Seasonal Movements and Reproduction in the Striped Mud Turtle (*Kinosternon baurii*) from the Southern Everglades, Florida

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ABSTRACT. – Movements and reproductive characteristics were measured in a population of the striped mud turtle (*Kinosternon baurii*) in the Everglades of southern Florida, USA. Most movements occurred during the May–October wet season, with peak movement of females in October. Although movements and ovarian cycles of *K. baurii* in the Everglades were similar to those of *K. baurii* at other sites in Florida, egg length and annual reproductive potential differed from individuals of a north Florida population and individuals from eutrophic canals in Miami. Among the three sites, Everglades females produced the largest eggs but also were the least fecund. The production of a large egg might be a response by Everglades females to their low annual fecundity in an oligotrophic system. These results underscore the importance of site-specific ecological data in predicting species' responses to wide-scale changes in the environment, which is especially important in the southern Everglades where proposed restoration plans involve not only water depth but water quality.

KEY WORDS. – Reptilia; Testudines; Kinosternidae; Kinosternon baurii; turtle; ecology; movement; reproduction; conservation; Everglades; Florida; USA

The striped mud turtle (Kinosternon baurii) is a smallbodied aquatic species of the southeastern United States (Conant and Collins, 1991). A large proportion of its geographic range is in Florida, where it is found in a wide range of habitats (Carr, 1940; Duellman and Schwartz, 1958). In northern Florida, seasonal movements of K. baurii are bimodal, associated with spring rains and the fall drying period, and the nine month egglaying season excludes the mid-summer months (Iverson, 1979). In extreme southern Florida, seasonal movements are as yet unknown, and the reproductive ecology of K. baurii is currently understood primarily from clutch characteristics of a population sampled during the summer months in eutrophic canals in Miami (Meshaka, 1988). However, populations of K. baurii in the southern Everglades, an expansive but nutrient-poor system that encompasses much of the southernmost portion of this species' geographic range, have yet to be studied in a way that analyzes movement and reproduction with respect to both latitude and habitat quality. To examine this relationship, we measured the seasonal movements and reproductive characteristics of K. baurii in Everglades National Park (ENP) and we compared our findings with those of other studies from eutrophic canals of extreme south Florida (Miami) (Meshaka, 1988) and those of central Florida (Wygoda, 1979; Mushinsky and Wilson, 1992; Wilson et al., 1999) and northcentral Florida (Iverson, 1979).

METHODS

We measured seasonal movements by recording and collecting all *K. baurii* observed twice daily, five days per

week, on a section of ENP roads during May 1995 – April 1997. The 15 km road from the park entrance to the Daniel Beard Center (DBC) traverses freshwater marsh, prairie, tropical hardwood hammock, pineland, and disturbed habitat on Main Park Road, Royal Palm Road, and Long Pine Key Road (a.k.a. Research Road) of ENP. We also combined the sample of turtles collected during the standardized road search with available museum specimens collected from roads in ENP from 1958 to 1998 as another measure of seasonal movements of *K. baurii*.

Reproductive characteristics were assembled using specimens collected from the systematic road collections and opportunistic captures made on Main Park Road, from the entrance to Flamingo. For all turtles, carapace length (CL) was measured to the nearest 1.0 mm with vernier calipers. Males with coiled epididymides were deemed sexually mature. Females with enlarged follicles (> 7.0 mm), shelled eggs, or corpora lutea were deemed sexually mature (Iverson, 1979). We measured diameters of ovarian follicles and corpora lutea, and the lengths and widths of shelled eggs, and length and width of the left testis to the nearest 0.5 mm with vernier calipers. Lengths and widths of testes were presented as percent of CL. Rainfall data were provided by rain gauges at the DBC, and water flow data were recorded at the Taylor Slough Bridge.

We compared our Everglades data with data from Meshaka (1988) and Iverson (1979); we refer to these data sets throughout our paper as Miami (south Florida) and north Florida, respectively. Conversion of female plastron length (PL) to CL from Iverson's (1979) data was accomplished by using the PL/CL ratio of 0.941 derived from Iverson (1978). Means are followed by one standard deviation. A MANCOVA was performed on SPSS. Because reproductive responses to different nutrient bases were predicted to occur, one-tailed p values < 0.05 were deemed significant. All specimens are deposited in the Everglades Regional Collection Center (ERCC).

RESULTS

Movements. — Movements of K. baurii were highly seasonal as measured during the standardized road search and by numbers of all museum specimens captured on the road (Fig. 1). Seasonal activity was pronounced in this species. Most turtles were observed during the May-October wet season, as indicated by road searches ($\chi^2 = 10.8, p >$ 0.01) and museum specimens ($\chi^2 = 18.5$, p < 0.01), and the greatest number were observed during the very end of the wet season in October. Females outnumbered males in both abundance measures (road: $\chi^2 = 7.0$, p < 0.01 and museum: $\chi^2 = 16.34, p < 0.01$). Females moved most in October when water levels were highest. Dry season movements were few and nearly exclusively by females (Fig. 1). Most females found on the road were either gravid or had just deposited their eggs, as evidenced by fresh corpora lutea and the presence of sand on the carapace. The few females not meeting those criteria were collected during what appeared to be a short mid-summer intermission in reproduction from July to August, at which time ovarian follicles were small (Fig. 2). Consequently, female movement for all months except for the middle of the wet season was associated with nesting activities.

By contrast, movements of males and juveniles, including hatchlings, were primarily restricted to the wet season (Fig. 1), although one hatchling was found in February. In the few adult males that were collected, the testes size, as percent length and width (L x W) of CL, were largest during late summer: June (9.1 x 9.1%; n = 1), July (9.8 x 6.4%; n =1), August (13.7 + 0.3 x 10.7 + 0.6%; n = 2), and October (14.7 + 1.2 x 10.2 + 0.05%; n = 2). These data are suggestive of copulation commencing in late summer/fall and coinciding with resumption of the gravid condition and a spike in female movements.

Body Size and Clutch Parameters. — Adult K. baurii in the Everglades were sexually dimorphic in body size ($T_{df=11}$ = 3.20, p < 0.008) (Fig. 3). Mean body size varied among populations (Table 1). Although Everglades and north Florida females were similar in mean body size (p > 0.05), females from Miami were significantly larger in mean body size than females of the Everglades ($T_{df=19} = 5.59$, p < 0.0000) and north Florida ($T_{df=50} = -4.70$, p < 0.0000). Likewise, Everglades males were significantly smaller in body size than Miami males ($T_{df=12} = 3.55$, p < 0.004).

Clutch size of Everglades females ranged from an average of 1.5 to 2.1 eggs as measured by number of shelled eggs, follicles > 10 mm, or fresh luteal scars (Table 1). Luteal scars, occasionally difficult to detect, provided a significantly different estimation of clutch size than did shelled



Figure 1. Monthly distribution of 88 striped mud turtles (*Kinosternon baurii*) captured on the road in Everglades National Park, during (A) our study, May 1995 – April 1997 (n = 18), and (B) based on museum specimens collected 1958–98 (n = 70).

eggs ($T_{df=30} = 2.05$, p < 0.04) and enlarged follicles ($T_{df=30} = 2.21$, p < 0.04), which did not differ significantly (p > 0.05) from one another. Clutch size was smaller in Everglades females than in Miami females when measured by shelled eggs (Z = 1.84, p < 0.03) and corpora lutea ($T_{df=14} = -2.58$, p < 0.01). Measured by number of shelled eggs, mean clutch size in north Florida was significantly different ($T_{df=42} = -2.92$) from that of the Everglades, but not Miami (p > 0.05).

For *K. baurii* in the Everglades, body length (CL) accounted for 36% (p < 0.008) of the variance in clutch size as measured by number of shelled eggs (Fig. 4). However, no such body-size component (p > 0.05) to clutch size existed in north Florida or Miami females (Fig. 4). ANCOVA disclosed no location effect on clutch size of *K. baurii* when the small sample (n = 7) from Miami was included in the



Figure 2. Diameters of ova and lengths of shelled eggs in mm in the striped mud turtle (*Kinosternon baurii*) from Everglades National Park.



Figure 3. Distribution of carapace length (CL) in mm of striped mud turtles (*Kinosternon baurii*) captured on the road in Ever-glades National Park, 1958–98.

analysis (Table 2). However, when the Miami sample was removed from the analysis, we discovered that, independent of body size, smaller clutches were produced by Everglades females than by those from north Florida (Table 2; Fig. 4).

The number of clutches produced annually by *K. baurii* was greatest in north Florida and equally low in Everglades and Miami; however, different values for annual clutch production in Miami might have been observed if a larger series was collected over a longer period than the summer months. Annual egg production, estimated by multiplying the mean clutch size by the mean or maximum number of

Table 1. Morphometric data and reproductive characteristics of the striped mud turtle (*Kinosternon baurii*) from the Everglades (this study), south Florida (Miami) canals (Meshaka, 1988), and north Florida (Iverson, 1979). Means are followed by std. dev., range, and sample size. N.S. = Not significant (p > 0.05). * = dissected females. Estimated reproductive potentials are presented as means and (maximum).

	Everglades	Miami	North Florida	
Carapace length (mm)				
Male	77.2±10.6	90.8 ± 4.8		
	(59-90; 10)	(80-98; 12)		
Female	89.0±7.0;	104.4 ± 9.0	91.8 ± 8.1	
	(77-107:25)*	(85-125:14)	(74-111:38)	
Egglaving season	Sept-June	Sept-June	1991 - 1992 - 1995 - 1995 - 1995 - 1995 - 1995 - 1995 - 1995 - 1995 - 1995 - 1995 - 1995 - 1995 - 1995 - 1995 -	
Clutch size				
Shelled eggs	1.9 ± 0.7	3.1±1.6	2.6 ± 1.0	
	(1-3; 16)	(1-5;7)	(n = 38)	
Follicles > 10.0 mm	2.1±1.2	2.9 ± 1.7	2.7±0.9	
	(1-5; 22)	(1-6; 12)	(n = 48)	
Corpora lutea	1.5±0.5	2.7±1.5	2.5±0.9	
	(1-2; 16)	(1-5; 13)	(n = 82)	
Estimated reproductive po	tential		1997 - 1997 - 1997 - 1997 - 1997 - 1997 - 1997 - 1997 - 1997 - 1997 - 1997 - 1997 - 1997 - 1997 - 1997 - 1997 -	
Number of clutches	3 (4)	3 (5)	3 (6)	
Number of eggs	203			
Shelled eggs	5.7 (7.6)	9.3 (15.5)	7.8 (15.6)	
Follicles > 10.0 mm	6.3 (8.4)	8.7 (14.5)	8.1 (16.2)	
Corpora lutea	4.5 (6.0)	8.1 (13.5)	7.5 (15.0)	
Shelled egg size	5461103 8 066193 8 0			
Length	29.1±1.9	27.6±1.6	27.6±1.9	
. (25.5-32.5; 30)	(25.0-31.0; 22)	(22.8-32.8; 112)	
Width	16.5±0.7	15.3±1.4	16.6	
(15.3-18.0; 30)	(11.7-17.3; 22)	(13.6-19.3; 112)	
Relationships				
Clutch size vs. body size	<i>p</i> < 0.01	N.S.	N.S.	
Egg size vs. body size	N.S.	N.S.	N.S.	
Egg size vs. clutch size	e N.S.	N.S.	N.S.	



Figure 4. Relationship of clutch size to carapace length (CL) in mm in the striped mud turtle (*Kinosternon baurii*) from Everglades National Park, a canal in south Florida (Miami) (Meshaka, 1988), and north Florida (Iverson, 1979). Adjusted regression equation for clutch size $= -3.797 + CL^{*}0.067 + site$ score. Site scores: Everglades = -0.296, north Florida = 0.

Table 2. Tests of between-subjects effects in clutch characteristics of the striped mud turtle, *Kinosternon baurii*, from three sites in Florida. * = analysis using only north Florida and Everglades samples. See text for explanation.

Source	Dependent Variable	Sum of Squares	df	Mean Square	F	Sig.
CL (mm)	Egg length (mm)	9.697	1	9.697	2.687	0.107
	Clutch size	11.427	1	11.427	12.719	0.001
	Clutch size*	14.696	1	14.696	24.112	0.000
Location	Egg length (mm)	23.278	2	11.639	3.225	0.047
	Clutch size	4.449	2	2.224	2.476	0.093
	Clutch size*	3.914	1	3.914	6.422	0.014
Error	Egg length (mm)	205.704	57	3.609		
	Clutch size	51.210	57	0.898		
	Clutch size*	31.084	51	0.609		

clutches possible, was lowest in the Everglades regardless of the measure of clutch size used in the calculation (Table 1).

Despite small body size, shelled eggs of Everglades females were significantly longer ($T_{df=50} = 3.04, p < 0.003$) and wider ($T_{df=29} = 3.60$, p > 0.001) than those of Miami females. Shelled eggs of Everglades females also were significantly longer ($T_{df=140}$ =-3.92, p>0.0001) but not wider (p>0.05) than those of north Florida (Table 1). Mean shelled egg length was similar (p > 0.05) between Miami and north Florida females, although Miami females produced significantly wider ($T_{df=26}$ = -4.26, p > 0.0002) shelled eggs than did females from north Florida. No body size component to maximum shelled egg length (Table 1) nor between maximum shelled egg length and clutch size (Table 1; Fig. 5) was detected for any of the three populations; however, an ANCOVA disclosed a significant location effect to maximum egg length (Table 2; Fig. 6). Consequently, as compared to a eutrophic south Florida (Miami) and a north Florida site, Everglades K. baurii produced the largest eggs at the greatest expense of annual egg production.

DISCUSSION

The relationship between movement and reproduction in female K. baurii from the southern Everglades was similar to that of other Florida populations (Iverson, 1979; Wygoda, 1979; Mushinsky and Wilson, 1992, Wilson et al., in press). For example, a midsummer intermission in egg development (Iverson, 1979) and nesting activities (Wilson et al., in press) was evident in central and northern Florida. The midsummer hiatus in the gravid condition in this species has been hypothesized to be a result of high summer temperatures that presumably hinder production of eggs (Iverson, 1979). Although summer monthly temperature maxima are lower in the southern Everglades than in north Florida (Wood, 1996), the shallow water of the Everglades prairies and marshes could still be too hot for females to produce eggs. In this regard, females from deeper, cooler canals in Miami were gravid in each month during the May-August study (Meshaka, 1988), and a very few females in Tampa nested during this time (Wilson et al., in press). Consequently, the mid-summer intermission in egg production is normal for this species but is also flexible.

The late summer, early fall pulse in female overland movement in the southern Everglades was also evident in Tampa (Wilson et al., in press) and may have represented a genuine peak in nesting activities following reproductive quiescence. A late summer, early fall peak in nesting for Florida populations of *K. baurii* would provide a distinct advantage when water levels are unlikely to rise any higher and inundate eggs. For southern Everglades populations, the advantage is greater in light of both the pronounced wet season and the low elevation of upland habitats imbedded in the wetland. The increased fertility of males in late summer may also have been timed to coincide with the female reproductive season.

Terrestrial captures of K. baurii seldom involve many males (Wygoda, 1979; Mushinsky and Wilson, 1992; Wilson et al., in press), and our results corroborate these observations. In the Everglades, the absence of male movements and scarcity of juvenile movements in the dry season suggested that movements of such individuals were associated with rainfall which, like females captured during July-August, allowed individuals to move actively in a mosaic of wet/dry habitats or passively with the sheet flow of water. Because most female movements are driven by a search for nests, and male movements are most likely dispersal events under the cover of rain, a highly uneven sex ratio among terrestrial individuals is not at all surprising. Meshaka (1988) found an equal sex ratio by aquatic trapping in Miami, and we predict that a 1:1 sex ratio likewise exists in the southern Everglades population of K. baurii.

One unresolved aspect in the movements of Everglades *K. baurii* is the relationship between hatching and appearance of hatchlings. We offer two hypothetical scenarios to explain mid- to late summer appearance of hatchlings and small juveniles and the singular February hatchling record.

If late summer to early fall represented a nesting peak in the Everglades as it does elsewhere (Wilson et al., in press), and if eggs laid in the fall entered diapause until spring as they do elsewhere (Ewert and Wilson, 1996), then a four



Figure 5. Relationship of maximum shelled egg length (mm) to clutch size in mm in the striped mud turtle (*Kinosternon baurii*) from Everglades National Park, a canal in south Florida (Miami) (Meshaka, 1988), and north Florida (Iverson, 1979).



Figure 6. Relationship of maximum shelled egg length in mm to carapace length (CL) in the striped mud turtle (*Kinosternon baurii*) from Everglades National Park, a canal in south Florida (Miami) (Meshaka, 1988), and north Florida (Iverson, 1979). Adjusted regression equation for maximum shelled egg length = 23.828 + CL*0.050 + site score. Site scores: Miami = -0.789, Everglades = 1.072, north Florida = 0.

month incubation period (Iverson, 1977) would place appearance of hatchlings in mid- to late summer the following year, as observed in this study and that of Mushinsky and Wilson (1992). The spring pulse of hatchlings observed by Mushinsky and Wilson (1992) may be young that overwintered after fall emergence. In this scenario, the February hatchling and the small juveniles captured in midto late summer could have represented overwintered fall hatchlings.

On the other hand, because oviposition was nearly continuous in the southern Everglades, and the wet/dry season is markedly pronounced there (Beard, 1938), the nearly exclusive mid-summer terrestrial appearance of hatchlings and very small juveniles could have been more a result of en-masse dispersal under the necessary wet conditions rather than a reflection of peak nesting several months earlier. This scenario also would explain the appearance of a single February hatchling, as well as mid- to late summer hatchlings and small juveniles that would have hatched earlier in the summer. However, until ecology of juveniles is addressed with the same intensity as that of adults, the answers to such basic questions as when Everglades *K. baurii* eggs hatch and when hatchlings normally appear remain speculative.

Clutch size and body size of both sexes in the Everglades were on average smaller than Miami counterparts but were similar to those of north Florida females, suggesting that differences in habitat, not latitude, controlled both characteristics in *K. baurii*. Not surprisingly, therefore, assuming equal body size among locations, a very striking reproductive response by *K. baurii* living in the oligotrophic system of the southern Everglades was detected in egg length, with Everglades females producing the largest shelled eggs. This finding coincided with the greatest loss in annual fecundity by Everglades females among the three sites and smaller clutch size compared to north Florida females. Consequently, fecundity was compromised in the southern Everglades and compensated by the production of a larger egg and possibly more successful hatchling. The somewhat confounding pattern in Miami canal-dwelling females of large body size, small eggs, and high annual egg production, but of clutches similar in size to those of Everglades and north Florida, corroborates our findings of reduced fecundity in nutrient-starved systems, and reveals the difficulty of generalization from small samples from the apparently high variability in artificial canals to which this species must respond. In this regard, canals may represent inconsistent variables in what are otherwise predictable responses in natural systems.

Studies of the American alligator (*Alligator mississippiensis*) have indicated that the mean clutch size and minimum and mean body size at maturity of Everglades populations are smaller than those of northern counterparts and those from managed areas outside of the Everglades (Jacobsen and Kushlan, 1989; Kushlan and Jacobsen, 1990; Mazzotti and Brandt, 1994). Moreover, Everglades *A. mississippiensis* were found to grow more slowly than more northern counterparts (Jacobsen and Kushlan, 1989; Dalrymple, 1996) resulting in the observed differences in reproductive parameters. In turn, the cause of slow growth of *A. mississippiensis* was most likely seasonal resource limitation in an environment where activity is continuous but productivity is seasonally limited (Dalrymple, 1996). In light of these similarities, the same could be true of growth

in Everglades *K. baurii* as compared to that of the Miami *K. baurii*. Egg size was not examined for *A. mississippiensis*, thereby leaving unresolved the question of whether or not Everglades populations of *A. mississippiensis* respond to, or compensate for, reduced annual fecundity with the production of large eggs as did Everglades *K. baurii*.

The Everglades is a young system, scarcely older than 5000 years (Gleason et al., 1994). Movements and ovarian cycles of *K. baurii* in this system have adhered to a pattern found elsewhere in its geographic range. Specific to the nutrient base of its habitat, Everglades *K. baurii* have responded in ways somewhat similar to another north temperate reptile species. Our findings underscore the importance of site-specific data when formulating models that relate to geographic variation of life history traits and those relating to the management of species. This latter consideration is especially important in the southern Everglades, where wide-scale hydrological restoration plans are being considered that take into account not only hydroperiod, but water quality as well.

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