher tortoise in Florida. Much of our present uncertainty is the same as that expressed by Auffenberg and Franz (1982), when they completed the first systematic gopher tortoise surveys throughout the state between 1959 and 1975. They warned about a rapid rate of extirpation of the gopher tortoise in certain portions of its range, sometimes caused by human consumption (Taylor, 1982; Diemer, 1986), but mostly caused by human disturbance of one sort or another. Auffenberg and Franz (1982) predicted a near total loss of gopher tortoise habitat in Florida by the year 2025. If humans continue to move into and develop the state as they have for the past 25 years, then it seems likely that their prediction will be accurate, except for those gopher tortoises that reside on protected areas. Of course, without proper management, populations on protected areas will also eventually perish (McCoy et al., 2005).

A major contributor to the survival of local populations will continue to be proper management of the habitat. In the absence of fire for only a few decades, good quality gopher tortoise habitat can become too overgrown to support the grasses and herbaceous vegetation needed as food. Gopher tortoises abandon overgrown habitat. When an individual in an overgrown patch of habitat attempts to move, there often exists no alternative suitable habitat to which they can move without crossing roads. The large number of tortoises killed by vehicles on roads likely reflects the increased frequency with which gopher tortoise are forced to move in search of good quality habitat.

The general decline in habitat quality may be accelerated by the invasion of non-native plants into upland habitats. Previously we emphasized the dependence of the gopher tortoise on relatively open land where grasses and herbaceous plants can thrive, however, an aggressive, invasive grass exists that may cause displacement of gopher tortoise populations. Cogon grass (*Imperata cylindrica*), an Asian invasive exotic, is a serious problem on rangelands, pastures, roadsides, and reclaimed phosphate mines (Shilling et al., 1997). It can form a continuous monospecific ground cover that is hostile to the gopher tortoise. With half-inch wide leaves that can grow to a meter in length, and a fibrous root system composed of branched rhizomes, Cogon grass can form monospecific expanses of dense ground cover that will eliminate all other vegetation. Such a dense ground cover could force a population of gopher tortoises to abandon their habitat in search of better quality land. Cogon grass is particularly aggressive in disturbed areas, such as roadsides or reclaimed phosphate mined land.

STATUS

In 1987, the U.S. Fish and Wildlife Service gave formal Threatened status to gopher tortoise populations that occur to the west of the Mobile and Tombigbee Rivers in Alabama, Mississippi, and Louisiana (Wilson et al., 1997). The total area occupied by the threatened western populations is about 148,000 ha (USFWS, 1987). In five of the six states in which the gopher tortoise occurs, it has some form of state protection. In Mississippi, the species is listed as Endangered; and in Alabama it is a Protected Nongame Species. In Georgia the species is listed as Threatened, and in South Carolina, as Endangered. In Louisiana the gopher tortoise is not protected by state laws, rather, it is Federally protected. Populations residing in Washington, northern Mobile, and southeastern Choctaw counties in Alabama also are afforded Federal protection.

The legal status of the gopher tortoise in Florida was previously ambiguous; the Florida Committee on Rare and Endangered Plants and Animals (FCREPA) listed it as a threatened species (McDiarmid, 1978; Moler, 1992), however, the gopher tortoise was listed as a Species of Special

Concern by FFWC in 1979, but very recently in 2006 uplisted it to Threatened (see below).

Threatened species, according to FCREPA, are "species that are likely to become endangered in the state within the foreseeable future if current trends continue" (Moler, 1992). Endangered species, on the other hand, are "species whose numbers have already declined to such a critically low level or whose habitats have been so seriously reduced or degraded that without active assistance their survival in Florida is questionable" (Moler, 1992). When a threatened species turns into an endangered species, therefore, is simply a matter of expert opinion. We suggest that the uncertain numbers of protected individuals; the increasing difficulty in managing the habitats of protected individuals; the possibility that remaining populations may be devastated by a variety of threats, and the relatively poor ability of long-lived, slowly-reproducing species to recover any of the threats means that the gopher tortoise already is endangered in much of Florida. If we wish to maintain the gopher tortoise's historical distribution in all 67 counties and its significant ecological role in enhancing Florida's biodiversity, then the degree of endangerment of the gopher tortoise in each of these counties must be assessed, and quickly.

As we were making final preparations for the publication of this chapter, the Florida Fish and Wildlife Commission (FFWC) adopted Florida Administrative Code 68A 1.004 and 68A 27 and implemented new standards for listing species (see *Guidelines for Using IUCN Red List Categories and Criteria*, March 2004). A species may be listed if it meets one of several criteria for threatened or endangered status. One aspect of the protocol places emphasis on population trends during the past three generations, nearly 100 yrs for the gopher tortoise. The *Gopher Tortoise Biological Status Report* recommended that the gopher tortoise be listed as a Threatened species because evidence exists that the number of individuals in the Florida population has declined by more than 50% in three generations. As a result, in 2006 the FFWC listed the gopher tortoise as Threatened in the State of Florida and changed regulations regarding testing individuals for URTD.

CONSERVATION OPTIONS AND SOLUTIONS

We believe that a three-part approach is needed to ensure a healthy future for the gopher tortoise. First, the most certain long-term conservation method is the outright purchase of land known to support populations of gopher tortoises by individuals or agencies willing to conserve them. Second, education of private land owners and public land managers about the value of active management of habitats known to support tortoise populations is needed to promote the health of existing gopher tortoise populations. State and local governments should be encouraged to adopt specific legislation to establish conservation easements and tax incentives to encourage landowners to maintain gopher tortoise habitat. Third, re-introduction (defined as the movement of individuals to replenish an area once inhabited by the species) of the gopher tortoise to suitable habitats on lands from which it has been extirpated or lands that have been restored to suitable habitats. This effort is needed to extend the species' ever-diminishing distribution.

A better understanding of the ecology of infectious diseases would be beneficial to any re-introduction program for the gopher tortoise. Likewise, a comprehensive understanding of the social structure of gopher tortoise populations would facilitate proper re-introductions. We know gopher tortoises interact with one another often, especially during the spring and fall breeding seasons, yet we can only guess about the influence of human intervention on the social structure of populations.

Public ownership of upland habitats known to support gopher tortoise populations is the most direct method of protection. Roughly 18.7% of the terrestrial area of Florida lies in conservation land (Cox, 1992). Exactly how many of these publicly held protected areas can support the gopher tortoise, and more importantly, how much of this land actually supports gopher tortoises today, are open questions. During the past decade or so we have witnessed the expansion of several Florida state parks that support populations of gopher tortoises. During more recent years, however, we have witnessed a decline in the resident gopher tortoise populations and a decline in active management practices at most state parks because of inadequate resources to execute controlled burns, and inadequate funds to support the parks properly (McCoy and Mushinsky, 1992b; McCoy et al., 2005; McCoy et al., 2006).

Recommendations for specific management procedures for gopher tortoises have been made by Landers and Speake (1980) for Georgia, Wright (1982) for South Carolina, Lohefener and Lohmeier (1984) for Louisiana, Mississippi, and Alabama, and Auffenberg and Franz (1982), Diemer (1986), and Diemer-Berish (1994) for Florida. Conservation measures include habitat management, establishment of preserves, protection from over-harvest, and public education (Landers, 1980; Diemer, 1986; Diemer-Berish, 1994).

Several counties in Florida have established local programs to purchase environmentally sensitive lands for public ownership. For example, Hillsborough County in central Florida has had an Environmental Land Acquisition and Protection Program (ELAPP) in place for most of the 1990s. By 1999, the Hillsborough County ELAPP had purchased about 35,000 acres of environmentally sensitive land. Soil surveys (Rob Heath unpubl. data) allow us to evaluate what proportion of that land might support the gopher tortoise. About 55% of the land was characterized as having mesic soils (typical of pine flatwoods and dry prairies which support relatively low densities of tortoises) and 10% was xeric soils (typical of sandhill and scrub habitats, which support relatively high densities of tortoises). It appears that although the gopher tortoise has benefited from the purchase of environmentally sensitive lands in Hillsborough Co., only a relatively small fraction of the purchased land supports them in relatively high densities.

Threats to the gopher tortoise, such as disease, harvesting, and habitat degradation, may have long-lasting consequences for the local tortoise population. Gopher tortoise populations in the panhandle of Florida likely are still recovering from the great harvest of adults for human food during and after the Depression. While it is appealing to attempt to protect nests and hatchlings from predation, human or otherwise, the fragile demography of the gopher tortoise is best served by protecting individuals that have already survived to adulthood. Because the gopher tortoise is long-lived, and eggs, hatchlings, and juveniles are vulnerable to predators, conservation efforts aimed at protecting adults likely will provide the greatest benefits for future populations of the gopher tortoise.

As is true for any species at risk, providing an opportunity and a forum for the education of individuals who own and/or manage their habitats potentially can have a great benefit. For example, as a result of gopher tortoise surveys on about a dozen state parks, McCoy and Mushinsky (1991) were able to make specific suggestions to improve the quality of the habitat for the gopher tortoise at each of those sites. Such efforts to work with land managers should not be limited to those who manage public lands, however. At present, many private land owners seem to be unaware of the land management practices needed to maintain healthy populations of gopher tortoises. Perhaps future state and locally funded programs might consider making such public education a high priority.

Efforts to educate the citizens of Florida need to reach out beyond traditional educational outlets. The Florida Fish and Wildlife Conservation Commission (FFWC) produced and distributed a poster depicting the protected status of the gopher tortoise when legal hunting for the tortoise was banned. Such posters are needed and valuable and additional posters that inform the public about the plight of the species might be considered in the future. Furthermore, a poster designed to inform the public about URTD might function to decrease the spread of the disease if people are discouraged from releasing “rescued” individuals into public lands. The public should be alerted to the potential damage that can be accidentally thrust upon a healthy tortoise population by moving individuals from sick to healthy populations or by releasing sick individuals into a population. Humans with good intentions but naive about URTD and other diseases could impart devastating affects on a tortoise population by “rescuing” a single sick tortoise and releasing it into another population. Brochures outlining habitat management techniques, and slide series/videos on gopher tortoise conservation are educational tools that should be developed and distributed throughout the species’ range. Educational efforts on behalf of the gopher tortoise should emphasize that xeric habitats, as well as wetlands, have aesthetic and biological value (Diemer, 1986).

Proactive management of upland habitats not only increases available gopher tortoise forage and nesting sites (Landers and Speake, 1980), but also affects growth rates and age to sexual maturity (Mushinsky et al., 1994). Healthy populations of the gopher tortoise are found most frequently in upland habitats with a grassy and herbaceous laden ground cover (Auffenberg and Franz, 1982; McCoy and Mushinsky, 1988). A proactive management plan for the remaining large parcels of land that support the gopher tortoise will benefit not only the resident tortoises but also the humans that reside nearby. The extensive wildfires following the wide-spread droughts experienced in Florida in the late 1990s and early 2000s have taught us the extreme dangers associated with poor land management practices. The upland habitats of Florida are fire dependent ecosystems. They accumulate fuel quickly and burn at a high frequency. If humans act to suppress fire, as we have done for most of the 1900s, then natural fires become catastrophic and extremely destructive. Frequent controlled burns of uplands benefit the wildlife that resides in the uplands and the humans that live nearby (Mushinsky and Gibson, 1991).

In north Florida, a private gopher tortoise management area has been developed by Ray Ashton (Ashton et al., 1994). The goal of the management area is to establish and maintain optimal habitats for gopher tortoises, burrowing owls (*Athene cunicularia*), and American kestrels (*Falco sparverius*). Three gopher tortoise preserves, totaling about 60 ha, have been created. Each preserve is surrounded by fencing, above and below the ground, to insure the integrity of the designated preserve sites. These preserves have not been in place for a sufficiently long time period to draw any meaningful conclusions about their success or future; however, the outlook is promising. The concept of a multiple species approach to on-site mitigation for non-competitive species is one that should appeal to developers and conservation biologists alike, and has great promise for these taxa.

Because the gopher tortoise is long-lived, it is important that biologists and land managers think about long-term survival as they plan for the future of this species. At any point in time, apparent differences between suitable, marginal, and poor quality gopher tortoise habitats may be temporary or misleading, and may cause some small or partially overgrown areas to be dismissed too quickly as unworthy of conservation effort. It is important to view habitat quality for the gopher tortoise as a dynamic gradient, based on a cycle of fire, hurricanes, or other land-altering events. Area reduction and habitat degradation are two of the greatest threats to the future of tortoise populations: as each of these threats becomes greater, the probability of extirpation increases. In combination, the effects of area reduction and habitat degradation are likely to increase local extirpation probability in a synergistic fashion. Hence, while tortoises on large areas of land are in need of continuous monitoring, tortoises on small areas are likely to be in need of continuous management as well. Future research priorities aimed at improving methods for managing small areas should include the delineation of the consequences of gopher tortoise translocation (defined as the deliberate and mediated movement of wild individuals into an existing population of conspecifics) on the existing populations at recipient sites. Future research priorities also should include derivation of methods that increase the likelihood that translocated and re-introduced tortoises establish residency at recipient sites.

Gopher tortoises can be maintained on relatively small managed parcels of land for a few decades or so (Landers and Speake, 1980), but large parcels (up to several hundred hectares) would reduce the population effects of emigration and certain sources of mortality. Areas as small as of 10–25 ha of favorable, actively managed habitat should be set aside for populations occupying lands slated for development (Cox et al., 1987). McCoy and Mushinsky (1988) surveyed a wide variety of sites for the gopher tortoise, including some of the largest federal lands in Florida and numerous relatively small parcels with small and unprotected populations of tortoises. They recognized the importance of protecting, if possible, large areas (tens to hundreds of hectares) of gopher tortoise habitat, but also recognized the value of the numerous small isolated populations that exist throughout the range of the tortoise. McCoy and Mushinsky (1988) pointed out four themes to be considered regarding the protection of gopher tortoises: (1) the gopher tortoise functions as a “keystone species” (Campbell and Christman, 1982; Eisenberg, 1983; Jackson and Milstrey, 1989), and therefore merits special consideration in ranking conservation priorities; (2) fragmentation of gopher tortoise populations will continue to increase, and relatively-large tracts of habitat will rapidly become rare; (3) conservation of large areas of gopher tortoise habitat is not without risk; and (4) conceiving of fragmented gopher tortoise populations as metapopulations suggests alternate conservation strategies.

The conservation of “large” areas of land has the potential to create false security about the future of resident tortoises. Because of the lack of a coordinated effort to catalog known populations of the gopher tortoise in Florida, the number of large areas, with reasonably large populations of tortoises, can only be approximated (e.g., Cox et al., 1994; McCoy et al., 2002; B. Stys, unpubl. data). We do know that development patterns throughout peninsular Florida are such that it is not practical to set aside even 10 ha of land in many places. Furthermore, continuous habitat management is essential to maintain the gopher tortoise, especially on relatively small isolated habitat patches. Yet, large areas with many resident gopher tortoises typically have not been managed with the gopher tortoise in mind (McCoy and Mushinsky, 1992b). Populations of tortoises on isolated parcels of land are vulnerable to stochastic disturbances that may have profound effects on their well-being, effects which are exacerbated if the areas are not properly managed. The sensitivity of gopher tortoise demographic factors in general, may make tortoise populations even more vulnerable to extirpation from disturbance events than other long-lived vertebrates. McCoy and Mushinsky (1988) believed it unwise to place full emphasis upon the single large area notion of conservation. Rather, they proposed that greater emphasis be placed upon alternate conservation strategies for the gopher tortoise in Florida. Whenever feasible, large areas of land should be secured, with the stipulation that rigorous management practices be employed to monitor continuously the demographic health of the resident population. In parallel with the securing of large areas, however, large numbers of small areas also should be secured. Such small areas allow “banking” of genetic diversity, as well as of individuals, for decades or perhaps longer. Management practices tailored to these small areas might even be able to perpetuate the populations for tens of decades or longer. Ultimately, however, large, properly managed preserves will be necessary to insure the future of the gopher tortoise in Florida.

While biologists recognize the value of preserving large parcels of land for the future well-being of the gopher tortoise, the literature is not clear about how large is large enough. Researchers have assumed that the smallest population that can maintain itself consists of about 50 adult individuals (this number is derived from genetic considerations). Cox et al. (1987) suggested that, to maintain 50 adult individuals, an area of 10–20 ha was required. Their estimate was based on inclusion of about 80 burrows and the average distance an individual travels within its home range. Eubanks et al. (2002) expanded the minimum area estimates to maintain 50 adult gopher tortoises. Based on a year-long study of home ranges of individuals tracked with radiotelemetry, they estimated the minimum area needed to maintain 50 adult tortoises was from 25–81 ha. Had the researchers not tracked individuals and based their calculations on burrow density alone, the minimum area to maintain 50 adults would have been 19–41 ha.

Other researchers used a different approach and logic to determine the minimum area needed to sustain a population of the gopher tortoise. Based on data from 19 populations for which the actual area inhabited by gopher tortoises was determined, McCoy and Mushinsky (unpubl. data) observed that tortoise densities tended to plateau at about 100 ha, and typically included about 500 burrows on large parcels of land. In parcels of land less than 100 ha, tortoise densities tend to be relatively high, suggesting that they are crowded by artificial boundaries and not free to move about as they would if the boundaries did not exist. Therefrore, 100 ha was considered to be the minimum area needed to maintain a population of gopher tortoises in the current setting. Additional security for the resident population can be gained by providing a buffer zone around the perimeter of the 100 ha.

In 2001, the Florida Fish and Wildlife Conservation Commission sponsored a population viability assessment for the gopher tortoise in Florida (Conservation Breeding Specialist Group, 2001). Population Viability Analysis (PVA) was conducted based on estimates of age specific mortality and fecundity rates. Spatial analysis was based on real and potential gopher tortoise habitat using GIS technology. Much of the data used for the PVA were estimated with high levels of uncertainty. Nevertheless, demographic sensitivity analysis indicated that mortality rates of juveniles (up to one year of age) and adult females were the primary drivers of overall growth dynamics in populations of the gopher tortoise. Research efforts and broad management actions should be directed preferentially at these aspects of the species’ life history.

Very little information is available regarding the capacity of the gopher tortoise to recover following a major decline in population numbers. The severely depressed densities of gopher tortoises in the panhandle of Florida, reflecting heavy human predation many decades ago, suggest that the recovery process is a slow one, as one might predict based on the general life history of the species. Using population models, Cox (1989) estimated minimum population sizes needed for a re-introduction of tortoises to an unoccupied site. He suggested that the persistence of small populations was longer for mixed populations consisting of subadults and adults than those of composed strictly of adults.

The details of any habitat management program aimed at maintaining or increasing the number of gopher tortoises present in an area must be site specific; however, the goal should be to produce a mosaic of vegetation density by altering the frequency and timing of controlled burns (Mushinsky and Gibson, 1991; Diemer-Berish, 1994). A multi-aged forest is desirable, ranging from treeless areas with high diversities and abundances of grasses and herbaceous plants, to areas with tree canopies that cover about 30–50% of the area. Summer burning mimics the natural fire cycle, promotes flowering of annual herbaceous plants, and facilitates the production of seeds by many of the grasses. Sandhill habitat responds well to summer burns on a 2–7 yr periodicity (Mushinsky, 1985; Mushinsky and Gibson, 1991). Pine flatwoods also should be subjected to summer burns on a 2–5 yr cycle to encourage the production of the plants used as forage by gopher tortoises. Sand pine scrub habitat burns less frequently, perhaps every 15–50 yrs. A highly overgrown site may be first burned during the winter months to reduce the risk of a very hot fire and to thin the canopy prior to implementing a cycle of summer burns which promote vegetative regrowth.

Management needs of gopher tortoises in disturbed habitats such as pastures, old fields, and power lines have been poorly studied. Gopher tortoises seem to be attracted to powerline and pipeline rights-of-way where there is no tree canopy and grass cover is dense compared to surrounding overgrown habitats. The attraction is an illusion—gopher tortoises accumulate in open areas when the surrounding lands are not burned and are overgrown. Gopher tortoise densities in these disturbed habitats typically exceed those of surrounding natural areas (Auffenberg and Franz, 1982). Research on densities and foraging behavior of gopher tortoises in pasture land preserves currently is being conducted, and preliminary findings indicate an average tortoise density of 2 tortoises/acre in improved pasture (Ashton et al., 1994). In managed grassland preserves, tortoises exhibited higher rates of recruitment and population growth after five years than rates described for some natural habitats (Ashton et al., 1994). Site-specific plans will be needed for tortoises in disturbed habitats and may include prescribed fire, mechanical shrub removal, and/or mowing.

Longleaf pine is the preferred pine species for planting in commercial pine stands on most well-drained sites (an exception is the Ocala Scrub in central Florida, for which the sand pine, *Pinus clausa*, is the preferred species). Sand pine should not be planted on former sandhill sites. The dense growth form of this species allows little or no sunlight to reach the forest floor, thereby reducing potential tortoise forage (Landers and Buckner, 1981). Thinning of trees should be undertaken to keep the canopy sufficiently open to allow sunlight to penetrate. Minimally disruptive site preparation (e.g., single drum chopping) is favored over more intensive methods such as bedding or root-raking. Previous studies have demonstrated that gopher tortoises can dig out following chopping treatment on deep, sandy soils (Landers and Buckner, 1981; Diemer and Moler, 1982). Recommended fire frequencies and seasons for pine plantations are similar to those on sandhill. A 1–2 yr interval is recommended if only winter fires are feasible.

We have discussed in detail two of the three issues associated with contemporary changes to the habitats typically occupied by the gopher tortoise, those of area reduction and habitat degeneration. The third component, habitat fragmentation, is a product of the problem caused by area reduction. As formerly large populations of gopher tortoises are forced to live on smaller and smaller parcels of land, the distance between neighboring populations increases, and the probability of successful exchange of individuals between populations diminishes. The steps needed to counteract the inevitable isolation of gopher tortoise populations created by fragmentation of upland habitats are not known at this time. In fact, our knowledge base is not sufficient to allow us to sort out the separate, but interactive, effects of area reduction and habitat fragmentation with any degree of certainty. Clearly, small populations are more vulnerable to extirpation than large populations. The added consequence of isolation by fragmentation will likely increase the probability that small populations will go extinct.

To evaluate the efficacy of the various management methods that may be used, gopher tortoise populations should be monitored periodically. Monitoring the status of the species statewide is an enormous undertaking. Remote sensing (e.g., Landsat/GIS data) appears to have the most potential for long-term large-scale monitoring of gopher tortoise habitat status. Monitoring of small populations may be warranted as well. Gopher tortoise translocation sites (see below), for example, should be surveyed 3–5 yrs post-movement. Possible methods include bucket-trapping gopher tortoises (accurate but labor-intensive), video camera surveys of burrows (limited to large burrows because of the large size of the camera relative to the size of the burrows), and burrow surveys (Cox et al., 1987). Because of time and labor constraints, burrow surveys are the most commonly used methods of surveying gopher tortoise populations.

Burrow surveys must be done carefully to be accurate. In particular, we know that not all burrows are occupied by a tortoise, and we know that an average tortoise will use several burrows during one activity season (McRae et al., 1981b). Nevertheless, if done with proper care, a researcher can estimate the number of gopher tortoises in various size classes based solely on their burrows, without ever encountering a gopher tortoise. To estimate numbers of tortoises in a given area based upon counts of burrows, the burrows are counted and classified as active, inactive, or abandoned to reflect the perceived time since a tortoise last occupied the burrow (McCoy and Mushinsky, 1992a). To evaluate the size distribution of the gopher tortoises in a population, the diameter of each burrow is measured. The burrow count data are multiplied by a correction factor. Unless site-specific correction factors are determined (see Cox et al., 1987), correction factors of 0.6 for disturbed sites, 0.5 for sandhill, and 0.4 for scrub and flatwoods are probably more accurate than using 0.614 for all habitat types. McCoy and Mushinsky (1992a) reported that the linear regression of log number of tortoises on log number of active burrows was the best predictor of number of gopher tortoises for the sites they studied. Witz et al. (1991) found young tortoises in a few burrows that appeared abandoned. If such behavior by young tortoises is widespread, then most current methods to survey gopher tortoises may underestimate the numbers of gopher tortoises. The cryptic nature of young gopher tortoises, their small size, and their propensity to place burrows near other structures on the ground all contribute to the difficulty of attaining an accurate estimate of young tortoises in a population.

Mitigation requirements of the State of Florida for gopher tortoises on development sites have evolved over the last decade or so. Many upland sites, however, are developed without prior review by wildlife agencies, and inequities in review and permitting requirements allow the unmitigated destruction of both tortoise habitat and tortoises (Diemer, 1989). Current mitigation options in Florida include the following: (a) avoidance of individual burrows during development, (b) habitat protection on- or off-site (usually an area equal to 15–25% of the occupied tortoise habitat being affected), and (c) translocation or re-introduction of tortoises to suitable habitat. In response to the wide-spread occurrence of URTD, a fraction of the gopher tortoise population to be relocated must be tested and found to be seronegative before a permit to move tortoises is issued. The habitat protection option may be fulfilled by contributing to a mitigation banking fund an amount sufficient to buy the requisite acreage in an existing or proposed mitigation park. As of July 2005, nine mitigation banks provided about 10,000 acres of protected land. A developer also may purchase an appropriate amount of land adjacent to public lands and then donate the parcel to the public landowner. Finally, a developer may protect an appropriate-sized area on-site in perpetuity (generally ± 10 ha). About 10,000 acres have been preserved on-site or on land provided by developers for protection of the gopher tortoise. On-site preserves, like other habitat set-asides, require approved habitat management plans. In some cases, on-site preserves incorporate pastures, golf course roughs, and retention areas. Although long-term management can be a challenge, these preserves have high educational value and provide scattered habitat for other upland listed species, such as the southeastern American kestrel, Florida scrub jay, gopher frog, Florida pine snake, and Florida burrowing owl.

Gopher tortoise translocation is controversial, labor-intensive, and time consuming, but the future of the species may depend upon perfecting translocation practices and procedures. Biological concerns include contamination of locally adapted gene pools, disease or parasite transmission, social structure disruption, and dispersal-related mortality (Diemer, 1989). Unfortunately, the rate of loss of uplands is so great that time does not permit the proper assessment of the potential concerns associated with translocation. If, as seems to be the case, the State adopts the policy of “no tortoise left behind” as recently suggested by McCoy et al. (2006), then finding suitable, secure recipient sites will become increasingly difficult with continued development. Such a policy has the effect of forcing the public to deal with the issue of whether gopher tortoise conservation is sufficiently important to slow development of unaltered upland habitats. From 1989 to July 2005, more than 60,000 gopher tortoise have been translocated to make way for development (FFWC, unpubl. data), but untold numbers have been entombed in their burrows under the provisions of “take” permits.

Two additional serious problems associated with moving tortoises have become increasingly apparent: the potential spread of disease and the lack of long-term protection and management of recipient sites. Although under review at the time of writing this chapter, current practices of testing a portion of a group of tortoises to be moved have proved to be inadequate and often with inconclusive results. Many healthy individuals have been killed because some in the groups to be moved tested positive for exposure to a disease such as URTD. Gopher tortoises showing clinical symptoms of any disease should not be translocated anywhere. The potential for disease transmission can be minimized or eliminated by moving tortoises only to sites without resident tortoises. The problem of long-term recipient site security can be addressed by moving tortoises only to previously established translocation sites, public lands, or private lands protected in perpetuity by conservation easements.

As increasing numbers of gopher tortoises are injured by vehicles or dogs; wildlife rehabilitation centers and veterinarians are treating more of these tortoises. Some individuals can be successfully treated and released, but many are of unknown origin, have been held in captivity with other tortoises, and/or have sustained injuries that prevent their release. A list of schools, nature centers, and private individuals willing to accommodate non-releasable gopher tortoises should be compiled. The State of Florida has developed a gopher tortoise adoption program, similar to that which has been developed in Arizona and Nevada for the desert tortoise.

Restocking (defined as the adding of individuals to an already existing population of conspecifics) is a conservation measure that differs from translocation in both intent and technique. The goal of restocking is to enhance severely depleted populations. The goal of translocation, on the other hand, typically is to salvage individuals displaced by development. [Note that if the goal of re-introduction is to replace an extirpated population, rather than to "dump" excess individuals, then it is closely related to restocking.] Restocking efforts must employ the best available source (genetically, socially, and geographically) of individuals for restocking. Translocation efforts may try to find "suitable" recipient sites, but the urgency of most translocation efforts often forces individuals to be placed in less-than-ideal situations. Possible restocking and re-introduction sites for the gopher tortoise include protected lands where they have been overharvested (e.g., Eglin Air Force Base in the Florida panhandle), reclaimed mining lands, abandoned orange groves and pastures, restored former pine plantations, and other "created" tortoise habitats (e.g., areas where the water table has been lowered by drainage) (Diemer, 1989). A list of potential restocking and re-introduction sites in Florida was compiled by FFWC (Berish, 1995). All of these sites should have habitat management commitments, and those on private lands should be secured by conservation easements or other binding agreements. Re-introduction of all ages of gopher tortoises to sites they formerly occupied has been tried in Florida, but the fate of most of these tortoises is unknown (Diemer, 1986). In southern Georgia, about 40% of the tortoises re-introduced into an area remained in that area for three years after their release (Landers and Buckner, 1981). In north Florida, about 30% of re-introduced tortoises were recaptured five years after their release (Diemer, 1987b). Clearly, these studies, and others (e.g., Godley, 1989; Macdonald, 1996), suggest that most tortoises quickly abandon sites to which they have been re-introduced. Relocation (including re-introduction, translocation, and restocking) is not an exact science, and until the methods for efficient and successful relocation are developed, only experienced, well-trained individuals with well-conceived plans should be permitted to make any relocation attempts.

At this time, it is hard to know if a unified conservation strategy for the gopher tortoise exists in Florida, and if one does exist, just what that strategy might be. Collection of the gopher tortoise was banned in 1988, and the use of live gopher tortoises for tortoise racing was abandoned in 1989. Recently, a few gopher tortoise reserves have been established. Furthermore, beneficial habitat management practices have been instituted at many public land holdings, illegal harvest has been reduced, and stronger legislation to protect uplands has been introduced in some parts of Florida. Despite these measures, the gopher tortoise continues to decline in distribution and numbers. Existing populations of gopher tortoises are increasingly fragmented and isolated on smaller and smaller parcels of land. Although it is still often encountered in Florida, the gopher tortoise is much less broadly distributed and much less numerous than before the dramatic influx of humans following World War II. Using GIS methods, Cox et al. (1994) estimated that 93 conservation areas with sufficient habitat of at least 68 ha (170 acres) supporting populations of at least 200 individuals existed in Florida. They concluded (Cox et al., 1994), "that the current system of conservation areas in Florida provides the *minimum level* (emphasis ours) of habitat protection required to maintain gopher tortoises." More recently, B. Stys (unpubl. data) used GIS methods to estimate that 140 conservation areas have at least 68 ha of gopher tortoise habitat. In fact, she noted that these 140 conservation areas contained more than 500 individual patches of suitable habitat of at least 68 ha. Ground-truthing of about 40 of the conservation areas identified by GIS has revealed that a proportion of the apparently suitable habitat actually is unoccupied and that areas not considered as suitable habitat actually are occupied (McCoy et al., 2002). Whether or not the current system of conservation areas in Florida provides the minimum level of habitat protection required to maintain gopher tortoises, therefore, is not clear. Furthermore, as development continues to creep ever closer to areas currently occupied by tortoises, our ability to manage them via prescribed burning diminishes, and habitat suitability will be reduced (McCoy and Mushinsky, 1992b; Mushinsky and McCoy, 1994; McCoy et al., 2006).

In spite of the legal protection afforded the gopher tortoise, and efforts by the Florida Fish and Wildlife Conservation Commission (Cox et al., 1987) to establish guidelines aimed at conserving gopher tortoise habitat, the question remains as to what can be done to insure the future viability of the gopher tortoise throughout Florida. How much protected habitat is needed to ensure the long-term persistence of gopher tortoises in Florida? The future of the gopher tortoise, like all other wildlife, is not simply a biological or scientific issue. Individuals, including land owners, developers, legislators and, in fact, all the inhabitants of Florida must make a conscientious decision to value wildlife and their habitats more than they value the things that displace or destroy wildlife and wildlife habitats. Biologists may be able to make a stronger argument for the protection of tortoises than for other species because of the many other species that are at least partially dependent upon tortoise burrows for their survival. Clearly, the presence of the gopher tortoise in the State of Florida enhances the biodiversity of the State. In other words, providing protection for the gopher tortoise and its habitats simultaneously provides protection for dozens, or even hundreds, of other upland habitat species. Biologically based arguments, however, may not be sufficiently strong to sway public opinion; much depends upon the context in which the arguments are made. For example, during the Depression, when tortoises were an important part of the diets of many Floridians, it would have been impossible to protect them.

Our existing laws and regulations need to be reviewed and re-evaluated in light of the tremendous growth in the human population during the past 50 years. Under the current Florida Endangered Species Act, agricultural interests in the State are exempt from many of the regulations that apply to most non-agriculture landowners or individuals wishing to develop natural habitat. "Incidental take" (killing) of the gopher tortoise by altering the habitat in a way that makes it unsuitable for the gopher tortoise is permissible in a variety of circumstances. Under current regulations farmers and silviculturists may elect to use "best management practices," to clear gopher tortoise habitat and, as a consequence, kill tortoises and other protected species. A permit from the Florida Fish and Wildlife Conservation Commission is not required if natural habitat is converted to farmland, plantation, or citrus grove. Converting ranch land into row crop fields also can be done without a permit.

A specific recent example illustrates the effect of silvicultural "best management practices" on the gopher tortoise. In western Alachua County, near the Ashton Biological Preserve, 2000 acres of longleaf pine-turkey habitat was converted to tree farm in the first two months of 2000. Aerial spraying of herbicides (eliminating most tortoise broadleaf food plant species), clearing, and deep plowing were used to prepare the land to become a tree farm. Prior to the clearing, the density of gopher tortoises was about 0.8 tortoises per acre (Ashton, unpubl. data). Given that density of gopher tortoises, 200 acres would have supported about 160 tortoises. A survey of about 200 acres of the cleared land was conducted in April 2000, and only two gopher tortoise burrows were observed (Ashton, unpubl. data).

Existing Federal and State of Florida tax laws regulating agricultural profit requirements and laws regulating tax exemptions on land used for agricultural purposes contribute to the loss of habitats used by the gopher tortoise. Furthermore, when the owners of natural habitats convert them to plantations, State regulations require planting 400–600 trees/acre if the owners wish to maintain their agricultural tax exemptions on that land. Dense, single-species tree plantations create a canopy that virtually eliminates many native species of plants and animals, including the gopher tortoise.

Under current regulations, a land owner may elect to use "best management practices" to convert his/her land to farmland, obtain an agricultural tax exemption, and then sell the property to a developer. Because the land was dedicated to agricultural use, it can quickly be developed. While an intermediate, and perhaps expensive, step has been inserted into a chain of events and it may take decades to complete, the outcome for the gopher tortoise is high mortality and loss of habitat.

In contrast to the kinds of regulations that promote habitat loss, there are incentives, in the form of "conservation easements," that reward land owners for maintaining gopher tortoise habitat. Although regulations for tax exemptions on conservation easements are in place, they are not widely used. A conservation easement removes the right of the landowner to develop the land within the easement. An easement may be perpetual or it may exist for ten years. Currently, conservation easements are used most frequently by Water Management Districts to protect the state's wetlands; they are less often used to conserve upland habitats. Agencies may pay a high percentage of the value of the property for a permanent easement. If agencies could match the tax exemptions granted to land owners who elect to convert their land to farms, plantations, or groves, then land owners may be more willing to establish conservation easements on portions of their land not dedicated to agriculture.

The use of "best management practices" is not limited to privately owned lands; they are applied to public lands as well. Frequently, the Florida Department of Forestry is established as the land manager for Conservation and Recreation Lands (CARL) and State Forests. In 1999, The Department of Agriculture and Consumer Affairs notified regional offices to increase revenues generated from tree harvests and to plan for increased tree productivity in future management plans. Among the practices now employed, at least at some state forests, is the elimination of natural pineland habitats by conversion to intense silviculture (400–800 trees/acre). Furthermore, burning and other land management practices are conducted, not to sustain or increase tortoise habitat, but rather to maximize the yield of timber. These current trends do not bode well for the future of gopher tortoises that reside on these publicly owned lands.

In conclusion, there appears to be much room to improve the protection of this species on both public and private lands within the State of Florida. To establish a meaningful plan to protect the tortoise into the 22nd Century will require the full participation of all those who can influence the future of the gopher tortoise and its habitats. Perhaps in response to the existing uncertainty about the future of the gopher tortoise, McCoy et al. (2006) have called for the State of Florida to adopt a "no tortoise left behind" policy. The authors recognized that implementation of such policy would require significant changes to current operating procedures and create considerable problems for developers.

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LITERATURE CITED

ALFORD, R.A. 1980. Population structure of *Gopherus polyphemus* in northern Florida. Journal of Herpetology 14:177-182.

ALLAN, S.A., SIMMONS, L.A., AND BURRIDGE, M.J. 1998. Establishment of the tortoise tick *Amblyomma marmoreum* (Acari: Ixodidae) on a reptile-breeding facility in Florida. Journal of Medical Entomology 35:621-624.

ALLEN, E.R., AND NEILL, W.T. 1951. The gopher. Florida Wildlife 5:10,32.

ALLEN, E.R., AND NEILL, W.T. 1953. Juveniles of the tortoise *Gopherus polyphemus*. Copeia 1953:128.

ARATA, A.A. 1958. Notes on the eggs and young of *Gopherus polyphemus* (Daudin). Quarterly Journal of the Florida Academy of Science 21:274-280.

ARESCO, M.J., AND GUYER, C. 1999a. Burrow abandonment by gopher tortoises in slash pine plantations of the Conecuh National Forest. Journal of Wildlife Management 63:26-35.

ARESCO, M.J., AND GUYER, C. 1999b. Growth of the tortoise *Gopherus polyphemus* in slash pine plantations of Southcentral Alabama. Herpetologica 55:499-506.

Ashton, R.E., Jr., and Ashton, K.J. 1991. *Gopherus polyphemus* (gopher tortoise). Drinking behavior. Herpetological Review 22:55-56.

Ashton, R.E., Jr., and Ashton, P.S. 2001. *Gopherus polyphemus* (gopher tortoise). Use of abandoned burrows by juveniles. Herpetological Review 32:185-186.

Ashton, R.E., Jr., Ashton, P.S., and Mosura-Bliss, E.L. 1994. Tortoise management as urbanization encroaches. In: North American Tortoise Conference Proceedings, Mapimi Biosphere Preserve, Durango, Mexico, pp. 13-17.

Auffenberg, W. 1966. On the courtship of *Gopherus polyphemus*. Herpetologica 22:113-117.

Auffenberg, W. 1969. Tortoise behavior and survival. Rand McNally, Chicago, IL.

Auffenberg, W. 1978. Gopher tortoise, *Gopherus polyphemus* (Daudin). In: McDiarmid, R.W. (Ed.). Rare and Endangered biota of Florida. Volume 3: Amphibians and Reptiles. University Presses Florida, Gainesville, pp. 33-35.

Auffenberg, W., and Franz, R. 1982. The status and distribution of the gopher tortoise (*Gopherus polyphemus*). In: Bury, R.B. (Ed.). North American Tortoises: Conservation and Ecology. U.S. Fish & Wildlife Service, pp. 95-126.

Auffenberg, W., and Iverson, J.B. 1979. Demography of terrestrial turtles. In: Harless, M., and Morlock, H. (Eds.). Turtles: Perspectives and Research. John Wiley & Sons, New York, pp. 541-569.

Auffenberg, W., and Weaver, W. 1969. *Gopherus berlandieri* in southeastern Texas. Bulletin Florida State Museum 13:141-203.

Berish, J.E. 1995. Identification of critical gopher tortoise habitat in south Florida. Florida Game and Fresh Water Fish Commission, Final Report. Tallahassee, 44 pp.

Berish, J.E.D., Wendland, L.D., and Cates, C.A. 2000. Distribution and prevalence of upper respiratory tract disease in gopher tortoises in Florida. Journal of Herpetology 34:5-12.

Berry, K.H. 1997. Demographic consequences of disease in two desert tortoise populations in California, USA. In: Van Abbema, J. (Ed.). Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles – An International Conference. N.Y. Turtle and Tortoise Society, pp. 91-99.

Beyer, S.M. 1993. Habitat relations of juvenile gopher tortoises and a preliminary report of upper respiratory tract disease (URTD) in gopher tortoises. Master's Thesis, Iowa State University, Ames.

Bjorndal, K.A. 1987. Digestive efficiency in a temperate herbivorous reptile, *Gopherus polyphemus*. Copeia 1987:714-720.

Bogert, C.M., and Cowles, R.B. 1947. Moisture loss in relation to habitat selection in some Floridian reptiles. American Museum Novitates 1358:1-34.

Boglioli, M.D., Guyer, C., and Michener, W.K. 2003. Mating opportunities of females gopher tortoises, *Gopherus polyphemus*, in relation to spatial isolation of females and their burrows. Copeia 2003:846-850.

Breininger, D.R., Schmalzer, P.A., and Hinkle, C.R. 1991. Estimating occupancy of gopher tortoise (*Gopherus polyphemus*) burrows in coastal scrub and slash pine flatwoods. Journal of Herpetology 25:317-321.

Breininger, D.R., Schmalzer, P.A., and Hinkle, C.R. 1994. Gopher tortoise (*Gopherus polyphemus*) densities in coastal scrub and slash pine flatwoods in Florida. Journal of Herpetology 28:60-65.

Brode, W.E. 1959. Notes on behavior of *Gopherus polyphemus*. Herpetologica 15:101-102.

Brown, D.R., Crenshaw, B.C., Mclaughlin, G.S., Schumacher, I.M., Mckenna, C.E., Klein, P.A., Jacobson, E.R., and Brown, M.B. 1995. Taxonomy of the tortoise mycoplasmas *Mycoplasma agassizii* and *Mycoplasma testudinis* by 16s rRNA gene sequence comparisons. International Journal of Systematic Bacteriology 45:348-350.

Brown, D.R., Schumacher, I.M., Mclaughlin, G.S., Wendland, L.D., Brown, M.B., Klein, P.A., and Jacobson, E.R. 2002. Application of diagnostic tests for mycoplasmal infections of desert and gopher tortoises with management implications. Chelonian Conservation and Biology 4(2):497-507.

Brown, M.B., Schumacher, I.M., Klein, P.A., Harris, K., Correll, T., and Jacobson, E.R. 1994. *Mycoplasma agassizii* causes upper respiratory tract disease in the desert tortoise. Infectious Immunology 62:4580-4586.

Brown, M.B., Mclaughlin, G.S., Klein, P.A., Crenshaw, B.C., Schumacher, I.M., Brown, D.R., and Jacobson, E.R. 1999. Upper respiratory tract disease in the gopher tortoise is caused by *Mycoplasma agassizii*. Journal of Clinical Microbiology 37:2262-2269.

Brown, M.B., Brown, D.R., Klein, P.A., McLaughlin, G.S., Schumacher, I.M., Jacobson, E.R., Adams, H.P., and Tully, J.G. 2001. *Mycoplasma agassizii* sp. nov., isolated from the upper respiratory tract of the desert tortoise (*Gopherus agassizii*) and the gopher tortoise (*Gopherus polyphemus*). International Journal of Systematic and Evolutionary Microbiology 51:413-418.

Burke, R. 1989. Burrow-to-tortoise conversion factors: comparison of three gopher tortoise survey techniques. Herpetological Review 20:92-94.

Burke, R.L., Jacobson, E.R., Griffith, M.J., and Guillette, L.J. 1994. Non-invasive sex identification of juvenile gopher and desert tortoises (genus *Gopherus*). Amphibia-Reptilia 15:183-189.

Burridge, M.J. 2001. Ticks (Acari : Ixodidae) spread by the international trade in reptiles and their potential roles in dissemination of diseases. Bulletin of Entomological Research 91:3-23.

Butler, J.A., and Hull, T.W. 1996. Reproduction of the tortoise, *Gopherus polyphemus*, in northeastern Florida. Journal of Herpetology 30:14-18.

Campbell, H.W., and Christman, S.P. 1982. The herpetological components of Florida sandhill and sand pine scrub associations. In: Scott, N.J., Jr. (Ed.). Herpetological Communities. U.S. Fish and Wildlife Service, Wildlife Research Report 13, pp. 163-171.

Carr, A.F. 1952. Handbook of Turtles. Cornell Univ. Press, Ithaca, New York, 542 pp.

Causey, M.K., and Cude, C.A. 1978. Feral dog predation of the gopher tortoise, *Gopherus polyphemus*, in southeast Alabama. Herpetological Review 9:94-95.

Colson-Moon, J.A. 2003. Reproductive characteristics, multiple paternity, and mating system in a central Florida population of the gopher tortoise, *Gopherus polyphemus*. Master's Thesis, University of South Florida.

Connor, K.M. 1996. Homing behavior and orientation in the gopher tortoise, *Gopherus polyphemus*. Master's Thesis, University of South Florida, Tampa.

Conservation Breeding Specialist Group. 2001. Population viability analysis for the gopher tortoise. Unpublished report, Species Survival Commission/IUCN World Conservation Union, 45 pp.

Cox, J. 1989. Survival characteristics of small gopher tortoise populations and their possible influence on relocation efforts. In: Diemer, J.E., Jackson, D.R., Landers, J.L., Layne, J.N., and Wood, D.A. (Eds.). Gopher Tortoise Relocation Symposium. Florida Game and Fresh Water Fish Commission, Non-game Wildlife Program Technical Report 5, Tallahassee, pp. 7-14.

Cox, J. 1992. A cross-tabulation of land-cover types by conservation lands in Florida. Florida Field Naturalist 20:72-75.

Cox, J., Inkley, D., and Kautz, R. 1987. Ecology and habitat protection needs of gopher tortoise (*Gopherus polyphemus*) populations found on lands slated for large-scale development in Florida. Florida Game and Fresh Water Fish Commission Nongame Wildlife Program Technical Report 4, Tallahassee, 74 pp.

Cox, J., Kautz, R., Maclaughlin, M., and Gilbert, T. 1994. Closing the Gaps in Florida's Wildlife Habitat Conservation System. Florida Game and Fresh Water Fish Commission. Tallahassee, 239 pp.

Davis, J.H., Jr. 1967. General map of natural vegetation of Florida.

Agriculture Experimental Station Circular S-178, University of Florida, Gainesville.

Deem, S.K. 1998. A review of heartwater and the threat of introduction of *Cowdria ruminantium* and *Amblyomma* spp. ticks to American mainland. Journal of Zoo and Wildlife Medicine 29:109-113.

Deyrup, M., Deyrup, N.E., Eisner, M., and Eisner, T. 2005. A caterpillar that eats tortoise shells. American Entomologist 51:245-248.

Diemer, J.E. 1986. The ecology and management of the gopher tortoise in the southeastern United States. Herpetologica 42:125-133.

Diemer, J.E. 1987a. The status of the gopher tortoise in Florida. Proceedings Southeastern Nongame and Endangered Wildlife Symposium, Athens, GA, 3:72-83.

Diemer, J.E. 1987b. Tortoise relocation in Florida: solution or problem? Desert Tortoise Council Proceedings, 1984 Symposium, pp. 131-135.

Diemer, J.E. 1989. *Gopherus polyphemus*. In: Swingland, I.R., and Klemens, M.W. (Eds.). The Conservation Biology of Tortoises. Occasional Papers IUCN Species Survival Commission 5, pp. 14-19.

Diemer, J.E. 1992a. Gopher tortoise *Gopherus polyphemus* (Daudin). In: Moler, P.E. (Ed.). Rare and Endangered Biota of Florida. Volume III. Amphibians and Reptiles. Gainesville: Univ. Press of Florida, pp. 123-127.

Diemer, J.E. 1992b. Demography of the tortoise *Gopherus polyphemus* in northern Florida. Journal of Herpetology 26:281-289.

Diemer, J.E. 1992c. Home range and movements of the tortoise *Gopherus polyphemus* in northern Florida. Journal of Herpetology 26:158-165.

Diemer, J.E., and Moler, P.E. 1982. Gopher tortoise response to site preparation in northern Florida. Proceeding of the Annual Conference of Southeast Association of Fish and Wildlife Agencies 36:634-637.

Diemer, J.E., and Moore, C.T. 1994. Reproduction of gopher tortoises in north-central Florida. In: Bury, R.B., and Germano, D.J. (Eds.). Biology of North American tortoises. National Biological Survey, Fish and Wildlife Research 13, pp. 129-137.

Diemer-Berish, J.E. 1994. Status and conservation of the gopher tortoise. In: North American Tortoise Conference Proceedings, Mapimi Biosphere Preserve, Durango, Mexico, pp. 24-28.

Dietlein, N.E., and Smith, A. 1979. Gopher tortoise races—what they mean to the tortoise. Proceedings of the Desert Tortoise Council 1979:181-185.

Dodd, C.K., Jr. 1995. Disarticulation of turtle shells in north-central Florida: how long does a shell remain in the woods? American Midland Naturalist 134:378-387.

Doonan, T.J. 1986. A demographic study of an isolated population of the gopher tortoise, *Gopherus polyphemus*; and an assessment of a relocation procedure for tortoises. Master's Thesis, University of Central Florida, Orlando.

Doonan, T.J., and Stout, I.J. 1994. Effects of gopher tortoise (*Gopherus polyphemus*) body size on burrow structure. American Midland Naturalist 131:273-280.

Douglass, J.F. 1976. The mating system of the gopher tortoise, *Gopherus polyphemus*, in southern Florida. Master's Thesis, University of South Florida, Tampa.

Douglass, J.F. 1978. Refugia of juvenile gopher tortoises, *Gopherus polyphemus* (Reptilia, Testudines, Testudinidae). Journal of Herpetology 12:413-415.

Douglass, J.F. 1986. Patterns of mate-seeking and aggression in a southern Florida population of the gopher tortoise, *Gopherus polyphemus*. Proceedings Desert Tortoise Council 1986:155-199.

Douglass, J.F., and Layne, J.N. 1978. Activity and thermoregulation of the gopher tortoise (*Gopherus polyphemus*) in southern Florida. Herpetologica 34:359-374.

Douglass, J.F., and Winegarner, C.E. 1977. Predators of eggs and young of the gopher tortoise, *Gopherus polyphemus* (Reptilia, Testudines, Testudinidae), in southern Florida. Journal of Herpetology 11:236-238.

Eisenberg, J.F. 1983. The gopher tortoise as a keystone species. In: Bryant, R.J., and Franz, R. (Eds.). The Gopher Tortoise: A Keystone Species. Proceedings of the 4th Annual Meeting, Gopher Tortoise Council, Valdosta, GA.

Epperson, D.M. 1997. Gopher tortoise (*Gopherus polyphemus*) populations: activity patterns, upper respiratory tract disease, and management on a military installation in northeast Florida. Master's Thesis, University of Florida, Gainesville.

Ernst, C.H., and Barbour, R.W. 1972. Turtles of the United States. Univ. Press of Kentucky, Lexington, 347 pp.

Ernst, C.H., and Barbour, R.W. 1989. Turtles of the World. Smithsonian Inst. Press, Washington, D. C., 313 pp.

Eubanks, J.O, Hollister, J.W., Guyer, C., and Michener, W.K. 2002. Reserve area requirements of gopher tortoises (*Gopherus polyphemus*). Chelonian Conservation and Biology 4(2):464-471.

Fernald, E.A. (Ed.). 1981. Atlas of Florida. Florida State University Foundation, Tallahassee.

Fitzpatrick, J.W., and Woolfenden, G.E. 1978. Red-tailed hawk preys on juvenile gopher tortoise. Florida Field Naturalist 6:49.

Franz, R. 1986. *Gopherus polyphemus* (gopher tortoise). Burrow commensals. Herpetological Review 17:64.

Fucigna, T.F., Jr., and Nickerson, D.K., Jr. 1989. Relocations of two groups of gopher tortoises from Palm Beach County to Martin County, Florida. In: Diemer, J.E., Jackson, D.R., Landers, J.R., Layne, J.N., and Wood, D.A. (Eds.). Gopher Tortoise Relocation Symposium Proceedings, Florida Game and Fresh Water Fish Commission, Nongame Wildlife Program Technical Report 5, Tallahassee, pp. 59-71.

Garner, J., and Landers, J. 1981. Foods and habitat of the gopher tortoise in southwestern Georgia. Proceeding of the Annual Conference Southeastern Association Fish Wildlife Agencies 35:120-134.

Gates, C.A., Allen, M.J., Diemer-Berish, J.E., Stillwaugh, D.M., and Shattler, S.R. 2002. Characterization of a gopher tortoise mortality event in west-central Florida. Florida Scientist 65:185-197.

Germano, D.J., and Bury, R.B. 1994. Research on North American tortoises: a critique with suggestions for the future. In: Bury, R.B., and Germano, D.J. (Eds.). Biology of North American tortoises, Fish and Wildlife. National Biological Survey, Fish and Wildlife Research 13, pp. 187-204.

Godley, J.S. 1989. A comparison of gopher tortoise populations relocated onto reclaimed phosphate-mined sites in Florida. In: Diemer, J.E., Jackson, D.R., Landers, J.R., Layne, J.N., and Wood, D.A. (Eds.) Gopher Tortoise Relocation Symposium. Florida Game and Fresh Water Fish Commission, Non-game Wildlife Program Technical Report 5, Tallahassee, pp. 43-58.

Guyer, C., and Hermann, S.H. 1997. Patterns of size and longevity of gopher tortoises (*Gopherus polyphemus*) burrows: implications for the longleaf pine ecosystem. Chelonian Conservation and Biology 2(4):507-513.

Hallinan, T. 1923. Observations made in Duval County, northern Florida, on the gopher tortoise (*Gopherus polyphemus*). Copeia 1923:11-20.

Hansen, K.L. 1963. The burrow of the gopher tortoise. Journal Florida Academy Science 26:353-360.

Hawkins, R., and Burke, R. 1989. Of pens, pullers, and pets: problems of tortoise relocation. In: Diemer, J.E., Jackson, D.R, Landers, J.L., Layne, J.N., and Wood, D.A. (Eds.). Gopher Tortoise Relocation Symposium Proceedings. Florida Game and Fresh Water Fish Commission, Nongame Wildlife Technical Report 5, Tallahassee, p. 99.

Hutchinson, V.H., Winegar, A., and Kosh, R.J. 1966. Critical thermal maxima in turtles. Herpetologica 22:32-41.

Hutt, A. 1967. The gopher tortoise, a versatile vegetarian. Florida Wildlife 21:20-24.

Iverson, J.B. 1980. The reproductive biology of *Gopherus polyphemus* (Chelonia: Testudinidae). American Midland Naturalist 103:353-359.

Iverson, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately printed, 363 pp.

Jackson, D., and Milstrey, E.G. 1989. The fauna of gopher tortoise burrows. In: Diemer, J., Jackson, D.R., Landers, J.L., Layne, J.N., and Wood, D.A. (Eds.). Gopher Tortoise Relocation Symposium. Florida Game and Fresh Water Fish Commission, Non-game Wildlife Program Technical Report 5, Tallahassee, pp. 86-98.

Jacobson, E.R., Gaskin, J.M., Brown, M.B., Harris, R.K., Gardiner, C.H., Lapointe, J.L., Adams, H.P., and Reggiardo, C. 1991. Chronic upper respiratory tract disease of free-ranging desert tortoises (*Xerobates agassizii*). Journal of Wildlife Diseases 27:296-316.

Jacobson, E.R., Brown, M.B., Schumacher, I.M., Collins, B.R., Harris, R.K., and Klein, P.A. 1995. Mycoplasmosis and the desert tortoise (*Gopherus agassizii*) in Las Vegas Valley, Nevada. Chelonian Conservation and BioIogy 1(4):279-284.

Kaczor, S.A., and Hartnett, D.C. 1990. Gopher tortoise (*Gopherus polyphemus*) effects on soils and vegetation in a Florida sandhill community. American Midland Naturalist 123:100-111.

Kautz, R.S. 1993. Trends in Florida wildlife habitat 1936-1987. Florida Scientist 56:7-24.

Kautz, R.S., Gilbert, D.T., and Mauldin, G.M. 1993. Mapping Florida wildlife habitats using Landsat Thematic Mapper imagery. Florida Scientist 56:135-154.

Kushlan, J.A., and Mazzotti, F.J. 1984. Environmental effects on a coastal population of gopher tortoises. Journal of Herpetology 18:231-239.

Landers, J.L. 1980. Recent research on the gopher tortoise and its implications. In: Franz, R. and Bryant, R.J. (Eds.). The Dilemma of the Gopher Tortoise - Is There a Solution? Proceedings of the 1st Annual Meeting, Gopher Tortoise Council, pp. 8-14.

Landers, J.L., and Buckner, J.L. 1981. The gopher tortoise: effects of forest management and critical aspects of its ecology. Southlands Experimental Forestry Technical Note, No. 56:1-7.

Landers, J.L., and Garner, J.A. 1981. Status and distribution of the gopher tortoise in Georgia. In: Odom R., and Guthrie, J. (Eds.). Proceedings of the Nongame and Endangered Wildlife Symposium. Georgia Department of Natural Resources, Game and Fish Division Technical Bulletin WL5, Atlanta, pp. 45-51.

Landers, J.L., and Speake, D.W. 1980. Management needs of sandhill reptiles in southern Georgia. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 34:515-529.

Landers, J.L., Garner, J.A., and Mcrae, W.A. 1980. Reproduction of gopher tortoises (*Gopherus polyphemus*) in southwestern Georgia. Herpetologica 36:353-361.

Landers, J.L., Garner, J.A., and Mcrae, W.A. 1982. Growth and maturity of the gopher tortoise in southwestern Georgia. Bulletin Florida State Museum, Biological Sciences 27:81-110.

Lavender, D.R., and Oliver, J.H., Jr. 1996. Ticks (Acari: Ixodidae) in Bulloch County, Georgia. Journal of Medical Entomology 33:224-231.

Linley, T.A., and Mushinsky, H.R. 1994. Organic composition and energy content of eggs and hatchlings of the gopher tortoise. In: Bury, R.B., and Germano, D.J. (Eds.). Biology of North American tortoises. National Biological Survey, Fish and Wildlife Research 13, pp. 113-128.

Lips, K.R.1991. Vertebrates associated with tortoise (*Gopherus polyphemus*) burrows in four habitats in south-central Florida. Journal of Herpetology 25:477-481.

Lohoefener, R. 1982. Gopher tortoise ecology and land-use practices in southern Desoto National Forest, Harrison County, Mississippi. In: Franz, R. and Bryant, R.J. (Eds.). The Gopher Tortoise and its Sandhill Habitat. Proceedings of the Third Annual Meeting of the Gopher Tortoise Council, pp. 50-74.

Lohoefener, R., and Lohmeier, L. 1984. The status of *Gopherus polyphemus* (Testudines, Testudinidae) west of the Tombigbee and Mobile Rivers. Report to U.S. Fish and Wildlife Service in support of petition to list this population under the Endangered Species Act of 1973, 116 pp.

Macdonald, L.A. 1996. Reintroduction of gopher tortoises (*Gopherus polyphemus*) to reclaimed phosphate land. Florida Institute of Phosphate Research Publication No. 03-105-126, 56 pp.

Macdonald, L.A., and Mushinsky, H.R. 1988. Foraging ecology of the gopher tortoise, *Gopherus polyphemus*, in a sandhill habitat. Herpetologica 44:345-353.

Martin, P.L., and Layne, J.N. 1987. Relationship of gopher tortoise body size to burrow size in a south-central Florida population. Florida Scientist 50:264-267.

McCoy, E.D., and Mushinsky, H.R. 1988. The demography of *Gopherus polyphemus* (Daudin) in relation to size of available habitat. Final report to Florida Game and Fresh Water Fish Commission, Nongame Wildlife Program, Tallahassee, 71 pp.

McCoy, E.D., and Mushinsky, H.R. 1991. A survey of gopher tortoise populations residing on twelve State Parks in Florida. Florida Department of Natural Resources. Technical Report 1, 78 pp.

McCoy, E.D., and Mushinsky, H.R. 1992a. Studying a species in decline: gopher tortoises and the dilemma of “correction factors.” Herpetologica 48:402-407.

McCoy, E.D., and Mushinsky, H.R. 1992b. Studying a species in decline: changes in populations of the gopher tortoise on federal lands in Florida. Florida Scientist 55:116-125.

McCoy, E.D., Mushinsky, H.R., and Wilson, D. S. 1993. Pattern in the compass orientation of gopher tortoise burrows at different spatial scales. Global Ecology and Biogeographic Letters 3:33-40.

McCoy, E.D., Stys, B., and Mushinsky, H.R. 2002. A comparison of GIS and survey estimates of gopher tortoise habitat and numbers of individuals in Florida. Chelonian Conservation and Biology 4(2):472-478.

McCoy, E.D., Mushinsky, H.R., and Lindzey, J.K. 2005. Population consequences of upper respiratory tract disease on gopher tortoises. Final Report, Florida Fish and Wildlife Conservation Commission, Tallahassee, 44 pp.

McCoy, E.D., Mushinsky, H.R., and Lindzey, J.K. 2006. Population declines of the gopher tortoise on protected lands. Biological Conservation 128:120-127.

McDiarmid, R.W. 1978. Rare and Endangered Biota of Florida. Volume 3, Amphibians and Reptiles. University Presses of Florida, Gainesville, 74 pp.

McLaughlin, G.S. 1990. Ecology of gopher tortoises (*Gopherus polyphemus*) on Sanibel Island, Florida. Master’s Thesis, Iowa State University, Ames.

McLaughlin, G.S. 1997. Upper respiratory tract disease in gopher tortoises, *Gopherus polyphemus*: pathology, immune responses, transmission, and implications for conservation and management. Ph.D. Dissertation, University of Florida, Gainesville.

McLaughlin, G.S., Jacobson, E.R., Brown, D.R., Mckenna, C.E., Schumacher, I.M., Adams, H.P., Brown, M.B., and Klein, P.A. 2000. Pathology of upper respiratory tract disease of gopher tortoises in Florida. Journal of Wildlife Diseases 36:272-283.

McRae, W.A., Landers, J.L., and Cleveland, G.D. 1981a. Sexual dimorphism in the gopher tortoise (*Gopherus polyphemus*). Herpetologica 37:46-52.

McRae, W.A., Landers, J.L., and Garner, J.A. 1981b. Movement patterns and home range of the gopher tortoise. American Midland Naturalist 106:165-179.

Means, D.B. 1982. Responses to winter flooding of the gopher tortoise (*Gopherus polyphemus* Daudin). Herpetologica 38:521-525.

Mickler, L.E. 1986. Gopher stew. North Florida Living 6:68-69.

Milstrey, E.G. 1986. Ticks and invertebrate commensals in gopher tortoise burrows: implications and importance. In: Jackson, D.R., and Bryant, R. (Eds.). The gopher tortoise and its community. Proceedings 5th Annual Meeting Gopher Tortoise Council, Florida State Museum, Gainesville, pp. 4-25.

Moler, P.E. 1992. Rare and Endangered Biota of Florida. Volume III. Amphibians and Reptiles. University Press of Florida, Gainesville, 291 pp.

Moon, J.C., McCoy, E.D., Mushinsky, H.R., and Karl, S.A. 2006. Multiple paternity and breeding systems in the gopher tortoise, *Gopherus polyphemus*. Journal of Heredity 97:150-157.

Mount, R.H. 1975. The Reptiles and Amphibians of Alabama. Alabama Agricultural Experimental Station, Auburn University, Auburn, 347 pp.

Mushinsky, H.R. 1985. Fire and the Florida sandhill herpetofaunal community: with special attention to responses of *Cnemidophorus sexlineatus*. Herpetologica 41:333-341.

Mushinsky, H.R., and Gibson, D.J. 1991. The influence of fire periodicity on habitat structure. In: Bell, S.E., McCoy, E.D., and Mushinsky, H.R. (Eds.). Habitat Structure: The Physical Arrangement of Objects in Space. Chapman and Hall Ltd., pp. 237-259.

Mushinsky, H.R., and McCoy, E.D. 1994. Comparison of gopher tortoise populations on islands and on the mainland in Florida. In: Bury, R.B., and Germano, D.J. (Eds.). Biology of North American Tortoises. National Biological Survey, Fish and Wildlife Research 13, pp. 39-47.

Mushinsky, H.R., and McCoy, E.D. 1996. Studies of wildlife and restoration of phosphate mined land. Florida Institute for Phosphate Research, Bartow, Florida, Publ. No. 03-100-129, 97 pp.

Mushinsky, H.R., Wilson, D.S., and McCoy, E.D. 1994. Growth and sexual dimorphism of *Gopherus polyphemus* in Central Florida. Herpetologica 50:119-128.

Mushinsky, H.R., Stilson, T.A., and McCoy, E.D. 2003. Diet and dietary preference of the juvenile gopher tortoise (*Gopherus polyphemus*). Herpetologica 59:475-483.

Myers, R.L., and Ewel, J.J.1990. Ecosystems of Florida. University of Central Florida Press, Orlando, 765 pp.

Palmer, B.D., and Guillete, L.J., Jr. 1988. Histology and functional morphology of the female reproductive tract of the tortoise *Gopherus polyphemus*. American Journal of Anatomy 183:200-211.

Peter, T.T., Burridge, M.J., and Mahan, S.M. 2000. Competence of the African tortoise tick, *Amblyomma marmoreum* (Acari: Ixodidae), as a vector of the agent of heartwater (*Cowdria ruminantium*). Journal of Parasitology 86:438-441.

Schumacher, I.M., Brown, M.B., Jacobson, E.R., Collins, B.R., and Klein, P.A. 1993. Detection of antibodies to a pathogenic mycoplasma in desert tortoises (*Gopherus agassizii*) with upper respiratory tract disease. Journal of Clinical Microbiology 31:1454-1460.

Schumacher, I.M., Hardenbrook, D.B., Brown, M.B., Jacobson, E.R., and Klein, P.A. 1997. Relationship between clinical signs of upper respiratory tract disease and antibodies to *Mycoplasma agassizii* in desert tortoises from Nevada. Journal of Wildlife Diseases 33:261-266.

Schumacher, I.M., Rostal, D.C., Yates, R.A., Brown, D.R., Jacobson, E.R., and Klein, P.A. 1999. Persistence of maternal antibodies against *Mycoplasma agassizii* in desert tortoise hatchlings. American Journal of Veterinary Research 60:826-831.

Seigel, R.A., Smith, R.B., and Seigel, N.A. 2003. Swine flu or 1918 pandemic? Upper respiratory tract disease and the sudden mortality of gopher tortoises (*Gopherus polyphemus*) on a protected habitat in Florida. Journal of Herpetology 37:137-144.

Shilling, D.G., Bewick, T.A., Gaffney, J.F., McDonald, S.K., Chase, C.A., and Johnson, E.R.L. 1997. Ecology, physiology, and management of cogongrass (*Imperata cylindrica*). Florida Institute of Phosphate research, Publications No. 03-107-140, 128 pp.

Small, C.R. and MacDonald, L.A. 2001. Reproduction and growth in relocated and resident gopher tortoises (*Gopherus polyphemus*) on reclaimed phosphate-mined lands. Florida Institute of Phosphate Research, Publication No. 03-105-145, 60 pp.

Smith, H.M., and Smith, R.B. 1980. Synopsis of the Herpetofauna of Mexico. Vol VI. Guide to Mexican turtles. John Johnson, North Bennington, VT, 1044 pp.

Smith, L.L. 1995. Nesting ecology, female home range and activity, and population size-class structure of the gopher tortoise, *Gopherus polyphemus*, on the Katherine Ordway Preserve, Putnam County, Florida. Bulletin, Florida Museum of Natural History 37:97-126.

Smith, R.B., Seigel, R.A., and Smith, K.R. 1998. Occurrence of upper respiratory tract disease in gopher tortoise populations in Florida and Mississippi. Journal of Herpetology 32:426-430.

Stewart, M.C., Austin, D.F., and Bourne, G.R. 1993. Habitat structure and the dispersion of gopher tortoises on a nature preserve. Florida Scientist, Biological Sciences 56:70-81.

Stout, I.J., Doonan, T.J., Roberts, R.E., and Richardson, D.R. 1989. Comparison of results of three gopher tortoise relocations in central and southeast Florida. In: Diemer, J.E., Jackson, D.R., Landers, J.L., Layne, J.N., and Wood, D.A. (Eds.). Gopher Tortoise Relocation Symposium. Florida Game and Fresh Water Fish Commission, Non-game Wildlife Program Technical Report 5, Tallahassee, pp. 15-42.

Taylor, R.W., Jr. 1982. Human predation on the gopher tortoise (*Gopherus polyphemus*) in north-central Florida. Bulletin Florida State Museum, Biological Sciences 28:79-102.

Timmerman, W.W., and Roberts, R.E. 1994. *Gopherus polyphemus* (gopher tortoise). Maximum size. Herpetological Review 25:64.

Ultsch, G.R., and Anderson, J.F. 1986. The respiratory microenvironment within the burrows of gopher tortoises (*Gopherus polyphemus*). Copeia 1986:787-795.

U.S. Fish and Wildlife Service. 1987. Determination of threatened status for the gopher tortoise (*Gopherus polyphemus*). Federal Register 52:25376-25380.

Wilson, D.S. 1991. Estimates of survival for juvenile gopher tortoises, *Gopherus polyphemus*. Journal of Herpetology 25:376-379.

Wilson, D.S., Mushinsky, H.R., and McCoy, E.D. 1991. Relationship between gopher tortoise body size and burrow width. Herpetological Review 22:122-124.

Wilson, D.S., Mushinsky, H.R., and McCoy, E.D. 1994. Home range, activity, and use of burrows of juvenile gopher tortoises in central Florida. In: Bury, R.B., and Germano, D.J. (Eds.). Biology of North American Tortoises. National Biological Survey, Fish and Wildlife Research 13, pp. 147-160.

Wilson, D.S., Mushinsky, H.R., and Fisher, R.A. 1997. Species profile: gopher tortoise (*Gopherus polyphemus*) on military installations in the southeastern United States. Technical Report SERDP-97-10, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

Wilson, D.S., Tracy, C.R., and Tracy, C.R. 2003. Estimating age of turtles from growth rings: a critical evaluation of the technique. Herpetologica 59:178-194.

Witz, B.W., Wilson, D.S., and Palmer, M.D. 1991. Distribution of *Gopherus polyphemus* and its vertebrate symbionts in three burrow categories. American Midland Naturalist 126:152-158.

Witz, B.W., Wilson, D.S., and Palmer, M.D. 1992. Estimating population size and hatchling mortality of *Gopherus polyphemus*. Florida Scientist 55:14-19.

Wright, J.S. 1982. Distribution and population biology of the gopher tortoise, *Gopherus polyphemus*, in South Carolina. Master's Thesis, Clemson University, SC.

Young, F.N.N., and Goff, C.C. 1939. An annotated list of the arthropods found in the burrows of the Florida gopher tortoise *Gopherus polyphemus* (Daudin). Florida Entomologist 22:53-62.

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Epilogue – Turtle Poetry

Dead Turtle

PATRICIA B. WALTERS[1]

Curious that I should want to eulogize a turtle
Perhaps it was his ignominious death
(Why did I think of it as male?)
That still form by the road

The grass that greens the median barrier had just been mowed
The blades that clipped had ripped the turtle's shell
And threw him….or he dragged himself
Exposed upon the slab

When first I sighted him, I thought he was alive
But absence of response was too abject
He eloquently spoke of death
Next day he was still there

Each time I passed, I tried to turn my eyes away
Not see this tiny, tiresome tragedy
But to ignore him was to slight
All victims man has left

So I watched while summer sun tanned him to leather
A kind of rigor mortis raised his head
Last gesture of primordial pride
Of death with dignity

There was a gradual sinking, shrinking of the corpse
Like the closing of the covers of a book
Some unknown force then lifted him
And one day he was gone

[1] Composed 1997
After seeing a dead turtle for several days on Interstate Highway 75 near Tampa, Florida

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Editorial Comment. — This poem about a dead turtle on the road, probably a Florida softshell, reminds us of the all-too-often sad outcome of interactions between turtles and man, especially man's development as represented by highways and automobiles and the destructive nature of our technology. As the turtle in the poem was gone one day, if we are not careful to preserve our natural heritage, all turtles will be gone one day. But though we are the problem, we are also the solution, and our efforts to preserve turtles and their habitats will make a difference for future generations. The survival of turtles in Florida and elsewhere will depend on our efforts. ANDERS G.J. RHODIN.

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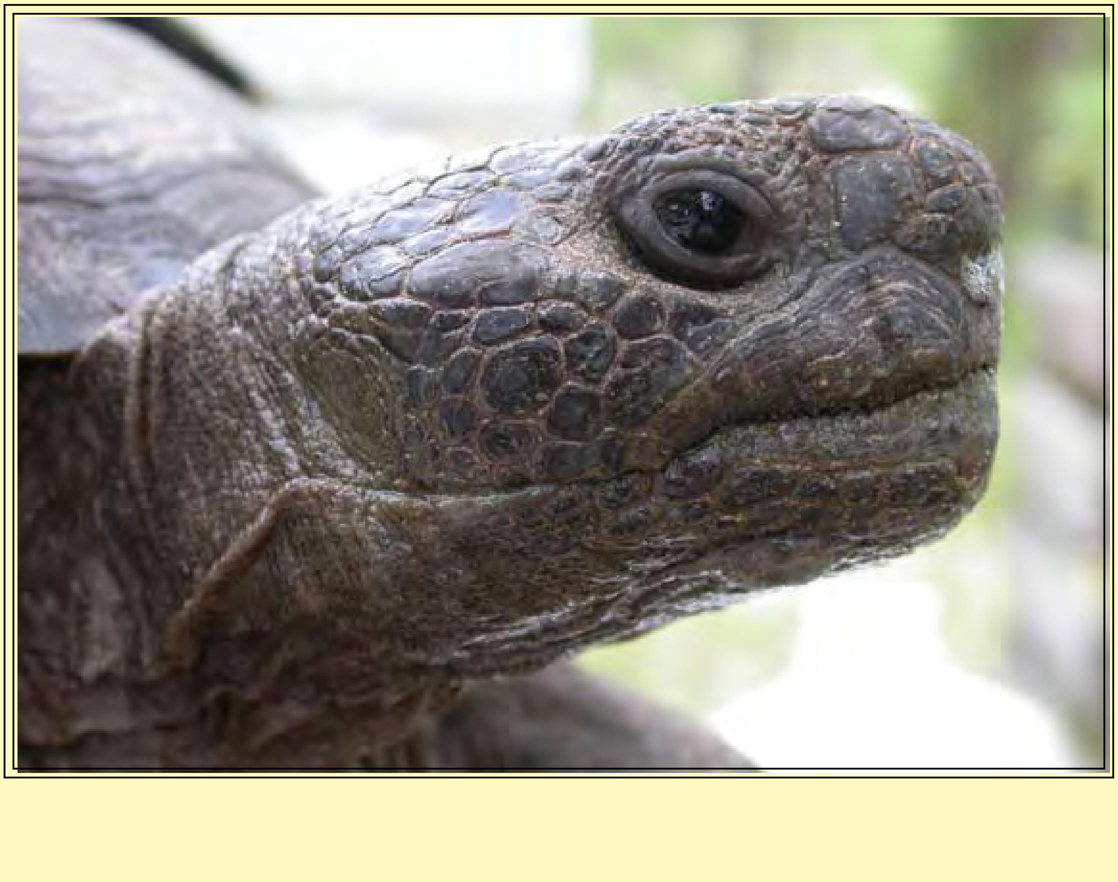

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