

this study. However, if the Withlacoochee River had lower total plant biomass and greater plant diversity before the introduction of these exotic plants, the diets of the three turtle species may have had less overlap.

These results must be interpreted with caution because of the small sample sizes and short duration of the study. To evaluate dietary overlap among these species more thoroughly, studies with larger sample sizes are needed that incorporate seasonal variation and that relate availability of plant species with diet selection. Studies in habitats that have not been invaded by exotic aquatic plants would be of great value.

Acknowledgments. — For assistance with identification of diet items, we thank C. Beck, J. Davis, T. Emmel, D. Griffin, G. Guala, B. Haller, M. Hein, K. Langeland, F. Maturo, and the staff of the Center for Aquatic Plants, University of Florida. K. Ainslee collected most of the turtles.

Literature Cited

- BJORNDALE, K.A. 1997. Foraging ecology and nutrition of sea turtles. In: Lutz, P.L., and Musick, J.A. (Eds.). *The Biology of Sea Turtles*. Boca Raton, FL: CRC Press, pp. 201-233.
- BUHLMANN, K.A., AND VAUGHAN, M.R. 1991. Ecology of the turtle *Pseudemys concinna* in the New River, West Virginia. *J. Herpetol.* 25:72-78.
- ERNST, C.H., LOVICH, J.E., AND BARBOUR, R.W. 1994. *Turtles of the United States and Canada*. Washington, DC: Smithsonian Inst. Press, 578 pp.
- 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. Thesis, Auburn Univ. Alabama.
- HART, D.R. 1979. Resource partitioning among Louisiana turtles of the genus *Chrysemys*. Ph.D. Thesis, Tulane Univ., New Orleans.
- HORN, H.S. 1966. Measurement of "overlap" in comparative ecological studies. *Amer. Natur.* 100:419-424.
- HYSLOP, E.J. 1980. Stomach contents analysis—a review of methods and their application. *J. Fish Biol.* 17:411-429.
- JACKSON, D.R. 1988. Reproductive strategies of sympatric freshwater emydid turtles in northern peninsular Florida. *Bull. Florida State Mus., Biol. Sci.* 33:113-158.
- JACKSON, D.R. 1995. Systematics of the *Pseudemys concinna-floridana* complex (Testudines: Emydidae): an alternative interpretation. *Chelon. Conserv. Biol.* 1:329-333.
- LAGUEUX, C.J., BJORNDALE, K.A., BOLTON, A.B., AND CAMPBELL, C.L. 1995. Food habits of *Pseudemys concinna suwanniensis* in a Florida spring. *J. Herpetol.* 29:122-126.
- MACARTHUR, R., AND LEVINS, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Amer. Natur.* 101:377-385.
- MARCHAND, L.J. 1942. A contribution to a knowledge of the natural history of certain freshwater turtles. M.S. Thesis, Univ. Florida, Gainesville.
- MYERS, R.L., AND EWEL, J.J. (Eds.). 1990. *Ecosystems of Florida*. Orlando: Univ. of Central Florida Press, 765 pp.
- RYAN, B.F., JOINER, B.L., AND RYAN, T.A., JR. 1985. *Minitab Handbook*, 2nd ed. Boston: Duxbury Press, 374 pp.

Received: 21 March 1996

Reviewed: 11 November 1996

Revised and Accepted: 11 December 1996

Predation by the Imported Fire Ant (*Solenopsis invicta*) on Loggerhead Sea Turtle (*Caretta caretta*) Nests on Wassaw National Wildlife Refuge, Georgia

ROBERT A. MOULIS¹

¹Savannah—Ogeechee Canal Museum and Nature Center, 681 Fort Argyle Road, Savannah, Georgia 31419 USA

Little information concerning predation by ants on eggs or hatchlings of turtles is available. McAllister et al. (1965) and Hughes (1970, 1971, 1972, 1974) referred to ants (*Dorylus* sp.) preying upon the eggs of loggerhead turtles (*Caretta caretta*) in southeastern Africa. Hughes (1975) indicated that a hatchery containing 10 *Caretta* and 2 leatherback (*Dermochelys coriacea*) nests, unprotected by ant poison, suffered 100% mortality during one nesting season. Congdon et al. (1983) reported that an unidentified ant caused destruction of the eggs of a Blanding's turtle (*Emydoidea blandingii*) in Michigan. Dodd (1988) listed ants as a predator on *Caretta* eggs but did not identify species or mention to what degree this predation occurred.

Imported fire ants (*Solenopsis invicta*) have been implicated by some researchers as potential or actual predators upon turtle and other reptile eggs in the USA. Mount et al. (1981) showed through field experiments that *S. invicta* will attack and consume eggs of the lizard *Cnemidophorus sexlineatus*. In addition Mount (1981) reported an observation of fire ants invading the nest of a chicken turtle (*Deirochelys reticularia*). Upon excavation, this nest contained several dead hatchlings. Landers et al. (1980) reported fire ants destroying 10 hatchlings from three separate nests of the gopher tortoise (*Gopherus polyphemus*). Mapes (1985) listed fire ants as a predator upon loggerhead eggs from Sarasota County, Florida. LeBuff (1990) provided slightly more information when he remarked that the native Florida fire ant (*Solenopsis geminata*) was a frequent invader of *Caretta* nests on Sanibel Island, Lee County, Florida. He noted that these ants caused insignificant losses to eggs, but hatchlings ascending the nest chamber were vulnerable to ant attack. LeBuff also stated that nests deposited in partially shaded or vegetated areas where ants foraged were seriously threatened. Although nests located in unshaded areas were not necessarily excluded from this threat, predation there was much less. He concluded that once ants reached the nest cavity, hatchlings quickly fell victim to the formic acid injected by the sting of the insects. Although no evidence exists on the susceptibility of hatchling turtles to the sting of fire ants, Mount (1981) indicated that a hatchling box turtle (*Terrapene*

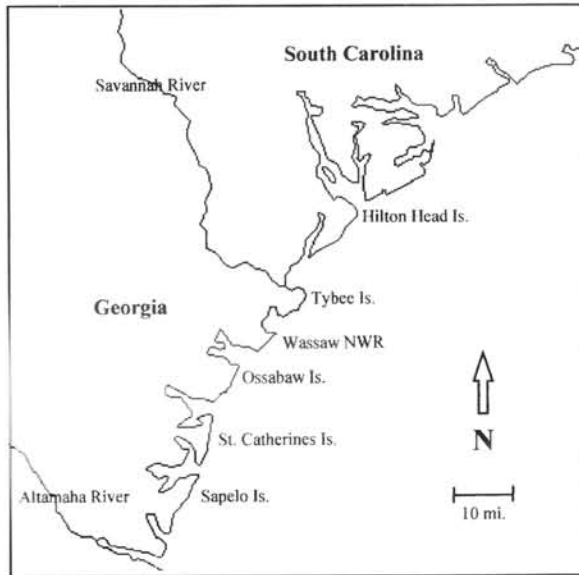


Figure 1. Location of Wassaw National Wildlife Refuge along the Georgia coast.

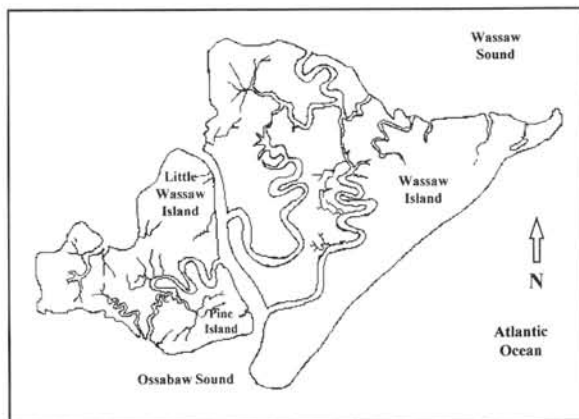


Figure 2. Detail of Wassaw National Wildlife Refuge.

carolina) and a yearling map turtle (*Graptemys barbouri*) died within a few days after being found covered with fire ants. LeBuff (1990) concluded that on Sanibel Island, fire ants were the most dangerous predators upon turtle hatchlings. Unfortunately, he gave no percentages as to the extent of this predation and mortality. More recently Wilmers et al. (1996) presented information on the destruction caused by fire ants to sea turtle nests in the lower Florida Keys.

Methods. — Since 1973 a sea turtle tagging program has been conducted on the Wassaw National Wildlife Refuge (WNWR) in Chatham County, Georgia, USA (see Figs. 1 and 2). This program initially was concerned with numbers and movements of adult female *Caretta* on Wassaw Island, but in later years also included nest relocation and hatchling release operations on both Wassaw and Pine Islands. In general the beach on Wassaw Island was patrolled throughout the night from mid-May to early August, while the smaller Pine Island beach was checked for nesting activity during daylight hours from

early June through early August. *Caretta* nests found during patrols were treated in one of three ways. Nests which were considered located in ideal locations were left *in situ*, while nests which were deemed in jeopardy of tidal inundation were either relocated to higher areas on the beach or moved to hatcheries. Both *in situ* and relocated nests were screened with galvanized fencing to deter raccoon predation.

Each hatchery consisted of a wooden-framed structure with galvanized sheet metal buried to a depth of 20 inches and attached to the two sides and backing of the wooden frame. Because the hatchery was a self-release structure, the oceanside was open to allow easy escape of hatchlings, as well as drainage from periodic summer storms. Either 2 x 4 inch mesh wire fencing or a removable wooden panel was placed on the oceanside of the hatchery during the incubation period to prevent larger predators from entering the hatchery. Screened tops (8 x 4 feet) were easily removed to allow researchers access to the hatchery's interior. Nests within the hatchery were usually checked several times during the course of the day. All nests located outside the hatchery were checked periodically (generally once a week) during their incubation to determine the effectiveness of screening against predators. Nests which were 50 days or older were checked daily to determine the date of first emergence. Three days after first emergence, nests were exhumed and the contents examined. Nests which had no evidence of emergence were exhumed after 70 days. The presence of ants, the number of unhatched eggs, and the number of dead hatchlings were recorded for each exhumed nest (see Table 1).

Results and Discussion. — During the summer of 1992, researchers noted high mortality among several *Caretta* nests on WNWR. Seven of 96 nests found in 1992 had been invaded by the fire ant, *Solenopsis invicta*, during some point in their development. From 1992 to 1994 ants were observed in a total of 21 nests (8.27% of all nests), and the percentage of nests infested varied from 2.86 to 10.57% annually. Although such information may indicate that ants invade only a small percentage of all nests, the impact on infested nests appears quite dramatic. The average hatchling release rate (number of hatchlings entering the water per number of eggs x 100) for nests containing ants was 40.55% compared to 54.02% for nests which did not contain ants. Other factors also contributed to these rather dismal success rates. For example, late season rains and beach erosion associated with tropical storms tremendously reduced hatchling success in 1992, although the effects from this abiotic factor were probably shared equally by both invaded and uninvaded nests. Furthermore, a combination of raccoon and ghost crab predation resulted in the destruction of 14.53% of all eggs laid during the 1994 season alone. However, because such losses generally occurred during the first few days after deposition, and resulted in the total devastation of the nest (especially in the case of

Table 1. Summary of loggerhead nest data on Wassaw National Wildlife Refuge, 1992-94.

Year	Total Nests	Total Eggs	Total Hatched Eggs	Total Dead Hatchlings	Total Live Hatchlings	Success Rate %	Infested Nests %	Total Eggs in Infested Nests	Hatched Eggs in Infested Nests	Dead Hatchlings in Infested Nests	Live Hatchlings in Infested Nests	Success % in Infested Nests
1992	96	11,626	5,840	677	5,163	44.41%	7.29%	831	507	313	194	23.25%
1993	35	4,040	2,952	64	2,888	71.49%	2.86%	111	2	0	2	1.80%
1994	123	14,088	8,273	544	7,699	54.65%	10.57%	1,470	1,035	245	782*	53.20%
Total	254	29,754	17,065	1,285	15,750	52.93%	8.27%	2,412	1,544	558	978	40.55%

* 8 hatchlings predated by raccoons/ghost crabs after emerging from nest not included.

raccoons) this form of egg mortality was usually restricted to nests which were not invaded by ants.

In addition, a dramatic increase of "pipped" eggs was also noted in some of the ant-infested nests and could indicate that ants may have chewed their way through some of these eggs. Although some of these pipped eggs contained fully developed embryos and entry by the ants may have occurred after such eggs were pipped naturally, others contained lesser developed, well-decayed embryos or contents which suggested little or no development. In several cases the shells of such eggs possessed small, circular holes (ca. 1 mm in diameter), and the remaining contents were more or less dehydrated.

In many cases ants apparently had entered the nests just prior to emergence, evidenced by the number of dead hatchlings observed upon nest exhumation. At present, it is unknown whether the ants caused the demise of these dead hatchlings. However, the proportion of dead hatchlings to total number of eggs was significantly higher ($\chi^2 = 2,258$, $df = 1$) for ant-infested nests than was the proportion for uninfested nests.

In 1992 all cases of fire ant infestation occurred in nests that had been relocated because their original locations were deemed unsafe as a result of local tide fluctuations. During the 1993 nesting season, no damage from fire ants was observed in relocated nests. However, a single *in situ* nest contained a related species of native ant, *Solenopsis globularia littoralis* (D.R. Smith, Systematic Entomology Laboratory, *pers. comm.*). Although no dead hatchlings were found in this nest, a total of 45 eggs (40.54% of the clutch) had small circular holes in their shells and contained a few to over one hundred ants. It should be noted that because of serious beach erosion during the 1992-93 winter, most nests (77.14%) from the 1993 season were placed in a self-release hatchery. Possibly the underground sheet metal of this hatchery served as a crude barrier to deter ants from invading the confines of the hatchery.

In 1994, 13 of 123 nests were affected by ants. In all, 6 of 55 *in situ* nests; 5 of 42 relocated nests; and 2 of 26 hatchery nests were found to contain ants during their excavation after hatching. These proportions are not significantly different ($\chi^2 = 0.313$, $df = 2$). However, it should be noted that the two hatchery nests were found to contain ants tentatively identified as *S. g. littoralis*, not *S.*

invicta. Both hatchery nests affected by ants were neighboring nests, and none of the remaining nests within the hatchery appeared to have been invaded by this seemingly less aggressive species. Also, the same hatchery location used during the 1993 season was again used during the 1994 season, and it is quite possible that a colony of *S. g. littoralis* was already established within the confines of the hatchery prior to the 1994 season. During the 1992 season no hatchery was used.

Infestation was not restricted to any one location on the beach but was scattered along the entire shoreline. During 1992 six of the seven affected nests had been relocated to the upper edges of well-established dunes. The single *in situ* nest infested during 1993 was located along the edge of a similar dune system. With the exception of the two hatchery nests invaded by ants during the 1994 season, nests containing ants were again located near the edges of dune systems, generally within a meter of the vegetation line. These data suggest that an "edge effect" as described by Odum and Odum (1971) could exist in such areas in regard to the fire ant. Similarly, in Wisconsin, Temple (1987) found a significant increase in predation in the nests of three species of turtle which were deposited near ecological edges. Also, Hamilton and Standora (1994) reported that the distance loggerhead nests were deposited from the dune vegetation line significantly affected predation rates by raccoons. Such information indicates that care should be taken when choosing a relocation site.

In 1992 one nest relocated to a site in front of the dune area had first been invaded by fire ants and then disturbed and partially depredated by a raccoon. However, this depredation was light (estimated from egg shells found scattered around the nest site to involve fewer than 15 eggs), and the presence of the ants had probably discouraged further predation by the raccoon. The presence of winged ants indicated that the ants had established themselves prior to the raccoon's disturbance. Egg shell fragments from an estimated 61 eggs found at the bottom of the nest cavity were suspected to be directly linked to ant activity.

The rather low amount of ant infestation during the 1993 season may be attributed to a sharp decrease in loggerhead activity or extensive use of a hatchery. The total number of nests laid during the 1993 season (35)

was a dramatic decrease from the 1992 or 1994 seasons (96 and 123, respectively). In addition only 8 nests (3 relocated and 5 *in situ*) were left outside the confines of the hatchery, and few opportunities would have existed for the ants to invade nests. Furthermore, of the 8 nests left outside the hatchery, 2 were totally destroyed by raccoons during their first night of deposition, and therefore only 6 nests were available to predation by ants.

As in 1992, the number of dead hatchlings found in ant infested nests during 1994 was significantly higher than the number found in all uninfested nests ($\chi^2 = 801$, $df = 1$). However, the proportion of dead hatchlings during the 1992 season was significantly higher than that of 1994 ($\chi^2 = 127.26$, $df = 1$). It is therefore possible that the use of the self-release hatchery may have decreased the amount of ant predation occurring in 1994. When only relocated nests are considered during the two seasons, no significant difference between the two exists ($\chi^2 = 1.286$, $df = 1$).

Based on these results ants in general and fire ants in particular may represent a major threat to both developing eggs and hatchling turtles. Because fire ants represent a rather recently introduced form of predator to the loggerhead population of the southeastern USA, predation from this species may dramatically alter the chances for survival of an already vulnerable species of sea turtle. It has been suggested that under natural conditions loggerhead hatching success may be as low as 10% (Hopkins et al., 1979; Richardson and Richardson, 1982). Therefore, even relatively small losses from factors such as ants may be unacceptable. Indeed, further research on the effects of this insect on loggerhead populations is desirable.

Acknowledgments. — I would like to thank Michael G. Frick and Randall S. Isbister for their help and support during the 1992–94 seasons. My thanks are also extended to the U.S. Fish and Wildlife Service and the Wassaw Island Trust for their assistance during the past 20 years, and more recently to the Skidaway Boat Club for their help in transporting crews to and from the island. In addition, I thank Sue Simon, Sally Krebs, Terry Arbogast, Mary Lee Warnock, John Robinette, Sally Murphy, and an anonymous reviewer for their helpful advice regarding earlier drafts of this manuscript. I also thank Harleston Cabaniss for advice concerning statistics. Lastly, my deepest appreciation goes out to the many volunteers of the *Caretta* Research Project who make this program possible.

Literature Cited

- CONGDON, J.D., TINKLE, D.W., BREITENBACH, G.L., AND VAN LOBEN SELS, R.C. 1983. Nesting ecology and hatching success in the turtle, *Emydoidea blandingi*. *Herpetologica* 39:417-429.
- DODD, C.K., JR. 1988. Synopsis of the biological data on the loggerhead sea turtle *Caretta caretta* (Linnaeus 1758). U.S. Fish and Wildl. Serv. Biol. Rep. 88(14). 110 pp.
- HAMILTON, C.M., AND STANDORA, E.A. 1994. Testing the importance of visual cues in raccoon predation of loggerhead sea turtle nests. In: Schroeder, B., and Witherington, B. (Compilers). Proceedings of the Thirteenth Annual Symposium of Sea Turtle Biology and Conservation. NOAA Tech. Mem. NMFS-SEFSC-341, p. 76.
- HOPKINS, S.R., MURPHY, T.M., JR., STANSELL, K.B., AND WILKINSON, P.M. 1979. Biotic and abiotic factors affecting nest mortality in the Atlantic loggerhead turtle. Proceedings of the 32nd Annual Conference of the South East Association of Fish and Wildlife Agencies, pp. 213-223.
- HUGHES, G.R. 1970. Further studies on marine turtles in Tongaland, III. *Lammergeyer* 12:7-36.
- HUGHES, G.R. 1971. The marine turtles of Tongaland, V. *Lammergeyer* 13:7-24.
- HUGHES, G.R. 1972. The marine turtles of Tongaland, 6. *Lammergeyer* 15:15-26.
- HUGHES, G.R. 1974. The sea turtles of south-east Africa. II. The biology of the Tongaland loggerhead turtle *Caretta caretta* L. with comments on the leatherback turtle *Dermochelys coriacea* L. and the green turtle *Chelonia mydas* L. in the study region. *Oceanogr. Res. Inst. Invest. Rep. No. 36*.
- HUGHES, G.R. 1975. The marine turtles of Tongaland, 8. *Lammergeyer* 22:9-18.
- LANDERS, J.L., GARNER, J.A., AND MCRAE, A. 1980. Reproduction of gopher tortoises (*Gopherus polyphemus*) in southwestern Georgia. *Herpetologica* 36:353-361.
- LEBUFF, C.H., JR. 1990. The Loggerhead Turtle in the Eastern Gulf of Mexico. Florida. Sanibel: *Caretta* Research Inc., 216 pp.
- MAPES, J. 1985. Loggerhead conservation on Florida's west coast. *Marine Turtle Newsletter* 33:8-9.
- MCALLISTER, H.J., BASS, A.J., AND VAN SCHOOR, H.J. 1965. The marine turtles of Tongaland, Natal. *Lammergeyer* 3(2):10-40.
- MOUNT, R.H. 1981. The red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae), as a possible serious predator on some native southeastern vertebrates: direct observations and subjective impressions. *J. Ala. Acad. Sci.* 52:71-78.
- MOUNT, R.H., TRAUTH, S.E., AND MASON, W.H. 1981. Predation by the red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae), on eggs of the lizard *Cnemidophorus sexlineatus* (Squamata: Teiidae). *J. Ala. Acad. Sci.* 52:66-70.
- ODUM, E.P., AND ODUM, H.T. 1971. *Fundamentals of Ecology*. 3rd ed. Philadelphia: Saunders, 574 pp.
- RICHARDSON, J.L., AND RICHARDSON, T.H. 1982. An experimental model for the loggerhead sea turtle (*Caretta caretta*). In: Bjorndal, K.A. (Ed.). *Biology and Conservation of Sea Turtles*. Washington, DC: Smithsonian Institution Press, pp. 165-176.
- TEMPLE, S.A. 1987. Predation of turtle nests increases near ecological edges. *Copeia* 1987:250-252.
- WILMERS, T.J., WILMERS, E.M., WELLS, P.W., AND MILLER, M. 1996. Imported fire ants (*Solenopsis invicta*): a growing menace to sea turtle nests in the lower Florida Keys. In: Keinath, J.A., Barnard, D.E., Musick, J.A., and Bell, B.A. (Eds.). *Proceedings of the 15th Annual Workshop on Sea Turtle Biology and Conservation*. NOAA Tech. Mem. NMFS-SEFSC-387, pp. 341-343.

Received: 9 May 1996

Reviewed: 26 November 1996

Revised and Accepted: 1 January 1997