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ECOLOGY OF THE EASTERN RIBBONSNAKE (*THAMNOPHIS SAURITUS*) IN SOUTHERN ALABAMA WITH EVIDENCE OF SEASONAL MULTIPLE BROODS

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***Abstract*.—Studies are lacking on the ecology of the Eastern Ribbonsnake (*Thamnophis sauritus*), especially in the southern United States. We describe some aspects of the sexual dimorphism, sex ratio, feeding habits, reproductive biology, and seasonal activity of the Eastern Ribbonsnake in a southern Alabama Tupelo-Gum swamp from 2003–2005. We captured 339 Eastern Ribbonsnakes 379 times; females were significantly longer than males, but males had longer tails. Snakes were active year-round, and the longest straight-line distance travelled by any snake was 1,050 m. Snakes consumed only frogs (*Hyla* spp. and *Lithobates* spp.); a shift occurred when juveniles switched from feeding on tadpoles to adult frogs. We found females had an extended reproductive season, producing broods April–October. Two females double brooded during the 2004 reproductive season, with 99 and 118 days between broods. The average brood size for Eastern Ribbonsnakes from six females that produced eight broods was 14 ± 3.18 (range 9–19). A reduction in brood size occurred in both females that produced multiple broods, but no decrease in neonate snout-vent length was detected between broods. Overall, our study provides needed natural history data from a southern location and the first evidence for multiple broods in a wild, temperate snake.**

Key Words.—Alabama; broods; clutch; ecology; reproduction; snake; *Thamnophis*

INTRODUCTION

The garter snakes (*Thamnophis* spp.) may be the most studied snakes in the world, and research on garter snakes has greatly expanded our knowledge of snake ecology and evolution (Rossman et al. 1996). Despite our wealth of knowledge on garter snakes, a geographical bias exists in the current literature. Early studies on *Thamnophis* spp. were conducted in the northern United States and Canada (Rossman et al. 1996), whereas few studies have been conducted on the ecology and natural history of garter snake populations in the southern United States and Mexico (Rossman et al. 1996; Seigel et al. 2000). The Eastern Ribbonsnake, *Thamnophis sauritus* (Fig. 1), is not an exception to this geographical bias; significant studies of its ecology and natural history occurred in Maryland (McCauley 1945), Michigan (Burt 1928; Carpenter 1952), and Ontario (Rossman 1963). The lack of data on southern populations of the Eastern Ribbonsnake hinders our understanding of its ecology and natural history (Rossman et al. 1996), which constrains our ability to conserve and understand Eastern Ribbonsnake populations in the southern United States.

The Eastern Ribbonsnake is a medium-sized, semi-aquatic species that is widespread throughout Eastern North America (Conant and Collins 1998). Generally, the species is described as an agile snake that inhabits swamps, stream margins, American Beaver (*Castor canadensis*) ponds, and wet marshes (Mount 1975). Like many natricines, the Eastern Ribbonsnake can be extremely abundant in ideal habitat, but may be conspicuously absent in apparently suitable habitat (Mount 1975). Absences are widespread in many regions, and Eastern Ribbonsnakes are a conservation

FIGURE 1. Eastern Ribbonsnake (*Thamnophis sauritus*) basking on Saw Palmetto from Mound Island in the Mobile-Tensaw Delta Wildlife Management Area, Baldwin County, Alabama, USA. (Photographed by Gabriel Langford)

FIGURE 2. Typical habitat of the Eastern Ribbonsnake (*Thamnophis sauritus*) on Mound Island, Baldwin County, Alabama, USA. (Photographed by Joel Borden)

concern in the following states: Illinois, Wisconsin, Florida, Connecticut, Kentucky, Maine, Rhode Island, and West Virginia (Ernst and Ernst 2003). Eastern Ribbonsnake populations are reportedly declining because of habitat destruction and fragmentation occurring throughout the Eastern Ribbon Snake's geographic range (Ernst and Ernst 2003). These threats are likely magnified by increasing rates of urbanization in southern states, which underscores the need for natural history data from southern locations to establish baseline knowledge for effective conservation.

Seigel and Ford (1987) have suggested that frequency of reproduction is the most important aspect of snake reproductive biology. Seigel and Ford's (1987) review of reproductive frequency found that most snakes produce a single annual or biannual brood. Yet, many authors have suggested that some wild snakes have the potential to produce multiple clutches in a reproductive season (Rossman 1963; Ford and Karges 1987; Seigel and Ford 1987; Rossman et al. 1996; Seigel et al. 2000), but until recently evidence for multiple broods in a single season was limited to data on seasonal reproductive patterns (e.g., Ford and Karges 1987). The first unequivocal evidence of multiple clutches in a wild snake was found in the Keelback (*Tropidonophis mairii*), a tropical natricine (Brown and Shine 2002). Brown and Shine's (2002) discovery was exciting, yet not unexpected, because several species of snakes in captivity, under artificially high amounts of food and ideal environmental conditions, are known to produce multiple broods (Tryon 1984). The ability to produce multiple broods in captivity suggests that when ecological constraints are relaxed, several snake species may produce multiple broods in the wild. Herein we provide data on some aspects of the ecology of the Eastern Ribbonsnake in a southern Alabama swamp, including the first evidence of multiple broods in a wild, viviparous, temperate snake. We also collected data on sex ratio, sexual size dimorphism, activity and habitat use, reproduction, and diet during a mark-recapture study from 2003–2005 in the Mobile-Tensaw Delta, Baldwin County, Alabama.

MATERIALS AND METHODS

Study area.—We studied snakes in the Upper Delta Wildlife Management Area (UDWMA) in Mobile and Baldwin counties, Alabama (N 31.54º, W 87.85º). The UDWMA constitutes a large (ca. 100,000 ha) seasonally–flooded bottomland hardwood forest with numerous swamps of Bald Cypress (*Taxodium distichum*), Black Gum (*Nyssa sylvatica*), and Water Tupelo (*Nyssa aquatic*; Fig. 2). The UDWMA was classified as a temperate rainforest (Bailey 1995), with long, hot summers and short, mild winters. Mean daily temperatures range from 1–22° C in January and 21–35° C in July and the annual mean precipitation for the study area was 163 cm (acquired from the nearest National Oceanic and Atmospheric Administration weather station at Mount Vernon, Alabama. Available at http://www.ncdc.noaa.gov/oa/climate/stationlocator.html [Accessed 20 January 2011). Flooding was common and occurred primarily during winter and early summer prolonged rain events that occurred upstream from the UDWMA.

We sampled herpetofauna throughout the UDWMA as part of a systematic herpetological inventory. However, the current study concentrated on Mound Island, located in the middle of the UDWMA. Mound Island is a small island (ca. 2.5 ha) that was accessible only by boat. The island was characterized by several Native American mounds (3–15 m elevation) that rise from an expansive tupelo-gum swamp in the interior of the island. Other significant elevations included several low-lying ridges and natural levees that occurred throughout Mound Island. Limited timber harvesting on Mound Island created gaps of successional forest (6–15 y) dispersed between much older stands (> 60 y). Wetland vegetation was composed of mature Bald Cypress, Black Gum, and Water Tupelo, which constituted 90% of the over-story vegetation and formed a closed canopy. The elevated terrestrial regions consist of large Sweetgum (*Liquidambar styraciflua*), Water Oak (*Quercus nigra*), and American Elm (*Ulmus americana*) with almost complete canopy coverage; except in areas with recent timber harvesting, which did not have an overhead canopy (C. Smoot Major, unpubl. data)

Sampling technique.—We collected snakes over a three-year period (2003–2005) at five locations on or adjacent to Mound Island. We surveyed two sites (A and B) from 25 May – 28 August 2003, and 3 June – 24 October 2004 using twelve 1 m^2 plywood coverboards (Grant et al. 1992), 20 Gee Minnow Traps (Seigel et al. 2000), and opportunistic hand captures at each location. We captured snakes by hand when walking to and from the boat landing at sites C, D, and E (see below), which equaled about 150 m per site. During these opportunistic hand captures, we searched under/in natural cover objects (e.g., vegetation, entrance to mammal burrows) that lay directly adjacent to or on the trail. We established three 30 m terrestrial Y-array drift fences with funnel traps (Enge 2001) at three additional sites (C, D, and E) for a total of nine drift fences. We never established drift fences on sites A and B because Native American artifacts might have been disturbed by digging. We opened and checked funnel traps along drift fences from 13 June – 26 November 2004 and 27 December 2004 – 6 March 2005. We closed funnel traps in December 2004 and April to May 2005 because extensive flooding prevented boat travel to Mound Island. In 2005, we made additional trips in April (n = 3) and May (n = 3) to hand capture snakes in the vicinity of all sites when flood waters permitted boat travel. Except for the aforementioned periods of flooding, we checked traps at least four times per week.

Upon capture we measured snout-vent length (SVL) and tail length (TL) to the nearest mm before determining the sex of snakes by visual inspection of the tail or by probing (Fitch 1987). We forced engorged snakes to regurgitate stomach contents and we palpated females for the presence of developing embryos (Fitch 1987). We marked snakes individually by ventral scale-clipping (Brown and Parker 1976) and released snakes 5 m from trapping arrays to prevent immediate recapture. In two instances, we recaptured females that had given birth earlier in our study, and both females gave birth to a second brood. The first female gave birth to both broods in funnel traps. We took the second female to the laboratory upon being recaptured where we watched for her to produce a second brood. We accommodated the second female according to Ford and Seigel (1989) and during six days of captivity, she consumed two medium-sized Bronze Frogs (*Lithobates clamitans*) and gave birth on the sixth day. We measured offspring in the same manner as the adults; in addition we weighed neonates on an electronic balance to the nearest 0.1 g. Before offspring were released at the point of capture, we clipped a ventral scale as a cohort identification mark. We deposited representative voucher specimens of adults and young in the Vertebrate Natural History Collection of the University of South Alabama.

Data analysis.—We found little data on size of sexual maturity in the Eastern Ribbonsnake. Carpenter (1952) found females attained maturity at a SVL of 42 cm in southern Michigan, but no data was provided for males. Given these few data, we established size at sexual maturity as 330 mm SVL for males and 380 mm SVL for females because these were the smallest reproductive individuals we encountered during this study. We analyzed sexual dimorphism in body size on SVL with a *t*-test, but we used an analysis of covariance (ANCOVA) between the sexes (SVL as a covariate) on TL, because TL has been shown to be highly correlated with body size (Avila et al. 2006). We excluded individuals with severely damaged tails from the ANCOVA. To meet assumptions of homoscedasticity for parametric tests, we log transformed body size variables (Sokal and Rohlf 1995). We used a *t*-test to determine if hatchling log SVL varied between broods from the same female. We used a Chi-square goodness of fit test to determine if sex ratios deviated from expected. To determine monthly snake activity, we divided the number of captures each month by the number of days traps were open that month. We used only data from 2004–2005 to evaluate trapping effectiveness because funnel traps were not used in 2003. We also excluded snakes born during the study when evaluating trap effectiveness. We tested for a difference between the sexes in straight-line movements with a Mann-Whitney U test because parametric assumptions could not be satisfied. We assigned a significance level of $\alpha = 0.05$ for all statistical tests and we reported mean and standard deviations as $\bar{x}$

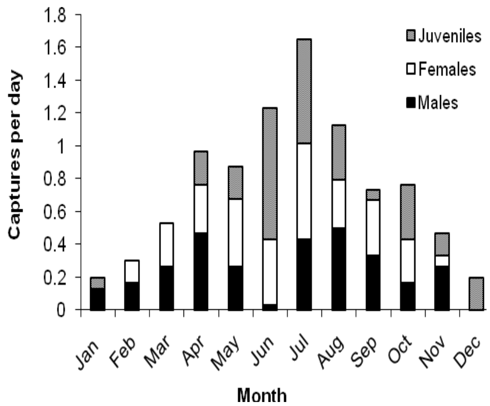

FIGURE 3. Number of male, female, and juvenile Eastern Ribbonsnakes (*Thamnophis sauritus*) captured per day on or near Mound Island, Baldwin County, Alabama from 2003–2005.

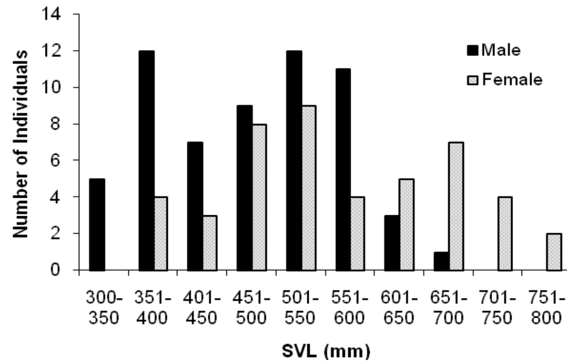

FIGURE 4. Snout-vent length (SVL) of adult Eastern Ribbonsnakes (*Thamnophis sauritus*) captured on or near Mound Island, Baldwin County, Alabama from 2003–2005.

and ± SD. We used Minitab 15 (Minitab Inc. State College, Pennsylvania, USA) for all statistical tests.

RESULTS

***Body size and adult sex ratio*.**—We captured 58 male, 51 female, and 230 juvenile and hatchling ribbonsnakes (339 total) 379 times, which includes 111 snakes born during this study. The adult sex ratio (1:0.87 M:F) was not significantly different from 1:1 ($X^2 = 0.44$, df = 1, $P = 0.503$). We found more females than males in May-July and October (Fig. 3); males were more common in other months. The largest snakes were all female (Fig. 4), including one female that represented a new maximum total length for the Eastern Ribbonsnake (Langford and Borden 2006). Overall, we found females to be significantly longer in body length (SVL) than males (Table 1; $t = 4.07$, df = 1, $P < 0.001$), but males had significantly longer tails than females ($F_{1,97} = 12.74$, $P < 0.001$).

***Activity and natural history observations*.**—We captured Eastern Ribbonsnakes every month of the year, although we caught only juveniles and hatchlings in December and no females in December and January (Fig. 5). During cold periods snakes took refuge in vegetation piles, tree root mats, and abandoned mammal burrows. Our most effective trapping technique was opportunistic hand capture, which yielded 94 of 181 (52%) snakes. Almost as successful, drift fences with funnel traps captured 83 of 181 (46%) snakes, whereas only two snakes were caught in minnow traps and two were found under cover boards.

We rarely witnessed snakes basking during summer months. In cooler months, we captured Eastern Ribbonsnakes by slowly approaching them as they basked along forest margins. Basking snakes were well camouflaged and quick to flee when their positions were compromised. We found arboreal activity to be common throughout the year. Snakes initially discovered in arboreal habitats easily escaped our capture by rapidly ascending vegetation (up to 6 m); thus we captured few climbing snakes. We captured nine snakes above ground, and of those, seven (78%) were taken from July-September. Snakes became almost entirely arboreal during flooding events. We did not witness snakes swimming across large static or flowing water bodies (even when chased by the authors); however, we frequently watched snakes cross small creeks and ponds.

Based on recaptures, the farthest straight-line distance moved by any snake was 1,050 m (male), while the next greatest movement was 300 m (female). Time between captures was seven months and six months, respectively.

TABLE 1. Mean snout-vent length (SVL) and tail length (TL) of the Eastern Ribbonsnake (*Thamnophis sauritus*) captured on Mound Island, Baldwin County, Alabama from 2003–2005. Data include sample size (n), range, and standard deviation (SD) of sizes.

		Mean SVL (mm)			Mean TL (mm)		
	n	SVL	Range	SD	TL	Range	SD
Males	58	476	330–680	90	215	110–272	56
Non-pregnant females	17	523	380–734	100	200	140–326	70
Pregnant females	34	569	380–777	105	226	131–360	60
Juveniles	119	310	190–364	67	140	90–198	40
Hatchlings	111	186	156–229	15	87	68–95	9

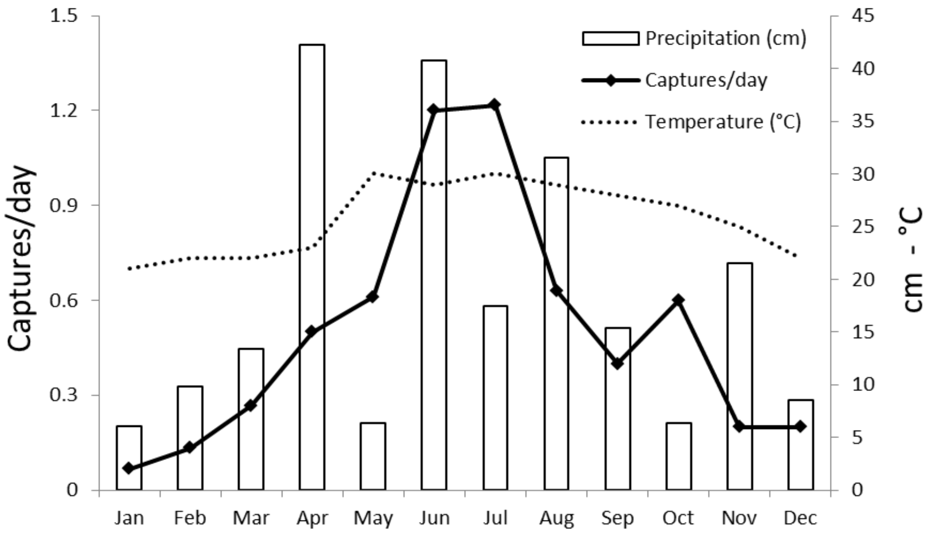

FIGURE 5. Monthly Eastern Ribbonsnake (*Thamnophis sauritus*) captures per day on or near Mound Island, Baldwin County, Alabama from 2003–2005, with precipitation (cm) and temperature (° C) data collected from Mount Vernon, Alabama, National Oceanic and Atmospheric Administration climate site.

On average, 16 snakes moved 145 m (median = 50 m, range: 0–1,050 m) between captures, which averaged 42 days (range: 5–208 d). Males ($\bar{x}$ = 201 m, SD = 380 m, range: 20–1,050 m, n = 6) moved farther than females ($\bar{x}$ = 41 m, SD = 86 m, range: 0–300 m, n = 10) between recaptures, but this difference was not significant (U = 99, P = 0.0832).

Diet.—Thirty-six of 339 (10.6%) snakes regurgitated food items or were seen consuming identifiable prey items. Frogs (adults and tadpoles) made up 100% of the diet of the Eastern Ribbonsnake. Adult and juvenile snakes (n = 23, SVL > 280 mm) consumed 15 (48% of total food items) adult *Lithobates clamitans*, nine (29%) unidentified adult *Hyla* spp., four (13%) adult *H. cineria*, two (6%) adult *H. avivoca*, and one (2%) adult *H. squirella*. We also found one (2%) *Lithobates grylio* tadpole eaten. Young snakes (n = 13, SVL < 280 mm) only consumed tadpoles: 30 (47%) *L. clamitans*, 15 (23%) *H. cineria*, 11 (17%) *H. avivoca*, five (8%) *Hyla* spp., and three (5%) *H. squirella*. Interestingly, we found frogs were always consumed feet first, whereas tadpoles were not consumed in a consistent position.

Reproduction.—Of 46 females we palpated for developing embryos, 34 (74%) were pregnant, and when considering only the reproductive season (April–October), 34 of 38 (89%) were gravid (Fig. 6). Pregnant females ranged in SVL from 380–777 mm, while the smallest reproductive male (330 mm SVL) was discovered via an unexpected laboratory copulation. We observed mating in the wild on 3 March 2005 between two adult snakes near the edge of a small creek. We did not observe mating at any other point during this study.

We observed two females giving birth in funnel traps on drift fence arrays in June; both females were recaptured later that season, and found to be gravid with their second clutch. Four additional females that gave birth in funnel traps were never recaptured. Female #1 (670 mm SVL) gave birth twice in the same funnel trap array; first on 23 June and again on 1 October. Female #2 (650 mm SVL) gave birth on 15 June in a funnel trap. We took her to the laboratory after palpation in the field indicated that she was pregnant on 7 October and she produced a second brood on 13 October. Days between births were 99 and 118 for the two females.

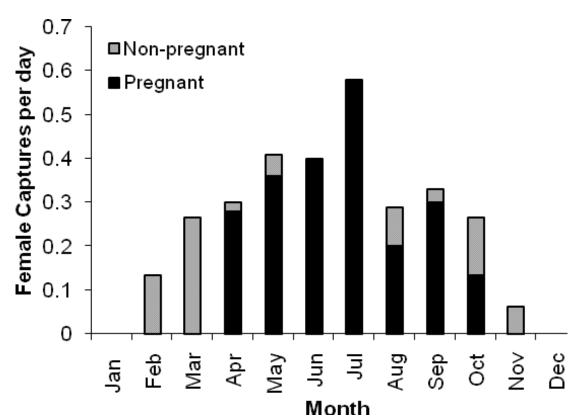

FIGURE 6. The number of pregnant and non-pregnant female Eastern Ribbonsnakes (*Thamnophis sauritus*) captured per day on Mound Island, Baldwin County, Alabama from 2003–2005.

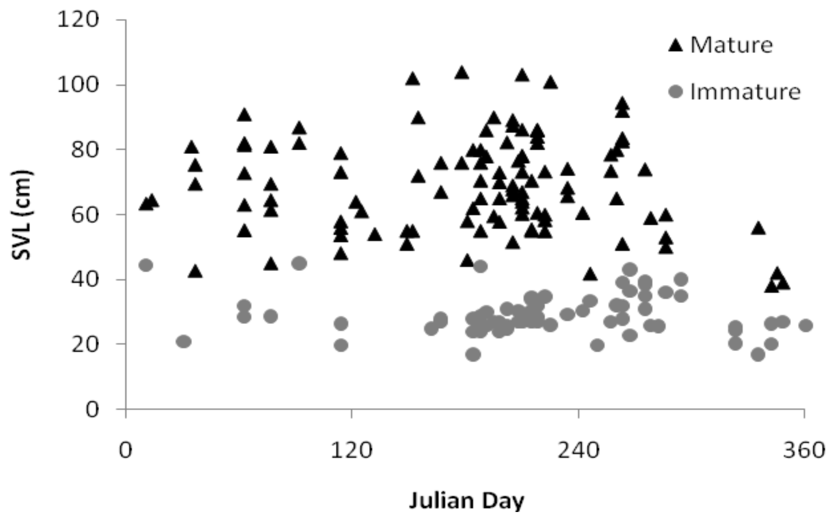

FIGURE 7. Snout-vent length (SVL) and Julian day of capture for Eastern Ribbonsnakes (*Thamnophis sauritus*) collected on Mound Island, Baldwin County, Alabama from 2003–2005.

The average brood size for the Eastern Ribbonsnake from six females that produced eight broods was 14 ± 3.18 (range: 9–19). We recorded a reduction in brood size in both females that produced multiple broods. The females produced broods of 16 and 19 in June, and 14 and 12, respectively, in October. No decrease in SVL was detected between these two broods (t = 1.88, df = 1, P = 0.065); therefore the 111 offspring from eight broods were combined to find an average SVL of 186 ± 15 mm (range: 156–229mm). Based on these sizes, it appears that multiple births in one reproductive season may have been common in this population, at least during this year, because small snakes (< 229 mm SVL) were captured year-round (Fig. 7).

DISCUSSION

During our study of an Alabama tupelo-gum swamp, we captured 339 Eastern Ribbonsnakes. To our knowledge this is the largest number of Eastern Ribbonsnakes continuously sampled in a southern location. During our concurrent herpetofaunal survey of the site, we found the Eastern Ribbonsnake to be the most commonly captured snake (51% of all snake captures) in the UDWMA, followed by the Cottonmouth (*Agkistrodon piscivorus*) and the Southern Watersnake (*Nerodia fasciata*; unpubl. data). In comparison, other recent surveys in southern locations have only captured a handful of Eastern Ribbonsnakes. A road-kill and drift fence survey of upland habitat in peninsular Florida that lasted 1,022 days found 27 individuals (Enge and Wood 2002). Another survey using drift fences in steephead ravines in the Florida panhandle caught 11 Eastern Ribbonsnakes (Enge 2005). A presence/absence survey of southeastern national parks used multiple sampling methods and found the Eastern Ribbonsnake in only two of 16 (13%) parks (Tuberville et al. 2005). A more successful study recorded 211 individuals during a three year road-cruising study on Long Pine Key, Florida (Dalrymple et al. 1991). When compared to these recent herpetological surveys, our data demonstrate that Eastern Ribbonsnakes appear to be very abundant in the UDWMA.

Eastern Ribbonsnakes in our population showed clear sexual size dimorphism. The largest snakes were all female. Female-biased sexual size dimorphism is common in many snake species (Shine 1993), especially natricines (Rossman et al. 1996; Gibbons and Dorcas 2004). This size dimorphism in snakes is usually attributed to an increase in female fecundity caused by the evolutionary potential for increases in offspring size and/or brood size with increasing female body size (Shine 1993). Male Eastern Ribbonsnakes at our site had proportionately longer tails than females, which also is common in other snakes (King 1989; Shine et al. 1999). Shine et al. (1999) suggest that sexual selection is working to maintain dimorphism because males with longer tails have increased mating success. A longer tail may also be maintained because of morphological constraints on the hemipenes (Shine 1993).

Eastern Ribbonsnakes are active year-round in the UDWMA. Year-round activity in the Eastern Ribbonsnake also occurs in Florida (Dalrymple et al. 1991). The closely related Western Ribbonsnake (*Thamnophis proximus*) is also active year-round in Louisiana (Tinkle 1957). Our data suggest that females may be less active than males and juveniles in winter months; however, Dalrymple et al. (1991) found fewer male Eastern Ribbonsnakes to be active in winter. It is possible that the opposite activity biases found by Dalrymple et al. (1991) and our study is an artifact of the decrease in overall snake captures during winter months. Movement data on the Eastern Ribbonsnake are sparse (Rossman et al. 1996). A recent radiotelemetry study in Nova Scotia found ribbonsnakes to be sedentary, sit-and-wait foragers that were frequently recaptured within a 50 m^2 summer home range along a lake shore (Bell et al. 2007). Carpenter's (1952) mark-recapture study in Michigan also found Eastern Ribbonsnakes to stay close to the shoreline, and he found snakes did not move long distances. We found the Eastern Ribbonsnake to be more active in southern Alabama than is reported at the northern portion of its range. The limited number of recaptured snakes in our study suggests a large, active population, similar to that found by Tinkle (1957) in the Western Ribbonsnake in southern Louisiana. However, our results may be biased toward active individuals because we used passive capture techniques and had limited recaptures. Thus, radiotelemetry studies are probably needed to determine the activity of the Eastern Ribbonsnake in the southern portions of its range.

The diet of the Eastern Ribbonsnake is composed primarily of amphibians (Rossman et al. 1996) and, in some populations fish (Bell et al. 2007). Our population fed exclusively on frogs, which were abundant in the UDWMA (unpubl. data). Although Southern Toads (*Anaxyrus terrestris*) and small fish (e.g., *Gambusia holbrooki*, *Aphredoderus sayanus*, *Notropis* spp.) were also abundant at most of our study sites, the Eastern Ribbonsnake did not feed on them. A disinterest in fish was supported by the initial refusal of live fish, but not anurans, by snakes we temporarily held in the laboratory. However, after one to two weeks, captive snakes readily fed on live and cubed frozen fish, which suggests the snake's diet could change with a switch in prey availability. Young snakes fed only on tadpoles, which were often consumed in large quantities at temporary, fishless ponds that filled and dried several times during the study. Adult and juvenile snakes fed almost exclusively on adult frogs, except for one adult male (410 mm) that consumed a large *L. grylio* tadpole.

Our study documents the first evidence of multiple broods in a temperate snake, and the first case occurring in a viviparous snake. The only other documented case of multiple clutches in any wild snake species occurred in the Keelback (*Tropidonophis mairii*), a tropical natricine (Brown and Shine 2002). Brown and Shine (2002) suggested that natricine snakes were likely candidates to produce multiple broods because of their rapid maturity and high reproductive outputs. Not surprisingly, the Keelback shares several traits with the Eastern Ribbonsnake. Both snakes: (1) are semi-aquatic species; (2) consume primarily frogs; (3) have extended reproductive seasons; and (4) have an abundant food source. The extent to which these traits facilitate multiple broods is not currently understood.

Our location, while temperate, can be categorized as a sub-tropical climate, which undoubtedly facilitates an extended reproductive season in most years (see Seigel and Ford 1987). Yet, an extended reproductive season alone does not contribute to multiple births; otherwise we might expect all tropical snakes to produce multiple broods (Shine 2003). Instead, many tropical snakes reproduce asynchronously over an extended reproductive season but may never produce multiple broods (Shine 2003). Furthermore, warmer climates do not always create an extended reproductive season (Aldridge et al. 1995). For example, data collected from a nearby population (47.7 km east of the UDWMA, but at the same latitude) suggest that the Eastern Ribbonsnake reproduces a single, synchronous brood over June and July (Joel Borden, unpubl. data). Variation in reproductive season and brood frequency between the populations inside and outside the UDWMA suggest that additional factors may be required to support multiple broods.

Most researchers have suggested caloric intake as a constraining factor for producing multiple broods in wild and captive snakes (Ford and Karges 1987; Seigel and Ford 1987; Brown and Shine 2002), and an abundant food supply was found in association with the Keelback (Brown and Shine 2002). Based on the concurrent herpetological survey we conducted, the Eastern Ribbonsnakes at our sites likely had an abundant food supply. If our population had an abundant food supply, as we suspect, then our results lend support to Brown and Shine's (2002) suggestion that an abundant, year-round food source may relax constraints on snakes attempting to acquire sufficient calories to produce two broods in a single year while also relaxing evolutionary pressure on offspring to be born during the peak of the amphibian breeding season.

We do not know if Eastern Ribbonsnakes in the UDWMA produce multiple broods every season. Tinkle (1957) suggested that Western Ribbonsnakes from southern Louisiana may alternate between producing a single brood in one year and two broods the next year. His reason for proposing this reproductive cycle is not clear, although he suggested that the reproductive systems of Western Ribbonsnakes would be stressed to produce multiple broods each year. Ford and Karges (1987) suggested that *Thamnophis marcianus* from southern Texas and northeastern Mexico may sometimes alternate between producing one and two broods in subsequent years. The authors reached this conclusion after finding fully developed young both early (April) and late (September) in the reproductive season. Based on the seasonal constraints discussed by Ford and Karges (1987) and close relationship between these snakes (i.e., garter snakes), it seems reasonable to assume that individual snakes are capable of producing multiple broods in the UDWMA population every other year (at most).

Recent studies have focused on how female snakes fuel reproductive outputs, which are represented by two strategies; income and capital breeding (Bonnet et al. 1998, 2001; Aldridge and Bufalino 2003; Lourdais et al. 2003; Winne et al. 2006). Income breeding occurs when an organism fuels reproductive expenditure via simultaneous feeding, whereas capital breeding occurs when reproductive expenditure is stored prior to embryonic development (Bonnet et al. 1998). The Eastern Ribbonsnake is a thin-bodied snake with little apparent fat stores. Minimal fat reserves probably indicate that the Eastern Ribbonsnake relies, at least partially, on income breeding to produce the second brood, as observed in the Keelback (Brown and Shine 2002). The use of income breeding is supported by our observation of a pregnant female consuming two frogs in captivity prior to producing a second brood. The ability to fuel reproductive efforts during pregnancy may be a required natural history trait for wild snakes to produce multiple broods in a single season.

Overall, this study provides greater understanding of the Eastern Ribbonsnake in a southern Alabama wetland; notably, we found an active population of snakes that fed exclusively on frogs and produced multiple broods in a reproductive season. We feel that the UDWMA provides an ideal habitat for the Eastern Ribbonsnake, and our numerous efforts to find a similar aggregation of snakes outside of the UDWMA were unsuccessful. It is unclear what factors play a role in the high abundance of Eastern Ribbonsnakes at our sites; however, when compared to areas outside of the UDWMA, our study sites had a unique combination of: (1) widespread shallow pools and creeks (both ephemeral and permanent); (2) an abundant food source (i.e. frogs); and (3) a mosaic of old growth and successional forest. Bell et al. (2007) suggested that these three factors were at least partially responsible for a locally abundant population of Eastern Ribbonsnakes in southern Ontario. Thus, we stress the apparent importance of expansive wetlands that support healthy anuran communities for the successful conservation of the Eastern Ribbonsnake. We encourage future studies to: (1) determine the importance of forest/wetland disturbance for long-term maintenance of Eastern Ribbonsnake populations; (2) survey favorable habitat to establish the conservation status of this understudied snake throughout its historic range; and (3) determine if other southern populations of Eastern Ribbonsnakes produce multiple broods in a reproductive season.

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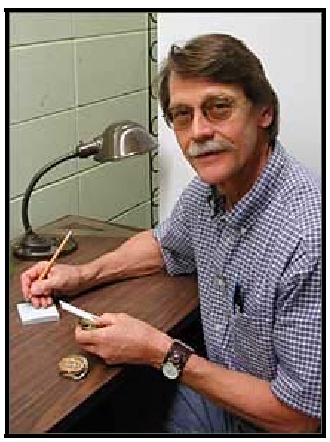

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