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Reproduction and feeding of the colubrid snake *Tomodon dorsatus* from south-eastern Brazil

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Abstract. Body size, sexual dimorphism, reproductive cycles, fecundity, diet and feeding behaviour of the colubrid snake *Tomodon dorsatus* from south-eastern Brazil were studied. Females of this viviparous species attained larger body sizes than males, the latter maturing with smaller body size than the former. Vitellogenesis occurred at the onset of rainy season, ovulation by mid rainy season, and parturition from late dry to early rainy season. Reproductive cycle was extended, maybe as a consequence of the low metabolism and food intake. Litter size ranged 4-26 offspring and was correlated with maternal body size. Relative clutch mass ranged 0.48-0.82, and neonates ranged 12-17 cm in snout-vent length. *Tomodon dorsatus* was shown to feed exclusively on veronicellid slugs quickly swallowed by long excursions of the specialized upper jaw units.

Introduction

The colubrid snake *Tomodon dorsatus* occurs along the Atlantic forest and surrounding areas in south-eastern and southern Brazil (Bizerra, 1998). This species belongs to the monophyletic Tachymenini, which includes seven genera (Bailey, 1967) with a wide variety of ecological traits (Bernarde et al., 2000). Although basic information on food habits and reproduction are available for *T. dorsatus* (Marques et al., 2001a; Marques and Sazima, 2004), data on ecological traits are unrecorded. This study provides further information on body size, sexual dimorphism, reproductive cycle, fecundity, food and feeding behaviour of *T. dorsatus*.

Methods

Preserved specimens ($n = 522$) from the collections of the Instituto Butantan (IB), São Paulo, and Museu de História Natural do Capão da Imbuia (MHNCI), Paraná, were examined in this study. Additionally, we examined freshly-killed specimens ($n = 217$) received by the IB. The examined samples included specimens collected along coastal Brazil, from São Paulo (23°20′S) south to Santa Catarina (27°20′S). This area lies within the Atlantic forest domain, and has a homogeneous climate characterized by high rainfall levels throughout the year (Nimer, 1989). Nonetheless, two "seasons" may be perceived: a rainy one (October-May) with higher rains incidence and temperature, and a dry one (June-September) with less rainfall and lower temperatures (see Marques et al., 2001b).

For each preserved specimen the following data set was taken: snout-vent length (SVL), head length (HL), tail length (TL) — to the nearest 1 mm, gut contents (see below), sex, and reproductive maturity (males were considered as mature when they had enlarged testes or opaque defferent ducts; females were regarded as mature when bearing oviductal embryos or ovarian follicles > 5 mm), diameter of largest ovarian follicle or presence of oviductal embryos. Degree of sexual size dimorphism (SSD) was 1 — mean adult SVL of the larger sex/mean adult SVL of the smaller sex (see Shine, 1994). We compared TL of males and females with analysis of covariance (ANCOVA) using SVL as the covariate. Similar procedure was used to compare HL of males and females using trunk length (= SVL-HL) as the covariate. All statistical analysis were performed with SPSS (Statistical Package for Social Sciences, version DOS, 4.0) and Statistica, version 5. Data on parturition were obtained from gravid captive females. Females, as well as neonates, were measured and weighed after parturition within a maximum of 72 h after birth to allow inclusion of the relative clutch mass (RCM — clutch mass/mother body mass) estimates (Seigel and Ford, 1987). Contents of the whole digestive duct were examined under a stereomicroscope, and the prey items were measured and weighed when intact or little digested. Snake specimens shipped to the Instituto Butantan come from several catching sources and may remain with the catchers for several days to weeks until received and processed in the laboratory. This delay causes most specimens to completely digest their prey, and for soft prey such as slugs no remains are found after a few days (pers. obs.). For this reason the proportion of snakes containing prey (see Shine, 1986) was disregarded in the present study. Two encounters between foraging snakes and slug prey were staged

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in the field (see Sazima, 1989). Slugs of the genus *Sarasinulla* (Veronicellidae) were offered as prey as these were found to be the only food in the examined guts. Captive individuals ($n = 40$) housed individually in 45 × 35 × 20 cm and 37 × 75 × 40 cm terrariums lined with 2 cm deep layer of soil were used for further observations on feeding behaviour.

Results

Body size and sexual dimorphism. Mature males averaged 45.3 cm SVL ($s = 7.5$, $n = 199$, range = 30.4-70.8) and mature females averaged 48.8 cm SVL ($s = 6.9$, $n = 259$, range = 32.8-73.1) ($t = 5.18$, df = 456, $P < 0.00001$). The degree of sexual dimorphism (SSD) was 0.08. Adult females have shorter tail length (ANCOVA; $F = 65.17$; df = 1, 367; $P < 0.00001$; $n = 370$), and larger head length than males (ANCOVA; $F = 43.77$; df = 1, 232; $P < 0.00001$; $n = 235$).

Reproduction. Females had a seasonal reproductive cycle, secondary vitellogenesis occurring mainly by the onset of rainy season, and most oviductal embryos occurred throughout the rainy season (fig. 1). Nineteen presumed neonates (11.2 to 12.3 cm SVL, see below) preserved in collections were obtained throughout the dry season and the beginning of rainy season. Parturition in eight captive females confirmed the above data, since births were recorded in June ($n = 1$), July ($n = 1$), August ($n = 3$), September ($n = 2$) and October ($n = 1$). Litter size ranged from 4 to 26 ($\bar{x} = 12.5$, $s = 5.3$, $n = 26$), and was positively correlated with female SVL (fig. 2). Relative clutch mass (RCM) ranged 0.48-0.82 ($\bar{x} = 0.65$, $s = 0.17$, $n = 3$). Average body size of neonates was 14.6 cm ($s = 1.2$, range = 12.1–17.0 mm SVL, $n = 122$).

Feeding. Eighteen prey items were recovered from the digestive tracts of 16 snakes that contained food, all identified preys being veronicellid slugs (mostly *Sarasinula* spp.). Prey mass ranged 1.7-31.3% ($\bar{x} = 5.7 \pm 6.8$, $n = 18$) of snake mass and prey size ranged 6.5-23.5% ($\bar{x} = 11.6 \pm 4.7$, $n = 18$) of snake SVL.

Tomodon dorsatus foraged actively and flicked its tongue continuously while moving. Occasionally, the snake stopped and raised its head making lateral movements with the fore-body. When close to a slug the snake flicked its tongue towards the prey and might touch it with the tongue and snout. It then arched its neck and inserted its mandible between the slug and the substrate, grasping the prey. The slug was usually grasped by the head or fore-body ($n = 18$),

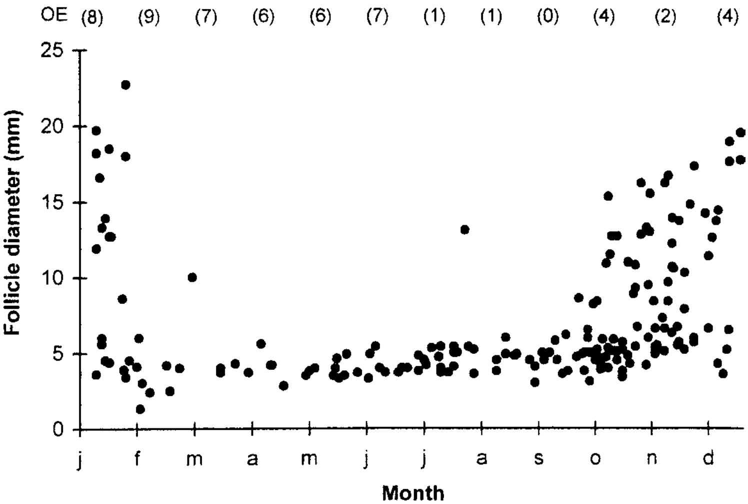

Figure 1. Seasonal variation in diameters of the largest ovarian follicles in adult females *Tomodon dorsatus*. OE = oviductal embryos. The number of females with oviductal embryos in parentheses.

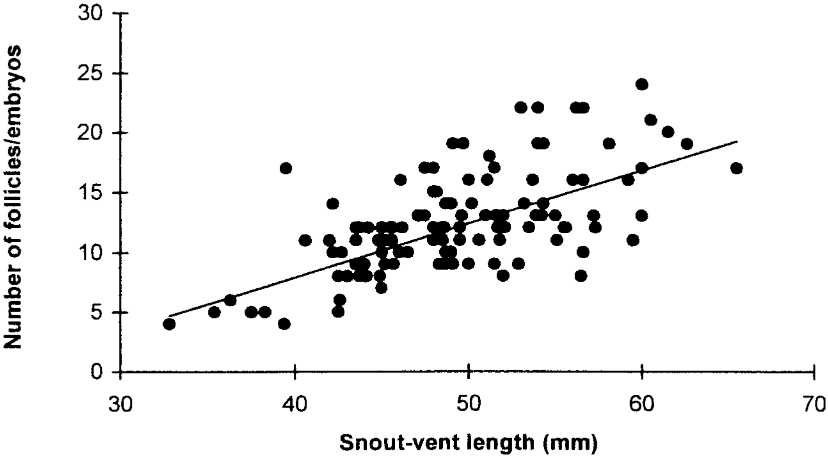

Figure 2. Relationship between maternal snout-vent and litter size in *Tomodon dorsatus* ($R = 0.51$, $F = 12.2$, $P = 0.0001$, $n = 51$).

Figure 3. *Tomodon dorsatus* swallowing a veronicellid slug tail-first (natural occurrence).

but grasping at the tail (fig. 3) or mid body also occurred ($n = 5$). The snake lifted the slug off the substrate and swallowed the prey by alternate excursions of the upper jaws. During the advance phase (see Kardong, 1979) each upper jaw made a quick excursion over the prey's body, and at the beginning of the close phase the specialized maxillary teeth held the prey, the jaw retracting and pulling the slug quickly inwards. Medium-sized to large slugs (7-18% of the snake SVL) were swallowed in 6-18 ($\bar{x} = 12.5 \pm 4.1$, $n = 8$) jaw moves of each side. After swallowing the snake gaped stretching the mandibles and might rub its chin on the ground, especially if slime adhered. Staged encounters yielded similar results.

Discussion

Body size and sexual dimorphism. Tomodon dorsatus females have larger body size than males, like most other viviparous colubrids (Fitch, 1981; Shine, 1994). The same pattern was recorded for *Thamnodynastes strigatus* (Bizerra, 1998) although another species within the Tachymenini, *Gomesophis brasiliensis*, showed no sexual dimorphism (Oliveira et al., 2003). These results seem inconsistent with the suggestion that males within the Tachymenini are larger than females (Bailey, 1981). A major correlate of the direction of sexual dimorphism among snakes is the presence or absence of male combat behaviour (Shine, 1978), and this combat remains unrecorded in *T. dorsatus*. However, the SSD value (0.08) in this snake is low and many species of colubrids with similar SSD value do show combat behaviour (see Shine, 1994). Oviparous xenodontine species from the Philodryadini (*Philodryas*) and Pseudoboini (*Oxyrhopus*) have higher SSD values (>0.23) (Hartmann, 2001; Pizzatto and Marques, 2002). Within the Colubridae the male combat is recorded mainly for the Colubrinae (Shine, 1994) and remains unrecorded for the neotropical Xenodontinae.

A smaller tail in females than in males is the most common condition recorded for snakes in general, and it is probably related to reproductive attributes (see King, 1989, for discussion about this type of sexual dimorphism). Head size dimorphism in *T. dorsatus* may be related to inter-sexual dietary divergence (see Shine and Crew, 1988 for this view), females preying on larger slugs, but we have no evidence for this. An alternative explanation is that head-size dimorphism is related to male mating choice (i.e., males choose females with larger heads, see Luiselli et al., 2002, for this view).

Reproduction. Tomodon dorsatus shows a seasonal reproductive pattern similar to those recorded for most neotropical snakes (e.g., Martins and Oliveira, 1998; Marques and Sazima, 2004). However, its reproductive cycle is longer and recruitment is later in the year than those of other neotropical snakes with seasonal reproduction. Vitellogenesis and recruitment restricted to the wet season is the general pattern for south-eastern Atlantic forest snakes (Marques, 1998). At least two viviparous species from south-eastern Atlantic forest, the colubrid *Helicops carinicaudus* and the viperid *Bothrops jararacussu*, follow this pattern, recruitment of newborns taking place late in the wet season (Marques, 1998; Marques and Sazima, 2004). Recruitment in *T. dorsatus* occurs when prey availability for juveniles is higher, as recruitment of *Sarasinula* spp. (main prey of *T. dorsatus*) occurs in late dry season and early wet season (Bizerra, 1998). However, the late snake recruitment may have another explanation as well. *Tomodon dorsatus* feeds on slugs, a resource of low caloric value (Arnold, 1993), and this snake is relatively sluggish, a trait indicative of low metabolic rates (see Lillywhite, 1987, for a review). Thus, the lengthened gestation of *T. dorsatus* may result from this latter characteristic, since another species of the Tachymenini, *Thamnodynastes strigatus*, preys on vertebrates and its recruitment occurs at the onset of the wet season as well (Bizerra, 1998). However, in *T. strigatus* vitellogenesis occurs in late wet season and the onset of dry season, and thus its gestation period is considerably shorter than that of *T. dorsatus* (Bizerra, 1998), supporting the view that the long vitellogenesis of the latter may be influenced by its presumed low metabolism. If true, this latter characteristic of *T. dorsatus* may influence other aspects of its life history and behaviour, as this snake has the richest defensive repertoire recorded for any Tachymenini species (Bizerra, 1998; Marques and Sazima, 2004; pers. obs.), a trait likely related to its inability to retreat quickly (Shine et al., 2000).

Feeding. Tomodon dorsatus is a specialized slug-eater and within the Tachymenini this food habit is also recorded for *Tomodon ocellatus* (Gallardo, 1972) and *Calamodontophis paucidens* (F.L. Franco, pers. comm.). However, the latter species probably belongs in the genus *Tomodon* (Bizerra, 1998; Franco, 2000). Most species within the Tachymenini (those in the genera *Thamnodynastes*, *Tachymenis*, and *Pseudotomodon*) feed on frogs and lizards (e.g., Donoso-Barros, 1966; Strüssmann and Sazima, 1993; Marques and Sazima, 2004). A phylogenetic analysis of the relationships within the Tachymenini (Bizerra, 1998; Franco, 2000) indicates that slug-feeding is a derived character of *Tomodon.* Another species of Tachymenini, *Gomesophis brasiliensis*, also feeds on soft invertebrates (earthworms, see Marques et al., 2001a; Oliveira et al., 2003) and we suggest that this feeding habit is a derived trait as well. Species of the Dipsadinae use the same prey categories recorded for the Tachymenini, some genera (e.g., *Imantodes* and *Leptodeira*) feeding on frogs and lizards, whereas other (e.g., *Geophis*, *Atractus*, *Ninia*) prey on earthworms, and three genera (*Dipsas*, *Sibynomorphus* and *Sibon*) feed on slugs and/or snails (see Greene, 1997). However, unlike in the Tachymenini, feeding on soft invertebrates within the Dipsadinae would be a basal trait, and preying on frogs and lizards may be regarded as derived condition, since *Imantodes* and *Leptodeira* are terminal genera (Fernandes, 1995).

The number of jaw moves in *T. dorsatus* during swallowing a slug is similar to the mandibular moves recorded for *Dipsas indica* feeding on the same prey type (Sazima, 1989). Both species swallow the prey quickly and with a low number of jaw excursions, probably an adaptation to avoid or lessen the effect of copious slime secreted by the slugs while handled. If the slime dries off before the slug is swallowed, the snake may be stuck to the substrate and must exert a considerable effort and time to free itself (IS, pers. obs.). Moreover, while stuck and struggling to free itself, the snake is likely more vulnerable to predation. *Tomodon dorsatus* has evident maxillary modification in relation to other species within the Tachymenini, since the length of its rear-fang may be up to nearly 70% of the length of the maxillary bone (Bailey, 1966). The length of the rear fang of this species is an extreme case among New Word colubrids, but the mechanical aspects of feeding that could have led towards the evolution of this condition are unknown (Bailey, 1966). Other specialized slug-eating snakes, including *Dipsas*, *Sibynomorphus*, *Pareas* and *Contia* have long mandibulary teeth that are regarded as an adaptation for feeding on slippery prey (Zweifel, 1954; Peters, 1960; Laporta-Ferreira et al., 1986). The long teeth of *D. indica* and the long mandibular excursions enable this snake to quickly handle a very viscous prey (Sazima, 1989). Likewise, the long posterior maxillary fang of *T. dorsatus* may allow deeper penetration and quick handling of its slippery and viscous prey. Contrary to other malacophagous snakes, *T. dorsatus* seems to be derived from a stock of rear fang snakes, and thus the lengthening of its rear maxillary fang may have evolved as an alternative to the long mandibular teeth found in other slug-eating stocks.

Some *T. dorsatus* individuals have a notable reduction of pre-diastemal teeth (0-5), whereas all other Tachymenini species have more than five teeth (Bailey, 1967; Franco, 2000). Thus, the pre-diastemal teeth probably have little or no importance in the swallowing process of *T. dorsatus*. A comparative study of captive individuals may test the assumption that there is no correlation between the number of pre-diastemal teeth and swallowing efficiency.

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