

## Overview of Reproductive Strategies in Xenodontini (Serpentes: Colubridae: Xenodontinae) with New Data for *Xenodon neuwiedii* and *Waglerophis merremii*

LÍGIA PIZZATTO,<sup>1,2</sup> ROSANA S. JORDÃO,<sup>3</sup> AND OTAVIO A. V. MARQUES<sup>3</sup>

<sup>1</sup>Pós-Graduação em Ecologia, Departamento de Zoologia, Universidade Estadual de Campinas, CP 6109, 13083-970, Campinas, São Paulo, Brazil; E-mail: ligia\_oceanica@yahoo.com

<sup>3</sup>Laboratório de Herpetologia, Instituto Butantan, Av. Dr. Vital Brazil 1500, 05503-900, São Paulo, São Paulo, Brazil

**ABSTRACT.**—Reproductive patterns are highly variable among Neotropical colubrids. Snakes of the Tribe Xenodontini are widely distributed in South America and show continuous reproductive cycles in many areas. We report interspecific and intraspecific variation in reproductive traits among these snakes and also show that seasonal cycles occur mainly in cooler areas. Clutch size relative to body size is similar among species, but *Erythrolamprus* spp. seem to lay fewer eggs than other species, and *Waglerophis merremii* from southeastern and southern Brazil lay more eggs than other species. Newborn *Erythrolamprus* are larger than all other Xenodontini, which may be related to ophiophagy. As in many other snakes, adult females are larger than males, but both sexes attain maturity with a proportionally similar body size. The sexual size dimorphism index is generally lower in smaller bodied species, and combat may be absent in the tribe. Male reproductive cycles are less well studied but seem to be more conservative, being continuous in all species studied (*W. merremii*, *Xenodon neuwiedii*, and *Liophis miliaris*). Phylogeny has an important role in reproductive patterns but climate and life-history traits can also influence tropical and subtropical species.

Elucidating reproductive characters is essential for understanding the animal life cycle. Reproduction in snakes has historically been studied mainly in north temperate areas. Species in these relatively cold regions typically reproduce in the warmer seasons (boreal spring-summer), and reproductive frequency is supra-annual, at least for females (Seigel and Ford, 1987). Despite the great diversity of snakes (especially the lineages of Colubriodea), the reproductive biology of many species are poorly studied, particularly for tropical and subtropical species from the New World. Earlier reviews expressed the belief that most tropical snakes reproduce annually and continuously (Fitch, 1970, 1982). More recent works have demonstrated that reproductive patterns of tropical species vary from strictly seasonal (Shine, 1991; Marques, 1996a) to broadly seasonal (Fowler et al., 1998), as well as continuous (Shine, 1991; Pizzatto and Marques, 2002). Moreover even continuous cycles can have reproductive peaks (Pizzatto and Marques, 2002), and males can also present seasonal or continuous cycles (Shine, 1977; Pizzatto and Marques, 2002; Salomão and Almeida-Santos, 2002). In addition, the complexity and high diversity of tropical climates probably contribute to reproductive variation observed in some

species (e.g., *Liophis miliaris*, Pizzatto and Marques, 2006a).

The aim of this work is to review the patterns of reproductive cycles, body size, size at maturity, and fecundity in Xenodontini, including new data on *Xenodon neuwiedii* and *Waglerophis merremii*. Despite being a polyphyletic group, Colubridae is by far the most diverse family of snakes (Lawson et al., 2005). Included in this family is the Xenodontini tribe (belonging to the Neotropical Subfamily Xenodontinae), and both tribe and subfamily are monophyletic (Myers, 1986; Zaher, 1999). The Tribe Xenodontini contains nearly 70 species in six genera of South and Central American snakes: *Erythrolamprus*, *Liophis*, *Lystrophis*, *Umbriovaga*, *Waglerophis* and *Xenodon* (Dixon, 1980; Cadle, 1984; Ferrarezzi, 1994).

### MATERIALS AND METHODS

Data on *X. neuwiedii* ( $N = 231$ ) and *W. merremii* ( $N = 464$ ) were obtained from preserved specimens from the collections of the Instituto Butantan (IB, São Paulo city, SP) and the Museu de História Natural do Capão da Imbuia (Curitiba city, PR). The examined samples included specimens collected in southeastern and southern Brazil. We made the following measurements: snout-vent length (SVL; nearest 1 mm), testis length (0.1 mm), diameter of deferent duct close to cloaca

<sup>2</sup>Corresponding Author.

(0.1 mm), diameter of the largest ovarian follicle or oviductal egg (0.1 mm), and number of eggs or follicles in secondary vitellogenesis (>10 mm). Additionally, freshly killed specimens (all from São Paulo state) received by the IB were examined to obtain data on snake mass and mass and width of the right testis. A small section of the deferent duct close to the cloaca was rubbed on a glass slide and examined microscopically ( $\times 20$ ) for the presence of sperm.

Gravid females received at IB were kept in captivity until egg-laying and eggs were incubated in vermiculite substrate at room temperature (range: 20–30°C). For each neonate, we recorded the birth date and SVL (nearest 1 mm). We also recorded data on newborn snakes received at IB (eggs received at the time of hatching) and occurrence of mating in two pairs of captive *W. merremii*. Reproductive data, comparable to ours, on other Xenodontini species were obtained from previously published works (citations listed in Appendices 1 and 2).

Females were considered mature if they had follicles in secondary vitellogenesis, oviductal eggs (cf. Shine, 1978), or folded oviducts (which indicate recent oviposition). Males were considered mature when they had turgid testes and convoluted deferent ducts (cf. Shine, 1980). Relative size at maturity, represented by the ratio of SVL of the smallest mature snake by the mean SVL, was compared between males and females for the pooled species using *t*-test. The ratios were log-transformed prior to the analyses to reach the normality (Zar, 1999). Sexual size dimorphism index (SSD) was calculated according to Shine (1994): (mean SVL of the larger sex/mean SVL of the smaller sex) – 1; by convention, negative values represent males larger than females (cf. Shine, 1994). We calculated the midpoint between female and male mean SVL for each species and used it in a linear regression for comparing its relationship with snake SSD (Zar, 1999). Relationship between clutch size and female SVL was analyzed in *X. newwiedii* and *W. merremii* by linear regression (Zar, 1999). Fecundity was compared among the pooled sample of Xenodontini species plotting the mean SVL of adult females by the mean clutch size.

Testis volumes were calculated using the volume of an ellipsoid ( $4/3\pi ab^2$  in which  $a$  = length/2 and  $b$  = width/2). Testis measures (length, volume, and mass) are known to reflect spermatogenic activity (Volsøe, 1944; Shine, 1977; Almeida-Santos et al., 2006). Variation of right testis length, testis mass, testis volume, and diameter of the deferent duct (dependent variables) were compared among seasons (factors) using ANCOVA because both variables

were significantly related to snake SVL (covariate in testis length and deferent duct analyses) and snake body mass (covariate in testis mass analysis; Zar, 1999). Data were log-transformed when necessary to be consistent with the premises of normality and homogeneity of variances (Zar, 1999).

The species in our pooled sample of Xenodontini are related to varying degrees and, thus, not strictly independent for inferential statistics (cf. Felsenstein, 1985). There are no published phylogenies that would allow an independent contrast or similar analysis. Our conclusions about patterns in the tribe must be regarded as tentative, and future research should address these questions in an explicitly phylogenetic framework.

## RESULTS

To place the data below in an appropriate context for seasonal interpretation, we briefly summarize the climates of four regions within the range of Xenodontini. The species included in the present work originated from northeastern, southeastern, and southern Brazil and Costa Rica, with different climates and ranging from 0–1,400 m in altitude. In northeastern Brazil (12–18°S), the climate is hot and dry throughout the year. Maximum monthly temperatures usually vary from 27–33°C and minimum from 18–21°C, with cooler winter months from July to September (INMET, 2007). Monthly rainfall is highly seasonal, with a long dry season from July to December (0–80 mm) and most rains falling in March and April (80–160 mm; INMET, 2007). The southeastern (22–26°S) is seasonal in both temperature and rainfall, probably representing a more subtropical climate. Maximum temperatures usually vary from 21–33°C and minimum from 6–21°C, with cooler autumn-winter from April to September (INMET, 2007). Monthly rainfall varies from 0–320 mm with a dry season from April to September (0–80 mm) and most rain occurring from November to March (80–320 mm; INMET, 2007). Southern Brazil (28–29°S) is characterized by rainfall distributed more homogeneously. Maximum temperatures vary from 15–36°C and minimum from 6–21°C, with cooler autumn-winter from April to September (INMET, 2007). Monthly rainfall varies mostly from 80–160 throughout the year (INMET, 2007). In Costa Rica, minimum temperatures range from about 13–23°C and maximum from 20–33°C, depending greatly on altitude (Coen, 1983). The coolest period is from November to January and warmest from March to May (Coen, 1983). Rainfall patterns differ between the Atlantic and Pacific sides, but both

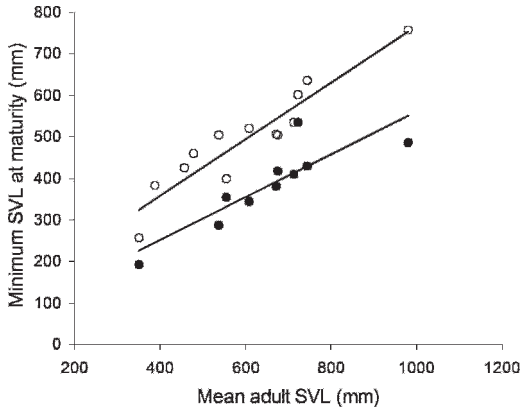


FIG. 1. Relationship between mean snout-vent length (SVL) in mature Xenodontini males (solid circles) and females (open circles) and the smallest mature snake. Raw data presented on Appendix 1.

places are very dry (50–100 mm) from February to April (Coen, 1983; Guswa and Rhodes, 2007).

**Body Size and Sexual Dimorphism.**—Mean snout-vent length differed considerably among species, ranging from 351–907 mm in females and 321–672 mm in males (Appendix 1). *Lystrophis dorbignyi*, *Liophis viridis*, *Liophis lineatus*, *Liophis mossoroensis*, and *Liophis poecilogyrus* were the smallest species, and *Erythrolamprus aesculapii*, *Erythrolamprus bizona*, *Liophis miliaris*, and *W. merremii* were the largest, especially when considering females (Appendix 1). Females averaged larger than males in all species, although the difference is not significant in *Li. mossoroensis*, *Li. viridis*, and *Liophis poecilogyrus schotti* from northeastern Brazil (consult citations in Appendix 1). The SSD index ranged from 0.05 in *Li. viridis* to 0.40 in *W. merremii*, but most species presented an index between 0.10 and 0.30 (Appendix 1). The SSD was positively related to SVL of the snakes ( $R^2 = 0.55$ ,  $P = 0.0006$ ), being higher in larger species. Females of most species attained maturity with 70–85% of the mean body size and males attained maturity with 65–80% and this difference was not significant ( $t_{22} = 1.13$ ,  $P = 0.271$ ; Fig. 1).

**Female Reproductive Cycle.**—Follicles in secondary vitellogenesis (>10 mm), oviductal eggs, and egg-laying were recorded for *W. merremii* from April to January in southeast Brazil and mainly from late August to February in southern Brazil (Fig. 2A,B). Hatchlings were recorded from January to May and mating in July and October the southeastern region (Fig. 2A). Apparently, in *X. neuwiedii*, vitellogenic follicles and eggs occurred throughout the year in both in the southern and southeastern regions (Fig. 3A,B).

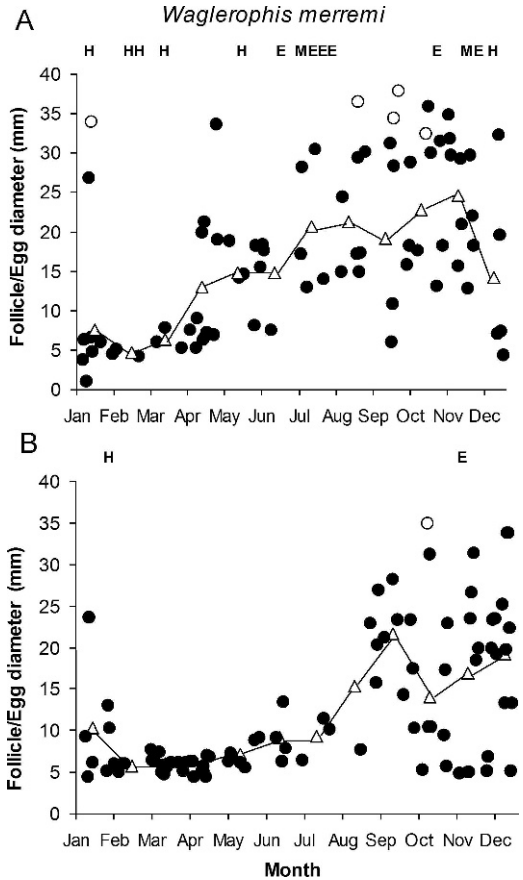


FIG. 2. Female reproductive cycles of *Waglerophis merremii* from southeastern Brazil (A) and southern Brazil (B). The diameter of the largest ovarian follicle (solid circles), oviductal egg (open circles) and the monthly mean of the follicle diameters (triangles with lines) are plotted over the course of the calendar year; each point represents one individual. Letters across the top of each panel denote observations of mating (M), egg laying (E), or hatchlings (H) from snakes received at IB.

Follicular cycles in Xenodontini were continuous, broadly seasonal (8–10 months), or strictly seasonal (5–7 months; Fig. 4). Continuous cycles were recorded in *X. neuwiedii*, *E. aesculapii*, *Liophis poecilogyrus poecilogyrus*, *Li. p. schotti*, *Li. miliaris* from northern coastal Atlantic Forest in Brazil and *Liophis typhlus* (Fig. 3). Broad seasonal cycles were recorded for *W. merremii* in northeast and southeast Brazil from autumn-spring, *Li. viridis*, *Li. mossoroensis* from late winter-summer, *E. bizona* and *Erythrolamprus mimus* from September to May (Fig. 4). Strict seasonal cycles, with vitellogenesis, ovulation and egg-laying from late winter to late spring, or early summer for snakes in southern Brazil, were recorded for *W. merremii* in southern Brazil

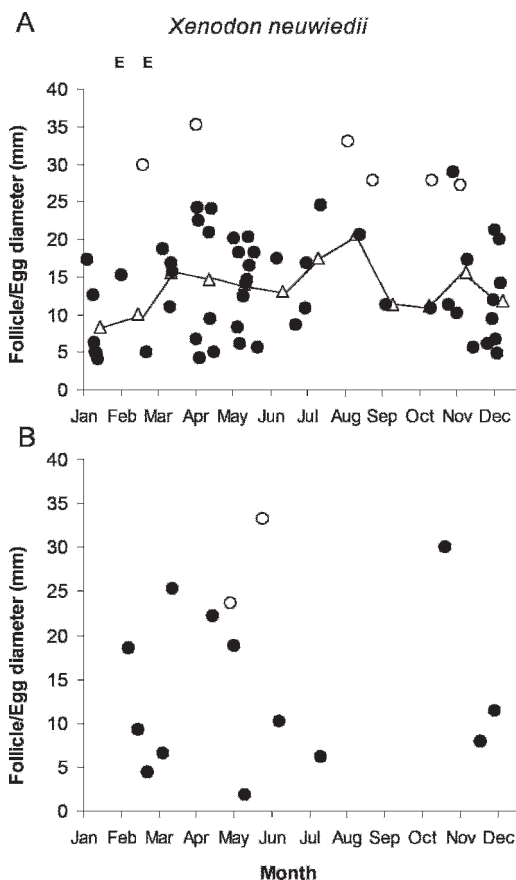


FIG. 3. Female reproductive cycles of *Xenodon neuwiedii* from southeastern Brazil (A) and southern Brazil (B). The diameter of the largest ovarian follicle (solid circles), oviducal egg (open circles) and the monthly mean of the follicle diameters (triangles with lines) are plotted over the course of the calendar year; each point represents one individual. Letters across the top of each panel denote observations of egg laying (E) from snakes received at IB.

(August to January), *Liophis poecilogyrus sublineatus* from south Brazil (August to February), *Li. lineatus* from July to January, *Liophis jaegeri* probably (September to January), *Liophis miliaris* from southern coastal and inland Atlantic Forest in Brazil, (September to February); and populations of *Li. miliaris* from southern inland Atlantic Forest in Brazil (October to February), and *Lystrophis dorbignyi* (August to February) in southern Brazil.

**Fecundity.**—As noted previously for other Xenodontini (see references in Appendices 1, 2), clutch size was positively related to SVL in *W. merremii* from southeastern and southern Brazil ( $R^2 = 0.57, P < 0.001, N = 36$  and  $R^2 = 0.51, P < 0.001, N = 27$ , respectively) and in *X. neuwiedii* from southeastern ( $R^2 = 0.43, P <$

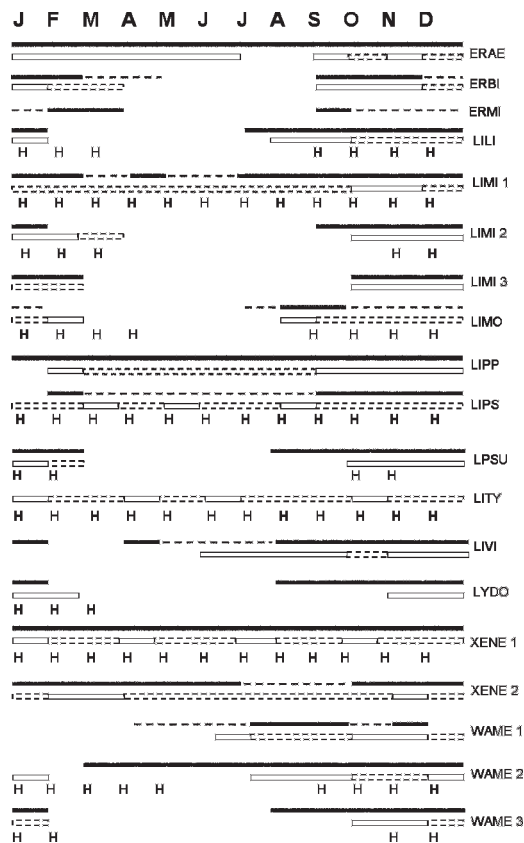


FIG. 4. Graphical summary of annual reproductive cycles of Xenodontini. For some species, multiple populations are displayed. Filled bars represent periods of vitellogenesis; open bars represent oviducal eggs or egg laying; H in bold indicates the collection month of hatchlings; and H in nonbold indicates hatchlings inferred. In some cases, we infer the extension of a reproductive event beyond the strict time limits of the data; the bars for such inferences are shown with broken outline. ERAE = *Erythrolamprus aesculapii*; ERMI = *Erythrolamprus mimus*; ERBI = *Erythrolamprus bizona*; LILI = *Liophis lineatus*; LIM1 = *Liophis miliaris* from (1) northern coastal Atlantic Forest, (2) southern coastal Atlantic and northern inland Atlantic Forest, and (3) southern inland Atlantic Forest, in Brazil; LIMO = *Liophis mossoroensis*; LIPP = *Liophis poecilogyrus poecilogyrus*; LIPS = *Liophis poecilogyrus schotii*; LPSU = *Liophis poecilogyrus sublineatus*; LITY = *Liophis typhlus*; LIVI = *Liophis viridis*; LYDO = *Lystrophis dorbignyi*; XENE 1–2 = *Xenodon neuwiedii* from southeast and south Brazil, respectively; WAME 1, 2, 3 = *Waglerophis merremii* from northeast, southeast, and south Brazil, respectively. Data taken from Vitt (1983), Marques (1996b), Maciel (2003), Goldberg, 2004; Pinto and Fernandes, 2004; Pizzatto and Marques 2006b; Oliveira et al., in press; and this work.



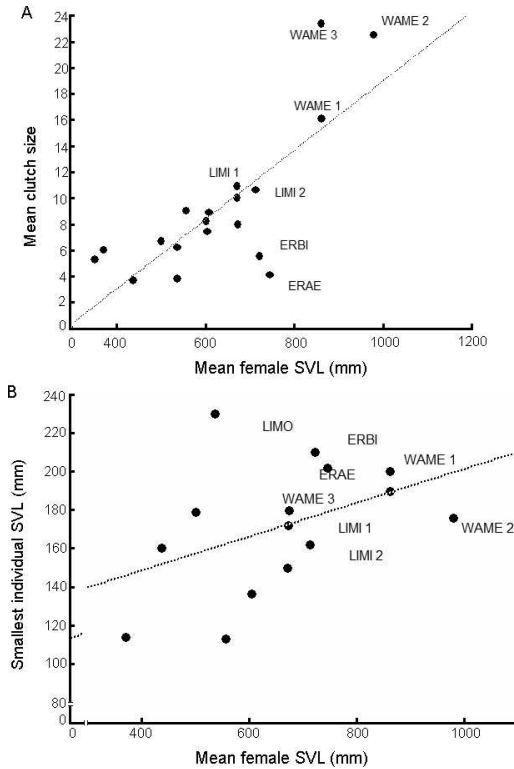


FIG. 5. Relationship between clutch size and female snout-vent length (A) and neonate snout-vent length and female snout-vent length (B) in Xenodontini. Each circle represents one species (or population). ERAE = *Erythrolamprus aesculapii*, ERBI = *E. bizona*, WAME = *Waglerophis merremii* from northeast (1), southeast (2), and south (3) Brazil, LIM1 = *Liophis miliaris* from northern inland Atlantic Forest (1) and southern coastal Atlantic Forest (2) in Brazil, and LIMO = *Liophis mossoroensis*. Additional data from: Vitt, 1983; Marques, 1996b; Maciel, 2003; Goldberg, 2004; Pinto and Fernandes, 2004; Pinto pers. com.; Solórzano, 2004; Pizzatto and Marques 2006a, Oliveira et al., in press; and this work.

0.0001,  $N = 43$ ) but not from southern ( $R^2 = 0.03$ ,  $P = 0.647$ ,  $N = 9$ ). Mean clutch size was positively related to SVL when analyzing all species of Xenodontini collectively (Fig. 5A;  $R^2 = 0.47$ ,  $P = 0.001$ , data log-transformed). However, when considering the effect of SVL, clutch size was similar among most Xenodontini species (Fig. 5A). Clutch size was slightly larger than expected by the SVL in *W. merremii* from southeast and southern Brazil and smaller, in *Erythrolamprus* spp. (Fig. 5A). Neonate *E. aesculapii* were 13.8–23.5% larger than other Xenodontini of similar body size see *Li. miliaris* and *W. merremii* in Appendix 2 and Fig. 5B); *E. bizona* also has relatively large neonates (21.5–23.0% larger than expected, see Appendix 2,

Fig. 5B). The smallest individual *Li. mossoroensis* is bigger than expected for the observed mean female size (see Appendix 2, Fig. 5B) and probably does not represent a neonate.

**Male Reproductive Cycle.**—Male cycles are less well studied than female cycles, and data were unavailable for most species. The length, mass, or volume of the testis did not vary among seasons in *W. merremii* and *X. neuwiedii* (Table 1). The same result was obtained for the diameter of the deferent duct in both the species in southeastern Brazil (Table 1). Sperm were found in the deferent duct in all mature specimens in both of these species from southeastern Brazil. Data on testis mass and volume and deferent duct for snakes from southern Brazil were not available. Testicular cycles were also continuous in *Li. miliaris* (Pizzatto and Marques, 2006a).

#### DISCUSSION

In most snakes, females are larger than males in terms of mean body size (Shine, 1994). Unexpectedly, *Li. viridis*, *Li. mossoroensis*, and *Li. p. schottii* did not show significant intersexual differences in mean body size. However, data for these species result from studies on communities (Vitt, 1983; Vitt and Vangilder, 1983), and the means also include juveniles (L. J. Vitt, pers. comm.), causing a bias. This is obvious in species in which the mean body size is smaller than the size of the smallest mature snake (see Appendix 1 and also data on Vitt and Vangilder, 1983), also resulting in error in the calculation of SSD (e.g., *Li. viridis*) and percentage of body size at maturity (e.g., *Li. p. schottii*) for some species.

The sexual size dimorphism (SSD) in Xenodontini is usually moderate, between 0.2 and 0.3. Consistent with these values combat behavior remains unrecorded for any species in this tribe or even for the subfamily Xenodontinae (Bizerra et al., 2005). High SSD results from females being larger than males, and it is probably related to fecundity. Larger snakes start reproducing later, with larger body sizes (see Appendix 1), which can increase clutch size. Thus, an absence of selection for larger size in males (e.g., combat behavior; see Shine, 1994) of Xenodontini could result in a large SSD in larger bodied species. In contrast, great SSD values do not happen in small species in which fecundity is highly constrained by the small body size. Thus, small species, such as *Li. viridis*, *Li. poecilogyrus*, and *Li. mossoroensis* start reproducing with small body sizes, and SSD tends to decrease. Shine (1994) found that, in snakes in which combat behavior does not occur, SSD was greater in taxa with more intense fecundity

TABLE 1. ANCOVA results for the variation in length, mass, and volume of testis, and diameter of deferent duct among seasons in *Xenodon neuwiedii* and *Waglerophis merremii* from southeastern (SE) and southern (S) Brazil.

Species	Testis length	Testis mass	Testis volume	Diameter of deferent duct
<i>X. neuwiedii</i> , SE	s: $F_{3,33} = 0.43$ , $P = 0.733$ ; i: $F_{3,36} = 1.48$ , $P = 0.236$	s: $F_{3,33} = 0.77$ , $P = 0.518$ ; i: $F_{3,36} = 2.04$ , $P = 0.122$	s: $F_{3,33} = 1.20$ , $P = 0.325$ ; i: $F_{3,36} = 0.67$ , $P = 0.578$	s: $F_{3,27} = 1.60$ , $P = 0.210$ ; i: $F_{3,30} = 0.51$ , $P = 0.675$
<i>X. neuwiedii</i> , S	s: $F_{3,19} = 2.18$ , $P = 0.123$ ; i: $F_{3,22} = 2.51$ , $P = 0.085$ ;	-	-	-
<i>W. merremii</i> , SE	s: $F_{3,23} = 1.30$ , $P = 0.279$ ; i: $F_{3,26} = 0.27$ , $P = 0.846$	s: $F_{3,23} = 0.48$ , $P = 0.701$ ; i: $F_{3,26} = 0.34$ , $P = 0.795$	s: $F_{3,23} = 1.30$ , $P = 0.297$ ; i: $F_{3,26} = 0.27$ , $P = 0.846$	s: $F_{3,23} = 1.65$ , $P = 0.204$ ; i: $F_{3,26} = 1.75$ , $P = 0.338$
<i>W. merremii</i> , S	s: $F_{3,43} = 0.24$ , $P = 0.866$ ; i: $F_{3,46} = 0.22$ , $P = 0.880$	-	-	-

s = slopes, i = intercept.

selection, but this relationship was strongly influenced by phylogeny.

Generally, clutch size is positively correlated with female body size (Shine, 1994). However, several different factors can affect the clutch size of snakes including the trade-off between clutch size and offspring size (cf. Shine, 1994). Thus, some species with relatively small clutches produce relatively large offspring. The relatively small clutches of *Erythrolamprus* may reflect such a trade-off, because neonate *Erythrolamprus* are much larger than the neonates of other species of Xenodontini of similar or even larger adult size. The Xenodontini are mostly frog eaters (e.g., Vitt, 1983; Greene 1997), but specialized ophiophagous habits have evolved in *Erythrolamprus* (Marques and Puerto, 1994). Swallowing ability increases with snake body size, and a small predator might be unable to ingest a very elongated prey item, as a snake. Neonate *E. aesculapii* eat very long preys (at least 30% of its SVL cf. Marques and Puerto 1994); thus, ophiophagy may be a selective pressure for their larger SVL. Our data are insufficient for performing appropriate analysis of this question, but if our hypothesis is true, we expect a large offspring in *E. minus*, and these data are essential to reinforce our findings.

With some exceptions, females in most species of Xenodontini exhibit aseasonal reproduction, a condition recorded in many other tropical colubrids, including species in Subfamilies Dipsadinae and Colubrinae (cf. Zug et al., 1979; Censky and McCoy, 1988; Marques and Muriel, 2007). Continuous reproductive cycles have also been reported in the Xenodontine, Tribe Pseudoboini (Pizzatto and Marques, 2002;

Pizzatto, 2005) but not in other Xenodontine lineages such as Philodryadini, Tachymenini and Elapomorhini (cf. Fowler et al., 1998; Marques and Sazima, 2004; Bizerra et al., 2005; Marques et al., 2006; R. J. Sawaya, pers. obs.; OAVM, pers. obs.). The duration of the reproductive cycles may be conservative in a lineage, but it might also be driven by other factors. As noted in other snakes (e.g., Ji and Wang, 2005), some species of Xenodontini (e.g., *W. merremii*, *Li. poecilogyrus*, *Li. miliaris*) present plasticity in reproductive timing. For example, in *W. merremii*, reproductive timing differed between geographically adjacent regions with distinct climates (i.e., southeastern Brazil vs. southern Brazil; see Results). Interspecific differences (e.g., feeding frequency, type of prey, physiological traits, habitat use) may also influence reproduction (see Ji and Wang, 2005; Santos et al., 2005) since different species occurring in the same locality had different reproductive patterns (e.g., *E. aesculapii*, *Li. miliaris*, and *X. neuwiedii* in the southeastern Atlantic forest in Brazil; see Marques and Sazima, 2004). The lack of seasonality or distinct cycling in males appears to be more conservative. In all species and populations analyzed, there was no significant difference in size or mass of testes throughout the year suggesting that sperm production is continuous. Sperm production can be costly in snakes from temperate areas (Olsson et al., 1997). Also, a continuous search for females (e.g., in environments where the females exhibit seasonality) can add costs in terms of reduced food intake, energy expenditure for locomotion, and greater predation. Indeed, such evolutionary costs may

be great, but apparently they are not high enough to limit sperm production among the Xenodontini.

Tropical and subtropical snakes are ideal subjects for studying reproductive patterns. Although in temperate areas climate (and especially temperature) is probably the main factor influencing reproduction, in the tropics, the influence of other factors, such as moisture, is clearer (see Brown and Shine, 2006). Some snakes can reproduce throughout the year even in seasonal areas where some other related species cannot. However, the possible effects of these other factors (prey type, feeding frequency, physiological traits, habitat use) on reproduction of snakes remain poorly studied. Phylogenetic constraints, for example, are usually neglected in part because of the absence of phylogenetic hypotheses for most groups. It is also essential to study species in equatorial areas where climate is more homogeneous: do all equatorial species reproduce year-round? Also, finding reproductive patterns in monophyletic groups can be essential for conservation, maybe allowing generalization and inference about reproduction in rarer species.

*Acknowledgments.*—We thank F. L. Franco (Instituto Butantan) and J. C. M. Leite (Museu de História Natural do Capão da Imbuia) for allowing analysis of specimens under their care; V. Germano for help in the laboratory; S. Goldberg for help with the literature; M. DiBernardo, R. R. Pinto, and L. Vitt for additional information on the species; and three anonymous reviewers for important comments and suggestions.

#### LITERATURE CITED

- ALMEIDA-SANTOS, S. M., L. PIZZATTO, AND O. A. V. MARQUES. 2006. Intra-sex synchrony and inter-sex coordination in the reproductive timing of the Atlantic Coral Snake *Micrurus corallinus* (Elapidae) in Brazil. *Herpetological Journal* 16:371–376.
- BIZZERRA, A. F., O. A. V. MARQUES, AND I. SAZIMA. 2005. Reproduction and feeding of the colubrid snake *Tomodon dorsatus* from south-eastern Brazil. *Amphibia-Reptilia* 26:33–38.
- BROWN, G. P., AND R. SHINE. 2006. Why do most tropical animals reproduce seasonally? Testing hypotheses on an Australian snake. *Ecology* 87:133–143.
- CADLE, J. E. 1984. Molecular systematics of Neotropical xenodontine snakes I. South American xenodontines. *Herpetologica* 40:8–20.
- CENSKY, E. J., AND C. J. MCCOY. 1988. Female reproductive cycles of five species of snakes (Reptilia: Colubridae) from Yucatan Peninsula, Mexico. *Biotropica* 20:326–333.
- COEN, E. 1983. Climate. In D. H. Janzen (ed.), *Costa Rican Natural History*, pp. 35–46. University of Chicago Press, Chicago.
- DIXON, J. 1980. The Neotropical colubrid snake genus *Liophis*: the generic concept. *Milwaukee Public Museum, Contribution in Biology and Geology* 31:1–40.
- FELSENSTEIN, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1–15.
- FERRAREZZI, H. 1994. Uma sinopse dos gêneros e classificação das serpentes (Squamata): II. Família Colubridae. In L. B. Nascimento, A. T. Bernardes, and G. A. Cotta (eds.), *Herpetologia no Brasil*, 1, pp. 81–91. PUC-MG, Fundação Biodiversitas, Fundação Ezequiel Dias, Belo Horizonte, Brazil.
- FITCH, H. S. 1970. Reproductive cycles of lizards and snakes. *Miscellaneous Publications of the Museum of Natural History of the University of Kansas* 52:1–247.
- . 1982. Reproductive cycles in tropical reptiles. *Occasional Papers of the Museum of Natural History of the University of Kansas* 96:1–53.
- FOWLER, I. R., M. G. SALOMÃO, AND R. S. JORDÃO. 1998. A description of the female reproductive cycle in four species from the Neotropical colubrid snake *Philodryas* (Colubridae, Xenodontinae). *Snake* 28:71–78.
- GOLDBERG, S. R. 2004. Notes on the reproduction in the false coral snakes, *Erythrolamprus bizona* and *Erythrolamprus mimus* (Serpentes: Colubridae) from Costa Rica. *Texas Journal of Science* 56:171–174.
- GREENE, H. 1997. *Snakes. The Evolution of Mystery in Nature*. University of California Press, Berkeley.
- GUSWA, A. J., AND A. L. RHODES. 2007. Monthly meteorological summaries. Available on <http://www.mvinstitute.org/wsrd/indexz.php>. Accessed on March 2007.
- INMET. 2006. Normais climatológicas. Available on: <http://www.inmet.gov.br/html/clima.php?lnk=/html/clima/mapas>. Accessed on March 2007.
- Ji, X., AND Z. W. WANG. 2005. Geographic variation in reproductive traits and trade-offs between size and number of eggs of the Chinese Cobra (*Naja atra*). *Biological Journal of the Linnean Society* 85:27–40.
- LAWSON, R., J. B. SLOWINSKY, B. I. CROTHER, AND F. T. BURBINKY. 2005. Phylogeny of the Colubroidea (Serpentes): new evidence from mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution* 37:581–601.
- MACIEL, A. P. 2003. *Ecologia e história natural da "cobra-do-capim" Liophis poecilogyrus* (Serpentes: Colubridae) no litoral norte do Rio Grande do Sul, Brasil. Unpubl. master's thesis. Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.
- MARQUES, O. A. V. 1996a. Reproduction, seasonal activity and growth of the coral snake, *Micrurus corallinus* (Elapidae), in the southeastern Atlantic forest in Brazil. *Amphibia-Reptilia* 17:277–285.
- . 1996b. cobra-coral *Erythrolamprus aesculapii* Linnaeus (Colubridae), no sudeste do Brasil. *Revista Brasileira de Zoologia* 13:747–753.
- MARQUES, O. A. V., AND A. P. MURIEL. 2007. Reproductive biology and food habits of the Swamp Racer Snake *Mastigodryas bifossatus* (Amaral, 1934) (Colubridae), from eastern South America. *Herpetological Journal* 17:104–109.
- MARQUES, O. A. V., AND G. PUERTO. 1994. Dieta e comportamento alimentar de *Erythrolamprus aesculapii*, uma serpente ofiófaga. *Revista Brasileira de Biologia* 54:253–259.

- MARQUES, O. A. V., AND I. SAZIMA. 2004. História natural dos répteis da Estação Ecológica Juréia-Itatins. In O. A. V. Marques and W. Duleba (eds.), Estação Ecológica Juréia-Itatins: Ambiente Físico, Flora e Fauna, pp. 254–274. Editora Holos, Ribeirão Preto, Brazil.
- MARQUES, O. A. V., F. S. OLIVEIRA, R. J. SAWAYA, AND F. G. R. FRANÇA. 2006. Ecology of the colubrid snake *Pseudablables agassizii* in south-eastern South America. *Herpetological Journal* 16:37–45.
- MYERS, C. W. 1986. An enigmatic new snake from the Peruvian Andes, with notes on Xenodontini (Colubridae: Xenodontinae). *American Museum Novitates* 2853:1–12.
- OLIVEIRA, R. B., G. M. F. PONTES, A. P. MACIEL, L. R. GOMES, AND M. DI-BERNARDO. In Press. Reproduction of *Lystrophis dorbignyi* (Duméril, Bibron and Duméril, 1854) (Serpentes, Colubridae) on the north coast of Rio Grande do Sul, Brazil. *Herpetological Journal*.
- OLSSON, M. M., T. MADSEN, AND R. SHINE. 1997. Is sperm really so cheap? Costs of reproduction in male adders, *Vipera berus*. *Proceedings of the Royal Society of London B* 264:455–459.
- PINTO, R. R., AND R. FERNANDES. 2004. Reproductive biology and diet of *Liophis poecilogyrus poecilogyrus* (Serpentes, Colubridae) from southeastern Brazil. *Phyllomedusa* 3:9–14.
- PIZZATTO, L. 2005. Body size, reproductive biology and abundance of the rare Pseudoboioinae snakes, genus *Clelia* and *Boiruna* (Serpentes: Colubridae) in Brazil. *Phyllomedusa* 4:111–122.
- PIZZATTO, L., AND O. A. V. MARQUES. 2002. Reproductive biology of the false coral snake *Oxyrhopus guibeii* (Colubridae) from southeastern Brazil. *Amphibia-Reptilia* 23:495–504.
- . 2006a. Interpopulational variation in reproductive cycles and activity of the water snake *Liophis miliaris* (Colubridae) in Brazil. *Herpetological Journal* 16:353–362.
- . 2006b. Interpopulational variation in sexual dimorphism, reproductive output, and parasitism of the water snake *Liophis miliaris* (Colubridae), in the Atlantic forest of Brazil. *Amphibia-Reptilia* 27:37–46.
- SALOMÃO, M. G., AND S. M. ALMEIDA-SANTOS. 2002. The reproductive cycle in male Neotropical rattlesnakes (*Crotalus durissus terrificus*). In G. W. Schuett, M. Höggren, M. E. Douglas, and H. W. Greene (eds.), *Biology of the Vipers*, pp. 507–514. Eagle Mountain Publishing, Eagle Mountain, UT.
- SANTOS, X., G. A. LLORENTE, M. FERICHE, J. M. PLEGUEZUELOS, F. CASALS, AND A. DE SOSTOA. 2005. Food availability induces geographic variation in reproductive timing of an aquatic oviparous snake (*Natrix maura*). *Amphibia-Reptilia* 26:183–191.
- SEIGEL, R. A., AND N. B. FORD. 1987. Reproductive ecology. In R. A. Seigel, J. T. Collins, and S. S. Novak (eds.), *Snakes, Ecology and Evolutionary Biology*, pp. 210–252. McMillan Publishing Company, New York.
- SHINE, R. 1977. Reproduction in Australian elapid snakes I. Testicular cycles and mating seasons. *Australian Journal of Zoology* 25:647–653.
- . 1978. Growth rates and sexual maturation in six species of Australian elapid snakes. *Herpetologica* 34:73–79.
- . 1980. Comparative ecology of three Australian snake species of the genus *Cacophis* (Serpentes, Colubridae). *Copeia* 1980:831–838.
- . 1991. Strangers in a strange land: ecology of the Australian colubrid snakes. *Copeia* 191:120–131.
- . 1994. Sexual size dimorphism in snakes revisited. *Copeia* 1994:326–346.
- SOLÓRZANO, A. 2004. Serpientes de Costa Rica / Snakes of Costa Rica. Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica.
- VITT, L. J. 1983. Ecology of an anuran-eating guild of terrestrial tropical snakes. *Herpetologica* 39:52–66.
- VITT, L. J., AND L. D. VANGILDER. 1983. Ecology of a snake community in Northeastern Brazil. *Amphibia-Reptilia* 4:273–296.
- VOLSØE, H. 1944. Structure and seasonal variation of the male reproductive organs of *Vipera berus* (L.). *Spolia Zoologica Musei Hauniensis* 5:9–159.
- ZAHER, H. 1999. Hemipenial morphology of the South American xenodontine snakes, with a proposal for a monophyletic Xenodontinae and a reappraisal of colubroid hemipenes. *Bulletin of the American Museum of Natural History* 260:1–168.
- ZAR, J. H. 1999. *Biostatistical Analysis*. Prentice Hall, Englewood Cliffs, NJ.
- ZUG, G. R., S. B. HEDGES, AND S. SUNKEL. 1979. Variation in reproductive parameters of three Neotropical snakes, *Coniophanes fissiden*, *Dipsas catesbyi* and *Imantodes cenchoa*. *Smithsonian Contributions to Zoology* 300:1–20.

Accepted: 14 September 2007.



APPENDIX 1. Mean, standard deviation and range of snout-vent size (SVL, mm) in adult females and males, proportion of the mean SVL they attain sexual maturity and sexual size dimorphism index (SSD) in Xenodontini snakes. N = sample size. NCAF = Northern Coastal Atlantic Forest, SCAF = Southern Coastal Atlantic Forest, NIAF = Northern Inland Atlantic Forest, SIAF = Southern Coastal Atlantic Forest.

Species and origin	Adult ♀	SVL adult ♂	SSD	Reference
<i>Erythrolamprus aesculapii</i> , SE and S Brazil	745 ± 57.0 (635–855, N = 94), mature at 85.2%	626.0 ± 66.0 (430–730, N = 136), mature at 68.7%	0.19	Marques, 1996b
<i>E. bizona</i> ; Costa Rica	721.7 ± 75.0 (602–835, N = 11), mature at 83.4%	614.0 ± 54.0 (535–715, N = 15), mature at 87.1%	0.17	Goldberg, 2004
<i>E. mimus</i> ; Costa Rica	537.0 ± 31.6 (504–580, N = 4), mature at 93.8%	482.0 ± 105.0 (288–553, N = 6), mature at 59.7%	0.11	Goldberg, 2004
<i>Liophis lineatus</i> ; NE Brazil	458.0 ± 16.2 (426–567, N = 29), mature at 93.0%	389.0 ± 10.3 (??–473, N = 15)	0.18	Vitt, 1983
<i>Liophis miliaris</i> ; NCAF Brazil	555.8 ± 101.0 (400–1015, N = 126), mature at 72.0%	465.4 ± 78.4 (355–650, N = 23), mature at 76.3%	0.19	Pizzatto and Marques, 2006a
<i>Liophis miliaris</i> ; SCAF, Brazil	713.3 ± 111.7 (534–985, N = 83), mature at 74.9%	580.6 ± 84.8 (410–745, N = 59), mature at 70.6%	0.23	Pizzatto and Marques, 2006a
<i>Liophis miliaris</i> ; NIAF Brazil	676.2 ± 118.5 (505–1005, N = 49), mature at 74.7%	539.1 ± 94.4 (417–905, N = 37), mature at 77.3%	0.25	Pizzatto and Marques, 2006a
<i>Liophis miliaris</i> ; SIAF Brazil	670.9 ± 115.1 (507–876, N = 80), mature at 75.6%	532.3 ± 85.1 (380–744, N = 104), mature at 71.4%	0.26	Pizzatto and Marques, 2006a
<i>Liophis mossoroensis</i> ; NE Brazil	479.0 ± 24.6 (460–755, N = 29), mature at 96.0%	420.0 ± 34.8 (??–655, N = 15)	0.14	Vitt, 1983; Vitt and Vangilder, 1983
<i>Liophis poecilogyrus schottii</i> ; NE Brazil	407.0 ± 2.2 (?–855, N = 57)	336.0 ± 2.1 (??–611, N = 34)	0.21	Vitt, 1983; Vitt and Vangilder, 1983
<i>Liophis viridis</i> ; NE Brazil	388.0 ± 17.6 (382–535, N = 33), mature at 98.0%	368.0 ± 17.8 (??–535, N = 22)	0.05	Vitt, 1983; Vitt and Vangilder, 1983
<i>Lystrophis dorbiguyi</i> ; S Brazil	351.1 ± 45.0 (257–490, N = 188), mature at 73.2%	321.3 ± 57.2 (192–500, N = 239), mature at 59.7%	0.09	Oliveira et al., in press
<i>Waglerophis merremii</i> ; SE Brazil	979.0 ± 17.8 (758–1855, N = 78), mature at 77.4%	677.0 ± 8.7 (486–860, N = 53), mature at 71.8%	0.45	This study
<i>Waglerophis merremii</i> ; S Brazil	861.0 ± 14.0 (561–1162, N = 104), mature at 65%	668.0 ± 7.0 (515–900, N = 59), mature at 77%	0.29	This study
<i>Waglerophis merremii</i> ; NE Brazil	749.0 ± 50.4 (??–1052, N = 28)	536.0 ± 28.0 (??–640, N = 18)	0.40	Vitt, 1983
<i>Xenodon newiedii</i> ; SE Brazil	609.0 ± 5.7 (520–751, N = 57), mature at 85.4%	512.0 ± 7.4 (345–730, N = 61), mature at 65.4%	0.19	This study
<i>Xenodon newiedii</i> ; S Brazil	674.0 ± 5.0 (602–775, N = 17), mature at 89.3%	557.0 ± 6.1 (366–718, N = 30), mature at 65.7%	0.21	This study

APPENDIX 2. Clutch size and neonate snout-vent length (SVL, mm) in Xenodontini snakes. Means are followed by standard deviation, the range and sample size (N) are indicated in parenthesis. \* represents standard error instead of standard deviation. NCAF = Northern Coastal Atlantic Forest, SCAF = Southern Coastal Atlantic Forest, NIAF = Northern Inland Atlantic Forest, SIAF = Southern Coastal Atlantic Forest.

Species and origin	Clutch size	Neonate SVL	Reference
<i>Erythrolamprus aesculapii</i> , SE and S Brazil	4.1 ± 2.3 (1-8, N = 11)	213.0 ± 9.6 (202-225, N = 4)	Marques, 1996b
<i>E. bizona</i> , Costa Rica	5.5 ± 1.8 (3-9, N = 11)	(210-245, N = 7)	Goldberg, 2004; Solórzano, 2004
<i>E. mimus</i> , Costa Rica	3.8 ± 0.5 (3-4, N = 4)	?	Goldberg, 2004; Solórzano, 2004
<i>Liophis lineatus</i> , NE Brazil	6.8 ± 1.4* (3-10, N = ?)	Smallest individual: 179.0	Vitt, 1983
<i>Liophis miliaris</i> , NCAF Brazil	9.0 ± 3.4 (5-17, N = 20)	Smallest individual: 113.0	Pizzatto and Marques, 2006b
<i>Liophis miliaris</i> , SCAF Brazil	10.2 ± 2.8 (5-17, N = 19)	172.4 ± 6.6 (162-178, N = 5)	Pizzatto and Marques, 2006b
<i>Liophis miliaris</i> , NIAF Brazil	10.9 ± 6.5 (4-30, N = 14)	175.0 ± 4.6 (172-182, N = 5)	Pizzatto and Marques, 2006b
<i>Liophis miliaris</i> , SIAF Brazil	10.0 ± 4.4 (1-8, N = 28)	Smallest individual: 150.0	Pizzatto and Marques, 2006b
<i>Liophis mossoroensis</i> , NE Brazil	6.2 ± 0.5* (4-9, N = ?)	Smallest individual: 230.1	Vitt, 1983; Vitt and Vangilder, 1983
<i>Liophis poecilogyrus schottii</i> , NE Brazil	8.1 ± 0.9* (3-17, N = ?)	Smallest individual: 136.3	Vitt, 1983; Vitt and Vangilder, 1983
<i>Liophis poecilogyrus poecilogyrus</i> , SE Brazil	8.25 ± 2.3 (6-15, N = 16)	?	Pinto and Fernandes, 2004
<i>Liophis poecilogyrus sublineatus</i> , S Brazil	6.0 ± 2.0 (3-9, N = 12)	Smallest individual: 114.0	Maciel, 2003
<i>Liophis viridis</i> , NE Brazil	3.7 ± 0.3* (2-6, N = ?)	Smallest individual: 160.3	Vitt, 1983; Vitt and Vangilder, 1983
<i>Lystrophis dorbignyi</i> , S Brazil	5.3 ± 1.6 (3-10, N = 26)	?	Oliveira et al., in press
<i>Waglerophis merremii</i> , SE Brazil	22.5 ± 9.0 (6-44, N = 43)	175.8 ± 1.58 (137-215, N = 37)	This study
<i>Waglerophis merremii</i> , S Brazil	23.4 ± 7.9 (12-39, N = 27)	189.8 ± 2.02 (152-218, N = 28)	This study
<i>Waglerophis merremii</i> , NE Brazil	16.1 ± 8.2* (4-30, N = ?)	Smallest individual: ~ 200.0	Vitt, 1983; Vitt and Vangilder, 1983
<i>Xenodon newiedi</i> , SE Brazil	8.9 ± 3.9 (3-18, N = 41)	-	This study
<i>Xenodon newiedi</i> , S Brazil	8.0 ± 2.9 (4-12, N = 9)	179.7 ± 1.45 (159-202, N = 10)	This study