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Ecology of the Southeastern Crowned Snake, *Tantilla coronata*

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There are very few comprehensive studies of the ecology of small-bodied snakes. Here, we describe the ecology and demography of the Southeastern Crowned Snake (*Tantilla coronata*) based on 1,640 captures on the Savannah River Site in the Upper Coastal Plain of South Carolina, USA from 1951–2007. Female *T. coronata* were significantly longer, heavier, and heavier-bodied than males but had relatively shorter tails. Clutch size based on oviductal eggs was positively correlated to maternal body mass and length. Snakes exhibited a unimodal seasonal activity pattern that peaked in summer. Pitfall captures were significantly male-biased from July–October, corresponding to the suggested mating period for this species in this part of its range. We identified three classes of animals in the population: neonates, second year animals, and older animals that included both non-reproductive subadults and reproductive adults. Longevity was at least five years for two recaptured males originally captured as mature adults. Centipede species were the exclusive prey identified from *T. coronata* collected on the Savannah River Site. Our study demonstrates that research on underrepresented species is possible and can contribute to understanding of snake ecology.

STUDIES of snakes and their interactions with their environments and larger biological communities are poorly represented in broader ecological literature (Gibbons, 1988; Bonnet et al., 2002). Nevertheless, herpetologists have amassed considerable research illuminating the life history, biology, and ecology of many snake species. Despite an increased understanding of many snakes, diminutive species, such as the many ''leaf-litter'' or semi-fossorial snakes, are still seldom studied in any detail. In most cases, previous studies offer small glimpses into the ecology or biology of small-bodied snakes by reporting specific analyses of reproductive biology (Stewart and Brasch, 2003), seasonal activity and habitat use (Willson and Dorcas, 2004), or feeding ecology (Cobb, 2004). Importantly, there are very few comprehensive analyses of the life history, demography, or ecology of small-bodied snake populations, despite increasing awareness of the importance of such natural history studies (Greene, 2005).

Although small-bodied snakes receive less attention than their larger counterparts, they are often among the most abundant snakes occupying many habitats. For example, densities of Ringneck Snakes (*Diadophis punctatus*) in Kansas were estimated at 1,000 per ha (Fitch, 1975), and Godley (1980) calculated average densities of 1,200 Striped Crayfish Snakes (*Regina alleni*) and Black Swamp Snakes (*Seminatrix pygaea*) per ha in aquatic habitats in Florida. Similarly, Werler and Dixon (2000) report that the Rough Earth Snake (*Virginia striatula*) is the most abundant snake species in many parts of Texas. Often, comprehensive ecological studies of snakes are hampered by their secretive natures, their frequently cryptic behaviors and colorations, and, in temperate snakes, their regular periods of inactivity. These factors may be amplified for small-bodied snakes, most of which live semi-fossorial or litter-dwelling lives and remain unobservable for much of the year. Consequently, our understanding of snake ecology is likely influenced by easier-to-study large-bodied species, despite great abundances of small snakes.

The Southeastern Crowned Snake, *Tantilla coronata*, is a member of the geographically widespread genus *Tantilla*, a genus that includes approximately 63 species that occur throughout North and Central America. *Tantilla* are generally small-bodied with dark colored heads and are primarily semi-fossorial, nocturnal, and feed on invertebrates, although many species are newly described and most remain unstudied (Canseco-Marquez et al., 2002; Sawaya and Sazima, 2003; Stafford, 2004). *Tantilla coronata* occurs in the southeastern United States east of the Mississippi River, and despite its inconspicuousness, can be locally abundant in the Sandhills and Coastal Plain physiographic provinces.

Unlike most other small-bodied snakes, *T. coronata* have received some attention in previous studies and natural history reports. Observations of *T. coronata* have ranged from descriptions of habitat (Minton, 1949; Hardy, 1952; Telford, 1966) and activity (Wright and Wright, 1957), to examinations of clutch size (Neill, 1951) and body size variation (Telford, 1966). More recent studies have investigated patterns of seasonal activity and reproductive biology to a greater extent (Semlitsch et al., 1981; Aldridge, 1992; Aldridge and Semlitsch, 1992a, 1992b). Older accounts of the natural history of *T. coronata* have been hindered by small sample sizes, and even among recent studies, information about smaller (younger) individuals is typically scarce. The purpose of this manuscript is to present a much-needed comprehensive analysis of the ecology of one small-bodied species of snake. We resolve previous uncertainties about the demography of a population of *T. coronata* and present analyses of their activity, size and growth patterns, reproduction, and feeding ecology based on 1,640

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captures from 1951–2007 on the Savannah River Site in Aiken and Barnwell counties, South Carolina, USA.

MATERIALS AND METHODS

Study site.—The 803 km^2 Savannah River Site (SRS) was established in 1951 in Aiken, Barnwell, and Allendale counties in the Upper Coastal Plain of South Carolina, USA. The site consists predominantly of planted pine forests and second-growth hardwood habitats but historically supported extensive agricultural areas prior to site establishment (Gibbons et al., 2006). Reptiles and amphibians have been a primary focus of extensive and intensive research on the SRS since 1951 (Gibbons et al., 1997).

Data collection and analysis.—*Tantilla coronata* were initially thought to be uncommon on the SRS (Freeman, 1955) but have since been found to be more widely distributed (Gibbons et al., 1997) and have subsequently been captured in large numbers during the course of herpetological research on the SRS. The development of effective collecting techniques such as using coverboards (Grant et al., 1992) and drift fences (Gibbons and Semlitsch, 1982), as well as serendipitous captures, has led to 1,640 captures of Southeastern Crowned Snakes since 1951. In general, field-captured animals were returned to the laboratory to record mass to the nearest mg, snout–vent length (SVL) and tail length to the nearest mm, capture location, and capture method. Sex was determined by manual eversion of the hemipenes, cloacal probing, or dissection in the case of animals sacrificed for use in other studies (Semlitsch et al., 1981; Aldridge and Semlitsch, 1992a, 1992b). Additionally, we marked >600 *T. coronata* in the past 35 years by clipping ventral scales or by heat branding ventral and lateral scales (Winne et al., 2006), and we report information on recaptures from these efforts.

We compared SVL and mass of males and females using analysis of variance (ANOVA). We compared relative tail lengths of males and females using analyses of covariance (ANCOVA) with SVL as a covariate. We compared relative masses of males and non-gravid females using ANCOVA with SVL as a covariate. We transformed all masses and lengths prior to analysis by computing natural logarithms (Arnold and Peterson, 1989; King, 1989; King et al., 1999). We excluded intra-year recaptures from all morphological comparisons. We determined clutch size by counting the number of oviductal eggs via palpation or visual inspection of the semi-transparent venter. We used linear regressions of natural log-transformed body size and clutch size to determine whether clutch size was correlated with mass and SVL of maternal animals, following the methods prescribed by King (2000). We dissected three females that died in pitfall traps, and we report masses and lengths of late-stage eggs from these females.

To examine seasonal activity patterns, we used data collected during recent, intensive pitfall trapping studies (2004–2006; see Todd and Rothermel, 2006 for trapping design) so that we could adjust monthly captures for trapping effort and eliminate effort-related sampling biases. Specifically, we divided the number of captures in each month by the number of total trap nights in each month. We used chi-square analyses to determine whether monthly pitfall captures of *T. coronata* were sex-biased. We examined all data prior to analyses to ensure that statistical assumptions were met (Zar, 1998).

To determine feeding patterns and prey types, we dissected preserved animals (n = 222) collected from 1979 to 1983 that were part of the Savannah River Ecology Laboratory collection. We identified all prey items to the greatest taxonomic resolution possible. We also scored the gut contents of dissected animals, including both the stomach and intestines, as either empty, trace quantities, half-full, or full. We used a contingency table analysis to determine whether males and females differed in the proportion grouped into each category. We used a contingency table to test whether males and females differed significantly in the proportion that had no gut contents versus those that had some gut contents. Only a few gravid females that had been captured in this period were preserved (n = 10), and they were excluded from gut content analyses due to their low sample size.

RESULTS

We recorded 1,640 captures of *T. coronata* from 1951–2007 on the SRS. Morphological data from older captures (1950s–1970s) were not always recorded and in some cases, sex, reproductive condition, or the completeness of the tails were not noted and these animals were subsequently excluded from analyses. Males were significantly shorter than females (ANOVA: $F_{1,467} = 81.3$, $P < 0.001$; Table 1) but had relatively longer tails (ANCOVA: $F_{1,255} = 41.4$, $P < 0.001$; Table 1). Additionally, females were both absolutely heavier than males (ANOVA: $F_{1,260} = 5.8$, $P = 0.02$; Table 1) and relatively heavier for their size (ANCOVA: $F_{1,259} = 3.9$; $P = 0.05$).

Generally, seasonal activity of *T. coronata* was unimodal and peaked in late summer with a sizeable reduction in activity during the colder months of November through April (Fig. 1). No animals were captured in pitfall traps in February during intensive sampling from 2004–2006, but at least one animal was captured in a pitfall trap in all other months during these years, although sampling in August was incomplete and was excluded from analyses. Sex ratios of animals captured in pitfall traps from 1951–2007 were

Table 1. Mean Body Size of *Tantilla coronata* Captured on the Savannah River Site, South Carolina, USA, from 1951–2007. Reported mass for females includes only non-gravid females.

	Mass (g)		Snout–vent length (mm)		Tail length (mm)		Tail length/total length (%)
Sex	mean (range)	n	mean (range)	n	mean (range)	n	mean (range)
Male	2.3 (0.7–5.9)	179	172.3 (98–251)	326	42.8 (23–59)	151	24.2 (16.6–28.7)
Female	2.7 (0.8–6.0)	83	194.3 (124–276)	143	40.5 (12–61)	107	21.3 (6.8–34.7)

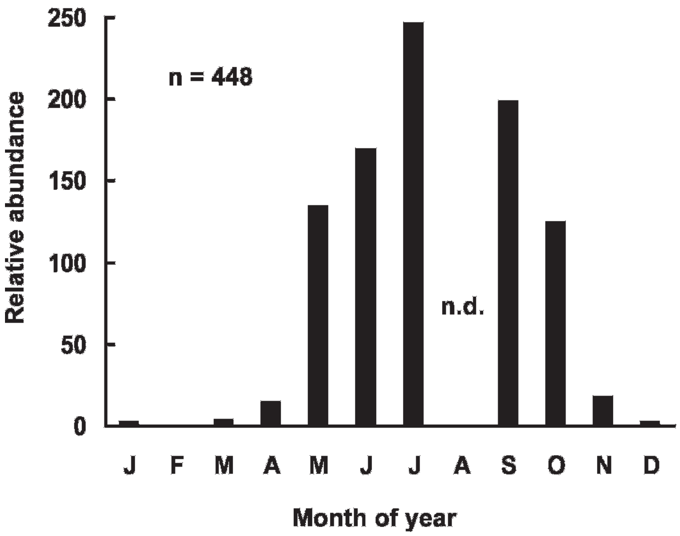

Fig. 1. Monthly relative abundance of *Tantilla coronata* captured during an intensive pitfall trapping session from 2004–2006 on the Savannah River Site, South Carolina, USA. Captures are adjusted for sampling effort by dividing total monthly captures by trap nights for that month and multiplying by 10^6. "n.d." indicates no data collected in August from 2004–2006.

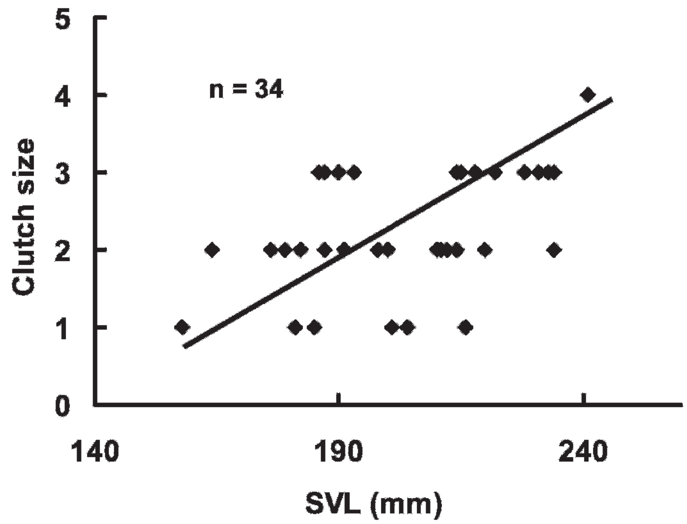

Fig. 3. Relationship between clutch size and maternal body length of *Tantilla coronata* captured on the Savannah River Site, South Carolina, USA. The number of oviductal eggs was positively correlated with maternal mass ($P = 0.003$) and snout–vent length ($P = 0.007$).

heavily male-biased in July, August, September, and October (P-values < 0.03; Fig. 2), but not during other parts of the year. During intensive (1,060 pitfall traps/night) and nearly continuous pitfall trapping from 2004–2006, snakes were captured together in pitfall traps seven times, occurring from May–July. Three of these were male–female pairs (18 May, 24 June, 13 July), although no copulation or other mating behavior was observed.

We recorded captures of 70 gravid females, nearly all of which were captured after 2003. Our dataset excludes females used in an earlier analysis from the SRS (Aldridge and Semlitsch, 1992a). The range of capture dates of gravid females was 7 May–24 July with a median capture date of 14 June. Relative clutch mass (clutch mass/maternal postpartum mass) ranged from 21–30% in three late-stage gravid females that were dissected. Eggs were cylindrical in shape and ranged from 18–22 mm in length. Clutch size (number of oviductal eggs) was significantly correlated with maternal body mass ($P = 0.004$; $R^2 = 0.24$) and SVL ($P = 0.007$; $R^2 = 0.21$; Fig. 3).

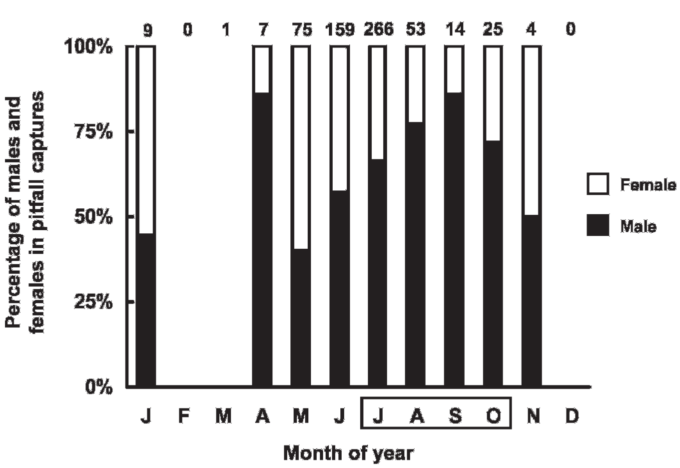

Fig. 2. Percentage of male and female *Tantilla coronata* captured in pitfall traps from 1951–2007 on the Savannah River Site, South Carolina, USA. The box indicates significantly male-biased captures from July through October ($P < 0.03$). Samples sizes for each month are provided above the bars.

Based on the captures that we observed, three general classes of animals were apparent: neonates (first year), juveniles (second year), and older animals (non-reproductive "subadults" and reproductive adults; Fig. 4). Newly hatched neonates were identifiable in the study population based on the known timing of egg deposition, the capture dates of gravid females, and the noticeably small size of neonates (Fig. 4). The four neonates ranged from 79 to 91 mm SVL. Second-year *T. coronata* were also distinguishable from adults and grew from approximately 90 to 130 mm SVL during their first full calendar year of growth (Fig. 4). As animals approached sexual maturity in their third calendar year of life, distinct classes could no longer be differentiated (Fig. 4).

Despite marking at least 600 animals from 1951–2007, only 15 animals were ever recaptured. Recapture intervals ranged from 4–1,074 days (mean = 314). Two snakes had intervals of nearly three years between initial capture and recapture and both snakes were mature males upon first capture. Thus, conservative estimates would place these animals in their sixth calendar year since birth (i.e., they had been living for five years). In all cases, recaptured snakes were found within 20 m of their initial capture location, even though numerous other nearby pitfall traps, coverboards, and natural cover objects were examined.

The sexes did not differ significantly in number of animals having empty, trace amounts, half-full, or full guts ($\chi^2 = 4.58$, df = 3, $P = 0.21$; Fig. 5). We also found no significant difference between the sexes in the number of animals having no food versus some food in the gut ($\chi^2 = 2.49$, df = 1, $P = 0.12$; Fig. 5). However, the highest proportion of animals with empty gut contents in both sexes occurred in October, corresponding with the tapering off of seasonal activity. Centipedes were the only prey items that we observed in *T. coronata* captured on the SRS, although prey items from very young snakes (<140 mm) were never recovered. We identified three species of centipedes as prey,

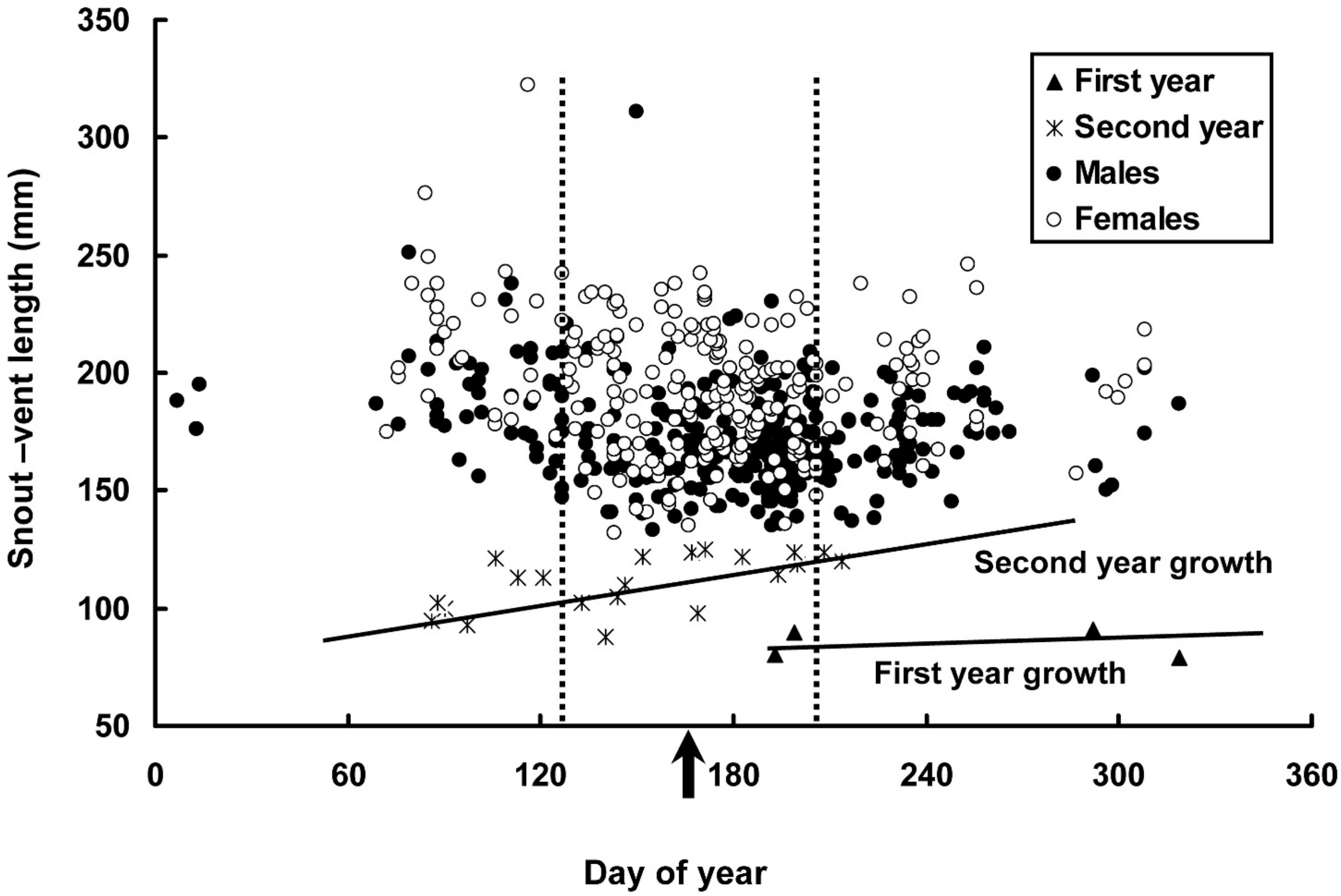

Fig. 4. Snout–vent length versus capture day of *Tantilla coronata* captured from 1951–2007 on the Savannah River Site, South Carolina, USA (first year animals $n = 4$; second year animals $n = 21$; males $n = 325$; females $n = 236$). The dashed lines represent the range of capture days for gravid females and the arrow points to the median day of capture of gravid females.

Cryptops hyalinus, *Scolopocryptops sexspinosus*, and *Theatops posticus*.

DISCUSSION

Because comprehensive studies of small snakes are generally rare, studies such as ours provide unique opportunities to test generalities of snake ecology on seldom-represented species. For example, our finding that females were significantly longer and heavier than males but had relatively shorter tails is consistent with many other colubrid snakes (Kaufman and Gibbons, 1975; Shine, 1994), including the closely related *T. relicta* (Mushinsky and Witz, 1993). Although the precise reason that males have relatively longer tails than females remains indefinite (King, 1989), several studies have proposed that females attain larger body size than males in the absence of male–male combat due to fecundity selection (Semlitsch and Gibbons, 1982; Shine, 1994; Pearson et al., 2002). In most oviparous squamates, larger females produce more offspring than smaller females (Fitch, 1985; Seigel and Ford, 1987; Ford and Seigel, 1989a). Similarly, in *T. coronata* that we captured on the SRS, maternal body size and mass were positively correlated with the number of oviductal eggs. In an earlier study, Aldridge and Semlitsch (1992a) found that clutch size, measured as the sum of vitellogenic follicles, oviductal eggs, and corpora lutea, was positively correlated with maternal body size in *T. coronata* collected on the SRS. However, there was no correlation of maternal body size with oviductal eggs alone. These results are consistent with the view that resource availability can affect maternal reproductive output (Seigel and Fitch, 1985; Ford and Seigel, 1989b; Seigel and Ford, 1991), and that year-to-year variation in resource availability affects the strength of the relationship between maternal body size and the number of fertilized embryos produced (Lourdais et al., 2002).

Climatic factors can strongly influence movements and behaviors of many snakes, particularly for temperate species subjected to widely varying seasonal temperatures and photoperiods. For many temperate species, activity in colder winter months is minimal or non-existent (Gibbons and Semlitsch, 1987). Although *T. coronata* were captured in all months on the SRS during 56 years of sampling, they were most active during the hottest months of the year and were infrequently encountered in January and February. In an earlier analysis, Semlitsch et al. (1981) found that surface activity of *T. coronata* in the SRS population was positively correlated to weekly air temperatures, a factor reflected by the unimodal peak of activity in summer months that we observed. Oviposition in *T. coronata* from South Carolina reportedly occurs from June to early July (Aldridge, 1992), corresponding with the observed median capture day of 14 June in gravid females in our study. However, females of the closely related *T. relicta* were captured with visible eggs from March to August in Florida (Mushinsky and Witz, 1993), a period considerably longer than that which we observed for

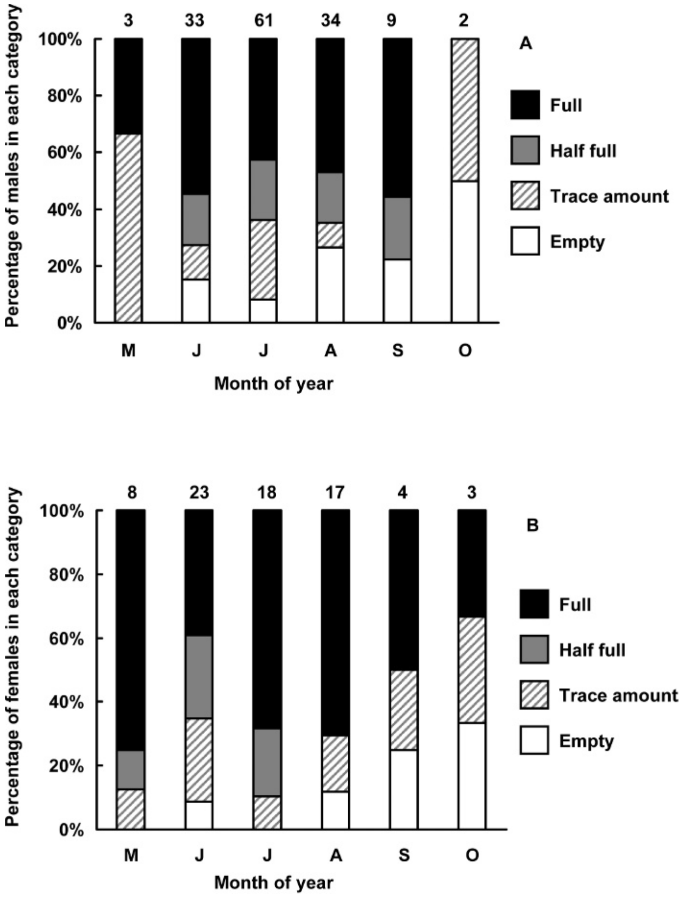

Fig. 5. Seasonal variation in gut contents of dissected *Tantilla coronata* captured on the Savannah River Site, South Carolina, USA. Snakes were grouped into one of the four listed categories based on the total amount of gut contents contained in the stomach and intestines for males (A) and females (B). Sample sizes for each month are listed above the bars. The few gravid females (n = 10) in the museum collection were excluded.

T. coronata (7 May–24 July), possibly due to a lengthier activity period in the warmer Florida climate. We found no difference in feeding frequency between the sexes, but both sexes were less likely to have food in their guts in October, coinciding with a gradual reduction in surface activity as colder winter weather approached.

Previous studies of the reproductive biology of *T. coronata* suggest the species follows a dissociated, or postnuptial, spermatogenic cycle similar to many other colubrids (Seigel and Ford, 1987) because sperm production and the size of the sexual segment of the kidney peak from July to August (Aldridge and Semlitsch, 1992b). However, this presupposes that *T. coronata* mate in the spring and not in the fall, a factor that is currently unresolved because evidence regarding the timing of mating in *T. coronata* has been conflicting. Neill (1951) reported capturing intertwined, mated pairs in April and early May in the state of Georgia and suggested the animals were copulating. We captured three male–female pairs in pitfall traps during the spring and early summer, although we also captured three pairs of same-sex animals during that time so it is unclear whether mated pairs were pursuing mates for courtship and reproduction or were serendipitously captured together as were same-sex animals. Aldridge (1992) further reported that in South Carolina, vitellogenesis in *T. coronata* occurred in the spring and ovulation occurred in June. Based on the presence and location of sperm in females, Aldridge (1992) concluded that several females mated in late August through October. Possible mating behavior from July to September is also supported by the significantly male-biased captures we observed in those months on the SRS, which was similarly identified in an earlier study (Semlitsch et al., 1981). Greater movements by males have been associated with mate-searching behavior in numerous snake species (Gibbons and Semlitsch, 1987; Gregory et al., 1987) and likely contribute to the pattern we observed. If sperm is acquired by females during the summer and early fall, it must be retained until ovulation the following year when eggs can be fertilized (Aldridge, 1992).

Juvenile and newly hatched small snakes are infrequently captured in most studies and are usually underrepresented in pitfall captures (Semlitsch et al., 1981; Willson and Dorcas, 2004). This possibly results from lower movement rates or smaller home ranges in juveniles compared to adults. In fact, only 48% of captures that we identified as first- or second-year animals were made with pitfall traps, in contrast to adults for which 82% of captures occurred in pitfall traps. Based on the average known timing of oviposition, a 60-day incubation (Palmer and Braswell, 1995), and the known capture dates and sizes of animals captured on the SRS, three distinct classes in the population are evident (Fig. 4). These findings are consistent with an earlier report by Telford (1966) that the average hatchling *T. coronata* in Florida had an SVL of ca. 82 mm and grew to ca. 98 mm by the following March. However, our interpretation stands in contrast to Semlitsch et al. (1981), who proposed that two animals collected on 2 August (119 mm SVL) and 7 September (100 mm SVL) may have been newly hatched juveniles and that the local population on the SRS comprised solely adults and neonates. Later, Aldridge and Semlitsch (1992b) proposed that *T. coronata* on the SRS in South Carolina reach sexual maturity in their third year of calendar life (i.e., two full years after hatching) based on the timing of reproduction and sexual maturity, an interpretation that agrees with our current assessment of this population. No previous estimates of longevity have been made for this species but a conservative estimate based on the long recapture intervals of two mature males (>1,000 days) in our study suggests that *T. coronata* are capable of living up to at least five years.

Small snakes are often secretive and can be infrequently encountered despite occurring in high abundances in many habitats. In 56 years of study, we have only recaptured 15 *T. coronata* out of at least 600 marked animals, likely because low encounter rates further reduce the likelihood of successfully recapturing individuals. Because capture and recapture rates of small snakes are often so low, comprehensive ecological studies are difficult to conduct and are rarely available. Nonetheless, our study demonstrates that research on underrepresented species is possible and can contribute to understanding of snake ecology.

MATERIAL EXAMINED

Tantilla coronata. SREL 586-2988 (222 specimens).

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