ARTICLES

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Population Structure, Activity, and Sexual Dimorphism in a Central Florida Population of Box Turtles, *Terrapene carolina bauri*

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Abstract. – We used mark-recapture techniques to study a population of box turtles, *Terrapene carolina bauri*, living on an 8 ha isolated patch of mesic forest in central Florida for a four-year period (1992–96). The study population had a density of approximately 16.3 turtles/ha with males and females equally abundant. The population was dominated by adults, with < 4% of the captured turtles < 9 years of age. Males had a higher capture probability than females. Males and females exhibited similar seasonal patterns of activity with significantly greater numbers of turtles being found in the fall than in the spring. Males had significantly longer carapaces than females. Compared to females, the posterior portion of the carapace was wider in males because of the broad posterior marginals. Comparison of our data with information from other populations of *T. carolina* revealed differences in demography, behavior, and sexual size dimorphism, indicating that species management plans should be based on data collected in the population of interest.

Key Words. – Reptilia; Testudines; Emydidae; *Terrapene carolina*; turtle; demography; sexual dimorphism; geographic variation; population density; activity; Florida; USA

Interest in the conservation of American box turtles (*Terrapene* spp.) has increased recently due to reports of declining populations at some sites (Stickel, 1978; Williams and Parker, 1987) and as a result of increased collection of these turtles for the pet trade (Rogers, 1996). To date, research on box turtles has focused largely on populations located in northern temperate regions of the United States (reviewed by Dodd et al., 1994; Ernst et al., 1994). Studies of *T. carolina* in the southern regions of their range could provide interesting comparative data on life history variation within the taxon. Box turtles in the United States have been listed as an Appendix II CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) species (Buhlmann, 1995). This listing makes acquisition of information on life history and ecology of box turtles crucial since these data are needed to develop management and conservation plans for these turtles.

This study presents preliminary data on a population of *Terrapene carolina bauri*, the Florida box turtle (Fig. 1). The range of *T. c. bauri* is restricted to peninsular Florida and the Florida Keys (Ernst et al., 1994). *Terrapene c. bauri* occupies a variety of habitats ranging from mesic hammocks to higher, drier pine uplands (Carr, 1940). The only literature available on the ecology and demography of this subspecies was based on the study of an island population (Dodd et al., 1994; Langtimm et al., 1996; Dodd, 1997a, 1997b) and of museum specimens (Ernst et al., 1995).

In this study, we used a mark-recapture method to determine the age structure, population density, sex ratio, and activity patterns of *T. c. bauri* in a central Florida population. In addition, we determined the degree of sexual dimorphism in several morphological traits. We focused specifically on differences between the sexes since such differences might influence the outcome of management plans. For example, Vogt (1994) suggested that sea turtle management plans should intentionally manipulate the sex ratio of hatchlings to produce female-biased sex ratios. Other authors have pointed out the potential dangers of intentional manipulations of sex ratios (Mrosovsky and Godfrey, 1995; Lovich, 1996). Similar problems could occur if unintentional manipulations of sex ratio occurred in an exploited species as a result of higher capture probability for one sex. Sex ratio is likely to be manipulated by the timing and location of collections if males and females have different spatial or temporal patterns of activity. Capture techniques, collector preferences, or management programs that are based on body size also may result in altered sex ratios in species with sexual size dimorphism. We currently lack the thorough understanding of sexual differences in behavior and morphology that is needed to determine how management practices will influence *Terrapene* populations.

METHODS

Study Site. — Our study site was an 8 ha mesic forest hammock located on the floodplain of the St. Johns River in Volusia County, Florida (Fig. 2). The forest was surrounded on three sides by a freshwater marsh. The fourth side was bounded by a levee and shallow impoundment. The dominant canopy vegetation was cabbage palm (*Sabal palmetto*), slash pine (*Pinus elliottii*), red maple (*Acer rubrum*), and live oak (*Quercus virginiana*). Common understory vegetation

Figure 1. Juvenile *Terrapene carolina bauri* at the study site in Florida. Photo by P.G. May.

included grasses, poison ivy (*Toxicodendron radicans*), wax myrtle (*Myrica cerifera*), saltbush (*Baccharis halimifolia*), and young cabbage palm. There were few fruiting plants at this site.

Data Collection. — Turtles were found by visually searching the study site from 3 April 1992 until 26 March 1996. Approximately twice a week (411 visits in four years), a group typically composed of three to six people searched the site on foot for box turtles that were visible without turning cover. We also searched carefully in leaf litter and turned palm fronds, looked under coverboards, and set up pitfall traps. Unmarked turtles were taken to the lab for data collection and then released at the site of capture within three days. We recorded only the identity, date recaptured, and location of resighted marked turtles.

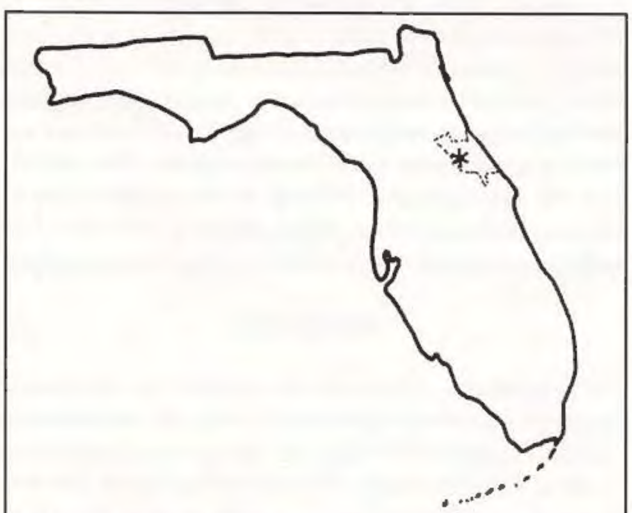

Figure 2. A map of Florida showing the location of the study site (asterisk). The dotted line indicates the boundary of Volusia County.

In the lab we recorded each turtle's sex (based on the concavity of the plastron), body mass (to 0.1 g), carapace length (straight, to 1 mm), carapace width along a line that crossed the center of the abdominal scutes of the plastron, width of the ninth marginal (to 1 mm), and carapace circumference along a line that crossed the center of the abdominal scutes of the plastron (to 0.1 mm). The minimum age of each turtle was determined by counting the lines of arrested growth (LAGs) on the left abdominal scute of the plastron. We assumed that LAGs are produced annually. Most turtles were so old that more than 10 LAGs were present, with the edges of the scutes marked with many tightly packed rings, or the plastron was worn smooth with no visible growth rings. These turtles were simply classified as greater than ten years of age. Each turtle was individually marked by drilling a unique combination of holes in the marginal scutes.

Data Analysis. — We used analysis of variance (ANOVA) to determine if there were significant differences between male and female morphological characters. In several cases our raw data exhibited significant heterogeneity in variances. These data were log-transformed and analyzed with ANOVA if heterogeneity in variances was reduced to nonsignificant levels. There were strong positive correlations between several morphological characters and total body size (as indicated by carapace length). To remove the effects of body size on these morphological measurements, we used analysis of covariance (ANCOVA) with carapace length as the covariate.

The degree of sexual size dimorphism was quantified using the compressed sexual dimorphism index (SDI; Lovich and Gibbons, 1992). SDI = $(-A/B) + 1$ if males are the larger sex and SDI = $(A/B) - 1$ when females are the larger sex (A is the size of the larger sex and B is the size of the smaller sex).

Autocorrelation analyses were used to determine if male and female box turtles showed seasonal activity patterns. These analyses correlated monthly mean activity levels with subsequent monthly mean activity levels using time lags of one to fifteen months. We used ANOVA to determine if the sexes differed in their activity patterns. The average abundance (turtles seen per observer hour) was averaged for all censuses during each season in each of four years for each sex. A statistically significant sex-by-season interaction effect would indicate that males and females had different seasonal activity patterns.

RESULTS

Population Structure. — From April of 1992 through April of 1996 we found 128 individual *T. carolina bauri* and located these turtles 730 times. Only 4 individuals (3.1%) had less than 9 LAGs. Therefore, this population appears to be dominated by adult individuals. There was no significant correlation between the carapace length of turtles and their date of first capture ($r = 0.12$, $n = 128$, $p > 0.05$).

The cumulative number of marked turtles appears to be asymptotically approaching a maximum of approximately 130 adult turtles for our study site (Fig. 3). In the last four months of the study we located box turtles 134 times and only 2 of these sightings involved unmarked turtles. Based on this information, we estimate the population density of box turtles in our hammock to be approximately 16.3 turtles/ha (130 turtles/8 ha).

We found 124 adult turtles of which 65 were females and 58 were males (no sex was recorded for one individual), giving a sex ratio of 1.12:1 females:males. This sex ratio is not significantly different from 1:1 (two-tailed binomial test with the expected probability = 0.50, $p = 0.47$). Individual males were captured on average significantly more frequently than individual females from 2 April 1992 through 15 October 1995 (Table 1; t-Test, $t = 5.18$, df = 119, $p < 0.01$).

Activity. — Box turtles in this population are active (found above ground) throughout the year (Fig. 4). The lack of a regular seasonal pattern of activity in both males and females was demonstrated using autocorrelation analysis. Consistent annual patterns of seasonal activity would result in strong positive correlations with a lag of 12 months in this analysis. For both male and female box turtles the only strong ($r > 0.5$) correlations occurred with a lag of one month, which indicates the only major predictor of the mean activity level during a month was the mean activity level

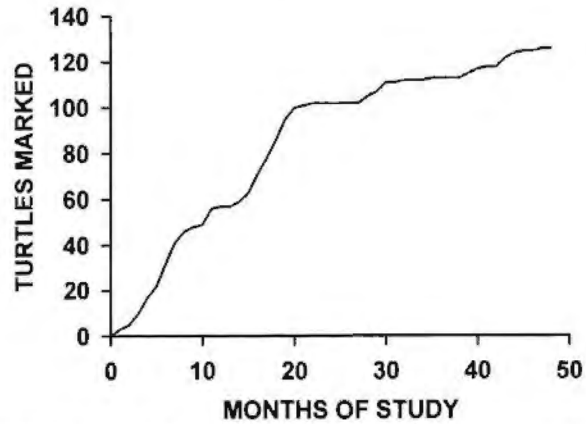

Figure 3. The cumulative number of *Terrapene carolina bauri* marked during this study.

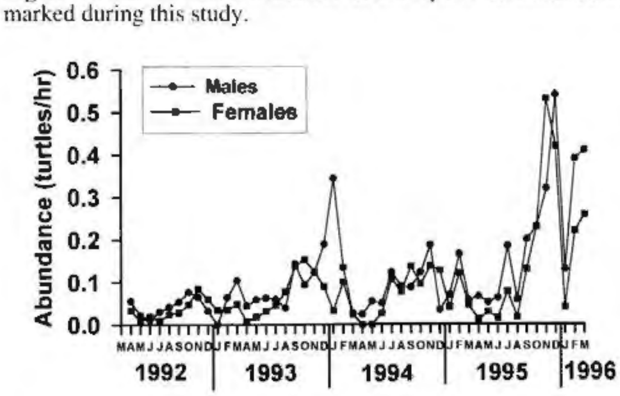

Figure 4. The seasonal activity patterns of male and female *Terrapene carolina bauri*.

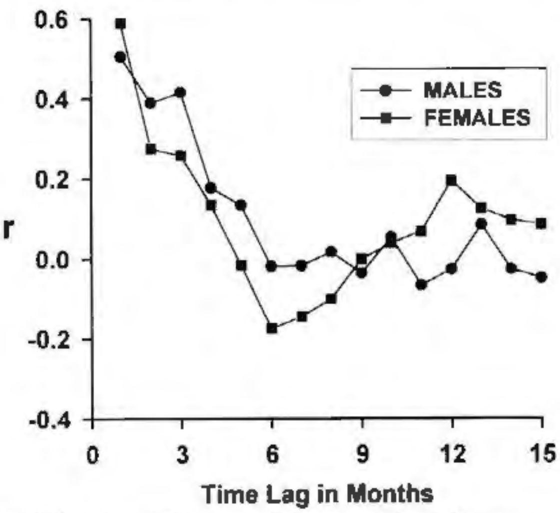

Figure 5. Autocorrelation analysis for seasonal activity in male and female *Terrapene carolina bauri*.

Table 1. Morphological characteristics of male and female *T. carolina bauri* at study site in Volusia County, Florida.

	Males			Females				
Trait	Mean	S.E.	n	Mean	S.E.	n	ANOVA	ANCOVA
Carapace Length (cm)	15.1	0.1	57	13.2	0.1	63	< 0.001	—
Mass (g)	546.9	13.9	57	439.0	8.9	64	< 0.001	0.035
Circumference (cm)	29.3	0.2	57	27.4	0.2	64	< 0.001	0.076
Carapace Width (cm)	11.2	0.1	51	9.7	0.1	58	< 0.001	0.007
Marginal Width (cm)	1.9	0.03	51	1.5	0.02	58	< 0.001	0.001
No. of Captures	5.7	0.7	57	3.7	0.5	64		

Table 2. The effect of sex and season on turtle abundance (captures/observer hour).

Source	df	mean-squares	F-ratio	*p*
Sex	1	0.006	0.873	0.359
Season	3	0.029	4.208	0.016
Sex * Season	3	0.002	0.262	0.852
Error	24	0.007		

observed in the previous month (Fig. 5). Extreme peaks in activity were observed in the fall and winter of both 1993 and 1995. These peaks coincided with heavy flooding of the study site when turtles were easily found on the isolated areas of ground that remained above water.

The lack of a significant sex-by-season interaction effect in our analysis of mean seasonal activity showed that male and female *T. carolina* did not show significantly different patterns of seasonal activity (Table 2). The capture rate for box turtles was significantly affected by season. A Tukey test revealed the only significant difference among the four seasons was that more turtles were found in the fall (mean abundance = 0.33 turtles/observer hr) than in the spring (mean abundance = 0.06 turtles/observer hr).

Sexual Size Dimorphism. — Males were significantly larger than females in all characters (Table 1). This population's sexual size dimorphism index was –0.25 for mass and –0.14 for carapace length. ANCOVA, using carapace length as the covariate, indicated that ninth marginal width was significantly greater in males than in females of the same carapace length (Table 1). There was no significant sexual dimorphism in size-specific carapacial circumference (Table 1). Size-specific mass was significantly greater in females than males; a typical female with a carapace length of 13 cm would have a predicted mass of 424 g, while a male of similar carapace length would have a predicted mass of only 387 g.

DISCUSSION

Sexual Size Dimorphism. — In our study population males were significantly larger than females. Some studies of *T. carolina* have found female-biased sexual size dimorphism (SSD) while others have found male-biased SSD (Table 3). *Terrapene carolina* is one of the few species in which it is known that the polarity of SSD varies among subspecies. Different subspecies of *Kinosternon subrubrum* (Lovich and Lamb, 1995) and different populations of both *K. scorpioides* (Pritchard and Trebbau, 1984) and *K. hirtipes* (Iverson, 1985) also appear to exhibit sexual size dimorphism in different directions. The apparent rarity of intraspecific variation in the direction of SSD in chelonians might reflect a lack of careful comparative studies rather than a real phenomenon.

When viewed interspecifically, SSD in turtles is correlated with latitude, habitat type, mating strategy, and the frequency of female reproduction (Berry and Shine, 1980; Fitch, 1981; Gibbons and Lovich, 1990; Forsman and Shine, 1995). Latitude and SSD were correlated among turtle species (Fitch, 1981). The correlation between latitude and the SDI was not significant among *T. carolina* populations ($r = 0.28$, $n = 10$, Table 3). Intraspecifically, the populations of *T. carolina* from the warmest regions, and therefore possibly the populations having the highest frequency of female reproduction (Tucker et al., 1978), have the strongest male-biased SSD. Careful field study, however, indicates *T. c. bauri* may have low rates of clutch production, with few females producing more than one clutch a year, while other females fail to reproduce in some years (Dodd, 1997a). Forsman and Shine (1995) found increasingly female-biased SSD with increased annual clutch frequency in an interspecific comparison of emydid turtles. More data on clutch frequency from field populations of *T. carolina* are needed to determine how clutch frequency is related to SSD in *T. carolina*.

Males were not only larger than females, they also had a different-shaped carapace. Compared to females, the posterior portion of the male carapace was wider relative to the front. This increase in posterior carapace width was largely due to the broad, outwardly-flaring marginals found on the male carapace. Strong sexual dimorphism was seen in our study population of *T. c. bauri* in both size and shape, but not in eye color, in contrast to *T. c. carolina* (Ernst et al., 1994).

Population Structure. — While *T. c. bauri* is thought to be a common species, few empirical data exist to support this opinion (Dodd and Franz, 1993). Our study population resides on protected land and is relatively isolated. The same is true of the population studied by Langtimm et al. (1996)

Table 3. Sexual size dimorphism in *Terrapene carolina*. Mean male and female carapace length (CL) are measured in cm and approximate latitudes are in degrees North. The sample size (*n*) is the sum of male and female turtles. SDI is the size dimorphism index, with negative numbers indicating males larger than females.

Subspecies	State	Latitude	Male CL	Female CL	*n*	SDI	Study
bauri	Florida	28	14.0	12.9	103	–0.09	Ernst et al., 1995
bauri	Florida	28	13.9	13.3	849	–0.05	Dodd, 1997b
bauri	Florida	29	15.1	13.2	120	–0.14	This study
major	Louisiana	30	16.7	16.0	395	–0.04	Boundy, 1995
triunguis	Louisiana	30	12.3	12.4	309	0.01	Boundy, 1995
triunguis	Oklahoma	35	11.6	12.1	395	0.04	C. Carpenter, *pers. comm.*
carolina	North Carolina	36	14.7	15.4	68	0.05	Stuart and Miller, 1987
carolina	Virginia	38	13.2	13.0	100	–0.02	Mitchell, 1994
carolina	Illinois	39	13.7	13.2	44	–0.04	Elghammer et al., 1979
carolina	Maryland	39	14.1	13.0	352	–0.08	Stickel and Bunck, 1989
carolina	New York	41	13.7	13.2	387	–0.04	Nichols, 1939

on Egmont Key, an island off the west coast of central Florida. They estimated their population density at 16.4 turtles/ha, remarkably similar to our estimate of 16.3 turtles/ha. Our population estimate may be inflated by transient turtles, but given the rarity of unmarked turtles found in the last twenty months of the study (Fig. 3) we suspect transients have a minor impact on our population estimate. The box turtles involved in our study have home ranges that include areas outside the forested study site. We have used radiotelemetry to track 6 turtles for six months and 5 of these turtles moved into the marsh adjacent to the forested study site in periods of dry weather (unpublished data). Our estimate of population density may be inflated since at any one time some of these turtles may be located beyond the boundaries of our study site.

While total population densities of *T. carolina* are similar in this study and that of Langtimm et al. (1996), there appear to be strong differences in the age structure of the populations. At least 25% of the population on Egmont Key appears to be juveniles (Dodd, 1997b). At our study site, juvenile turtles comprise only 3% of the box turtles we found. The differences in the abundance of juveniles may be a result of lower predation intensity on Egmont Key. Mammalian predators that might eat eggs or juvenile turtles are not present on Egmont Key (Dodd, 1997b), but raccoons, armadillos, and bobcats are common at our study site.

Hatchling and juvenile box turtles are thought to be extremely hard to find (Ernst et al., 1994). This makes determining the age structure of box turtle populations difficult. We believe that the majority of box turtles in our hammock were encountered, and that the absence of young individuals results from low recruitment. Since we have been studying the population for four years, the young, supposedly secretive turtles would now be maturing and becoming more apparent. We have not started finding unmarked young adults in the last several years. All the turtles that had their first capture in the last year of the study were well over 10 years old based on the number of LAGs on their scutes and the worn appearance of their plastrons. The lack of a significant correlation coefficient between turtle carapace length and the date of initial capture is another indication that smaller turtles were not recruiting into the population during our study. Furthermore, juveniles do not appear to be more secretive than the adults in this population. Three of the marked turtles were between 3 and 7 years old and we captured these animals an average of 3.67 times during the study. This rate of capture is similar to that of the adult males and females in the population (Table 1). The apparently low recruitment at our study site may indicate it is a declining population or that it is a population in which very high adult survivorship balances the low recruitment rate.

The Egmont key population shows a strongly male-biased (1.6:1 male:female) sex ratio (Dodd, 1997b), in contrast to the 1:1 sex ratio of our study population. Langtimm et al. (1996) found that male and female *T. carolina* had equal capture probabilities, whereas we found males were captured significantly more frequently than females.

Population density estimates at our study site and those reported by Langtimm et al. (1996) indicate that box turtles are common at these two sites in Florida. However, unlike these protected areas, most *T. carolina* in Florida are exposed to the major threats facing other box turtle populations, including automobiles and habitat destruction and fragmentation, but fortunately, collection for the pet trade is illegal (see Dodd and Franz, 1993; Ernst et al., 1994). Unfortunately there are no demographic studies on box turtles in Florida that live in or near more human-influenced areas. We therefore have no information on how these threats are impacting Florida box turtles.

Activity. — We found box turtles active throughout the year, with the rate of turtle captures often higher in the fall and winter than in the warmer months of the year. There are several possible reasons for high fall activity. First, box turtles may forage extensively in the fall to regain the resources used in summer reproduction. Second, flooding of our study site also frequently occurs in the fall. Turtles that moved to the few dry areas may have been more easily found compared to when they were more dispersed. Dodd et al. (1994) also found that Florida box turtles were active throughout the year.

Implications for Management Plans. — The claim has been made that young *T. carolina* have a low per capita probability of harvest simply because they are rare in shipments for the pet trade (Boundy, 1995). The rarity of young box turtles in shipments is likely the result of their rarity in the population, rather than small body size. The box turtles in our study population appear to have low rates of recruitment to the adult population. These low recruitment rates may result, in part, from a late age at first reproduction, a low frequency of reproduction, and low clutch size in *T. c. bauri* (Dodd, 1997a, 1997b). Simulation studies based on life history data collected in long-term studies indicate that turtle populations fare poorly in the face of increased mortality rates of any age class in the population as a result of their life history characteristics (Congdon et al., 1993, 1994). Box turtle populations with demographic characteristics similar to those of our study population are unlikely to be subjects of sustainable harvests.

The use of our study site to provide data for management plans on *T. carolina* populations elsewhere would likely lead to underestimating the impact of harvesting turtles. Like most biologists, we chose to study organisms where they are most abundant, not where they occur at lesser and more typical population densities. Using the population density of our study site to estimate the total population size of a larger area would result in an overestimate of population size. Using such an overestimate in a management plan would grossly underestimate the impact of harvesting a certain number of turtles from that area.

There are differences in age structure, sex ratio, and sex-specific capture rates between the population of *T. c. bauri* on Egmont Key (Dodd et al., 1994; Langtimm et al., 1996) and our study population. These differences in behavior and demographics indicate that data from one population may be of little use in devising management plans for other populations of the same taxon. This may be particularly true of populations of *T. carolina* in the southern USA, where subspecies with marked differences in morphology occur. Meaningful management plans for *T. carolina* will depend on long-term studies that accumulate data on box turtle demographics in areas where exploitation is planned. Such studies are not currently available.

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