Feeding, reproduction and growth in the crowned snake *Tantilla melanocephala* (Colubridae), from southeastern Brazil

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Abstract. The crowned snake *Tantilla melanocephala* is a small fossorial sonorine snake, widely distributed through South America. Dissection of 186 specimens, combined with observations of captive specimens, provided information on the natural history of this species in southeastern Brazil. Females attained larger body sizes than males. Apparently *T. melanocephala* forage at night for active prey. Centipedes of the genus *Otostigmus* were the main prey item. These centipedes are subdued by injection of venom. Data from preserved specimens showed no significant seasonal variation in the number of collected snakes. Reproduction seemed to be highly seasonal with vitellogenesis occurring from onset to the middle of the rainy season and hatching at the end of the rainy season. Clutch size ranged from one to three and was correlated with female body length. Neonates measured 10-12 cm snout-vent length and juveniles attained about 17.5 cm SVL during the first year. Apparently males attain sexual maturity at an age of about 10 months and females at about 20 months.

Introduction

The genus *Tantilla* contains about 50 species occurring mainly in the southern United States and Central America (Peters and Orejas-Miranda, 1970; Vanzolini, 1986). These snakes belong to the monophyletic tribe Sonorini that includes 12 genera of small fossorial snakes (Savitzky, 1983). Works by Semlitsch et al. (1981), Aldridge and Semlitsch (1992a, b) and Mushinky and Witz (1993) on the North American species are the main studies on the ecology of the genus *Tantilla*. The only species mentioned for Brazil is *T. melanocephala* (Peters and Orejas-Miranda, 1970; Wilson, 1987). Apart from anecdotal reports (Vanzolini, 1948; Amaral, 1978; Cunha and Nascimento, 1978) nothing has been published on the ecology of this snake. The present study provides information on body size, sexual size dimorphism, food and feeding behavior, seasonal and daily activity, reproductive cycles, clutch size, inferred growth rate for yearlings and age at sexual maturity in *T. melanocephala* from open areas in southeastern Brazil.

Methods

A total of 186 specimens was examined from the collection of the Instituto Butantan (IB), in São Paulo. The sample included only specimens from southeastern Brazil (between 20° and 25°S). The following data were taken from each specimen: (1) snout-vent length (SVL); (2) sex; (3) reproductive maturity or immaturity (males were considered mature if they had enlarged testes or opaque efferent ducts; females were considered mature if they had either oviductal eggs or ovarian follicles >5 mm); (4) diameter of largest ovarian follicles or oviductal eggs; (5) stomach and/or intestine contents. Growth rate was inferred from seasonal distribution of body sizes (see Shine, 1978a).

Five captive snakes provided information on daily activity and feeding behavior. These snakes were individually housed in $25\times50\times30$ cm^3 terraria with 2 cm deep soil substrate. We recorded the time when the snakes were active. We offered centipedes *Otostigmus* sp. as prey, released about 10 cm from the snakes.

Results

Body size. This species is very small, with adult SVL averaging 25 cm. The mature males averaged 22.5 cm SVL ($s = 3.1$, $n = 93$, range 15.5-29), and mature females averaged 27 cm SVL ($s = 3.2$, $n = 78$, range 20.5-38.5). This difference is highly significant ($t = 9.40$, df $= 169$, $P < 0.00001$).

Food habits. A total of 129 prey items was recorded from digestive tracts. Apart from four insect records, all identified prey items were centipedes. The centipede *Otostigmus* sp. (Scolopendridae) comprised most of the records (table 1).

Feeding behavior. We recorded three feeding sequences for the captive snakes. Centipedes were held by *T. melanocephala* until immobilized, and thereafter the snake used alternating jaw movements to maneuver toward the prey's head. The time between seizure and the onset of pre-ingestion maneuvers varied from 2 to 7 minutes. The prey was always swallowed head first.

Table 1. Prey items from gut contents of *Tantilla melanocephala* in southeastern Brazil. $n = 129$ prey items found in 186 snakes. % frequency of occurrence in parenthesis.

Prey type	Number of records
Scolopendromorpha	
Scolopendridae: *Otostigmus* sp.	74 (57.4)
Cryptopidae: unidentified genus	3 (2.3)
Unidentified	48 (37.7)
Insects	
Unidentified	4 (3.1)

Daily activity. Three captive snakes were always found concealed during the day, but several times ($n = 5$) were seen actively prowling on the surface at night or twilight. Diurnal activity was observed only once, although collection effort was similar for day and night. In the field, activity ($n = 2$) was observed at 19:00 and 20:00 h (M.B. Ramos-Neto, pers. comm.).

Reproduction. Ovaries of adult female *T. melanocephala* are inactive over most of the year (fig. 1). Vitellogenesis and ovulation are restricted from onset to the middle of the rainy season (September to January) (fig. 1). Since all females of *T. melanocephala* examined lacked the left oviduct, the clutch sizes were estimated based on vitellogenic follicles of the right ovary or oviductal eggs (fig. 2). Clutch size ranged from 1 to 3, with a mean of 1.95 ($s = 0.85$, $n = 19$), and was positively correlated with female SVL ($r = 0.55$, $P < 0.05$, $n = 19$) (fig. 2). The number of vitellogenic follicles produced by the right ovary ($\bar{x} = 1.86$, $s = 0.77$, $n = 14$) was significantly higher than that of the left ovary ($\bar{x} = 1.07$, $s = 0.92$, $n = 14$) ($t = 2.45$, df = 26, $P < 0.05$).

Seasonal abundance. Juveniles were collected throughout the year, but the smaller individuals were collected especially in March (fig. 3). Adult males and females were more evenly distributed throughout the year (fig. 3). When these data are combined into frequency of collection in different seasons (rainy season and the dry season), there is

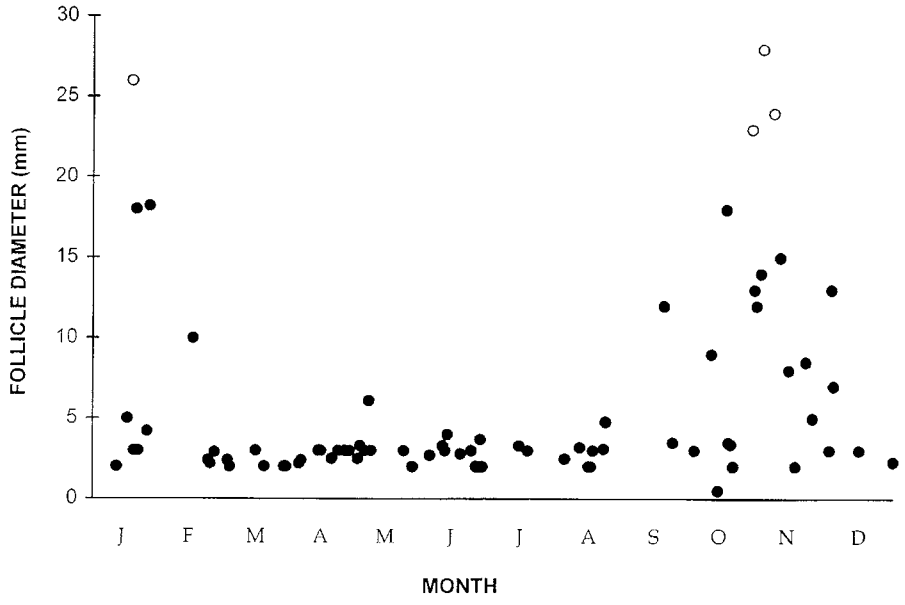

Figure 1. Seasonal variation in the diameter of the largest follicle in adult females of *Tantilla melanocephala*. Open circles represent oviductal eggs.

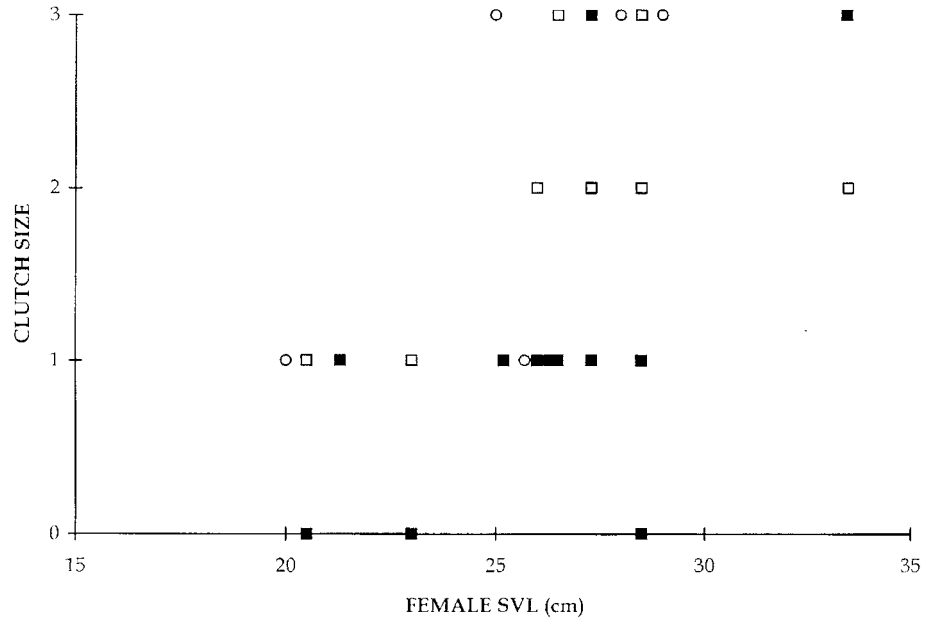

Figure 2. Relationship between maternal snout-vent length and clutch size in *Tantilla melanocephala*. Circles show oviductal eggs, open squares show right vitellogenic follicles, solid squares show left vitellogenics follicles.

no significant seasonal variation in the number of adults snakes collected, either males ($\chi^2 = 0.27$, 1 df, $0.90 > P > 0.75$, $n = 93$) or females ($\chi^2 = 0$, $P > 0.99$, $n = 78$).

Growth rates. The smallest field-collected snake with umbilical scar measured 10.2 cm SVL. Overall we conclude that the usual size at birth in *T. melanocephala* is 10-12 cm SVL. Thus, births apparently occur in March and April (see fig. 3). From the seasonal distributions of SVLs (fig. 3), we infer that juvenile *T. melanocephala* attain about 17.5 cm at 12 months, and sexual maturity is reached at about 10 months in males and 20 months in females (see fig. 3).

Discussion

Body size. Females attain larger body size than males. This is the most common situation among snakes and is correlated with the absence of male combat behavior (Shine, 1978b, 1994a). Apparently this behavior is absent in the genus *Tantilla* (cf. Shine, 1994a). However, male combat has been recorded at least in one species of sonorine snakes, *Sonora episcopa* (Kassing, 1961; Kroll, 1971; Shine, 1994a).

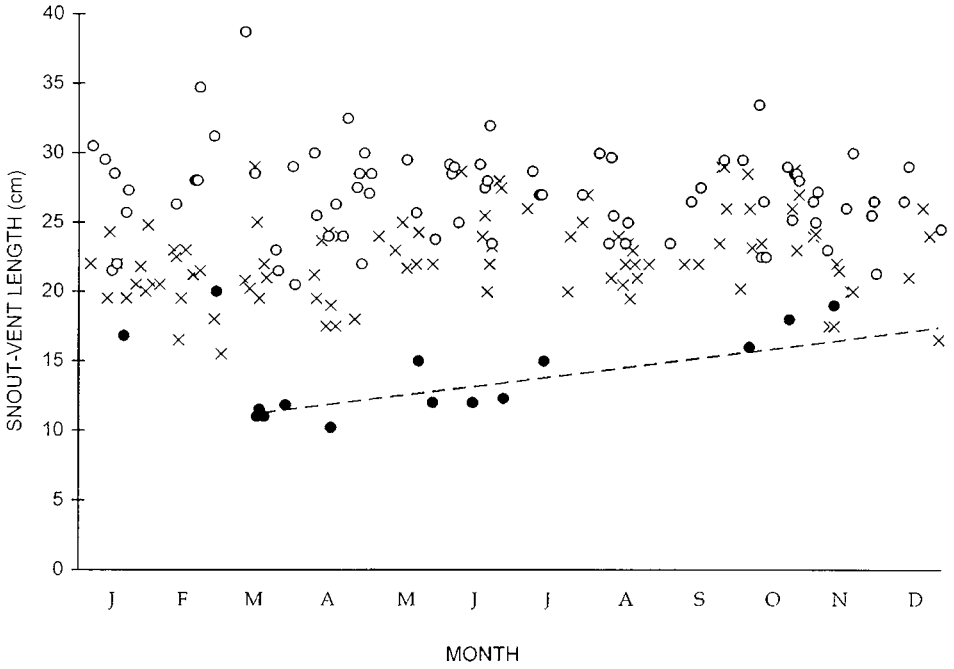

Figure 3. Seasonal distribution of body size, and inferred growth rates, in *Tantilla melanocephala*. Solid dots show juveniles, circles show mature females, crosses show matures males. Dashed line shows inferred growth pattern.

Food habits. The specialization of *T. melanocephala* upon arthropods is expected in view of these traits being phylogenetically conservative within the tribe Sonorini (Savitzky, 1983). However, no other South American colubrid snake is known to feed predominantly upon arthropods. One possible exception is *Pseudablabes agassisi*, that eats mainly lycosid spiders (F.L. Franco, pers. comm.). The specialization of *T. melanocephala*, feeding mainly on centipedes, has been noted previously by Vanzolini (1948) and Cunha and Nascimento (1978). One author described the diet of this species as composed by "earthworms" (Amaral, 1978), being most probably in error. Centipede prey is recorded for other species of *Tantilla*, but in minor proportion (Smith, 1982; Arnold, 1993). Beetle larvae are the main prey of *T. relicta* from Florida and *T. gracilis* from Texas (Smith, 1982; Arnold, 1993). These differences may reflect a substantial degree of dietary specialization among the species, or geographical and/or ecological differences in availability of different prey types.

The centiped *Otostigmus* sp., a prey type represented by about 57% in table 1, increased to about 96% in the subset of the 77 identifiable centipedes. We offer three hypotheses to explain the predominance of *Otostigmus* in the diet of *T. melanocephala*: (1) encounter rates with different prey, (2) prey choice and (3) hard to pursue prey. Data from field samples in southeastern Brazil indicate that individuals of the Scolopendridae (genus

Otostigmus) and Cryptopidae occur in similar proportion of abundance (A. Chagas Junior, pers. comm.). Individuals of the Cryptopidae and Scolopendridae (genus *Otostigmus*) show distinctive behavior in the field. The former are more agile and show higher escape ability (I. Knysac and R. Martins, pers. comm., pers. obs.). Thus it is possible that such prey is unprofitable since the rate of failed catch attempts may be high (cf. Arnold, 1993) and this may explain the predominance of *Otostigmus* sp. in the diet of *T. melanocephala*.

Feeding behavior. Nocturnal activity is recorded for *Tantilla coronata* from southern Indiana and *T. rubra* from Texas (Minton, 1949; Easterla, 1975). Diurnal activity was observed for Amazonian *T. melanocephala* (Silva et al., 1985; Martins and Oliveira, unpubl. data). Our data indicate that *T. melanocephala* from southeastern Brazil is mostly nocturnal. The centipede prey is nocturnal, so this snake may forage at night for active prey. The feeding tactics of *T. melanocephala* consists in holding on the prey until its struggling ceases. Apparently this snake has high venom toxicity for centipedes, which must be immobilized before ingestion. Predation on centipedes is made possible by the snake's injection of venom and its own immunity to the prey's venom (Greene, 1997).

Reproduction. The seasonal timing of reproduction in *T. melanocephala* is similar to that recorded for two other species of *Tantilla* from North America, *T. rubra* and *T. coronata* (Easterla, 1975; Aldridge and Semlitsch, 1992a). Like several species within the genus (Clark, 1970), *T. melanocephala* has only the right oviduct. The left ovaries produce fewer vitellogenic follicles than right ovaries. Thus it appears that the loss of the left oviduct is accompanied by changes in ovarian function, differently from that seen in *T. coronata*. In the latter, the number of vitellogenic follicles produced by the right ovary is similar to the left (Aldridge and Semlitsch, 1992a). Observed clutch size is similar to that reported for other species of *Tantilla* (cf. Easterla, 1975; Aldridge and Semlitsch, 1992a). This low fecundity seems to be a function of the small adult size of these snakes (cf. Shine, 1994b).

Seasonal abundance. The abundance of smaller specimens in March indicates a short period of recruitment in *T. melanocephala* from southeastern Brazil. The lack of seasonality in collection dates for museum specimens of adult snakes is surprising in view of field studies for other species of *Tantilla* which show considerable seasonal variation in habitat selection and activity levels (Semlitsch et al., 1981; Mushinsky and Witz, 1993). Another fossorial snake from southeastern Brazil, *Micrurus corallinus* (Elapidae), that occurs in a more stable climate in forested areas shows high seasonality (Marques, 1996).

Growth rates. Hatching size in other species of *Tantilla* has been reported as 7.6-9.0 cm SVL in *T. coronata* (Minton, 1949; Telford, 1966) and 8.8-9.5 cm SVL in *T. relicta* (Mushinsky and Witz, 1993). The smallest field-collected individual in the present study

measured 10.2 cm. Apparently, *T. melanocephala* increase by about 50% of their initial body size during the first year. This growth rate is similar to that recorded in *T. coronata* (Telford, 1966). Macroscopic examinations of testes and efferent ducts suggest that males attain maturity at an age of approximately 10 months. However, it is possible that successful mating occurs only at about 20 months (see Aldridge and Semlitsch, 1992b for *T. coronata*).

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