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Aspects of the reproductive biology and breeding habits of *Leptodeira annulata* (Serpentes, Imantodini) in eastern Amazonia

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Abstract. We analyzed reproductive and feeding habits of *Leptodeira annulata* based on a sample of 136 specimens from eastern Amazonia and compared our data with information from the literature of other populations of *L. annulata*, as well as of *Imantodes cenchoa*. As a result, we detected sexual bimaturism, a continuous reproductive cycle, and no sexual dimorphism regarding snout–vent length. Anurans represent the predominant food item of *L. annulata* in the region, and these snakes do not exclude small prey from their diet, behaving as opportunistic feeders. Interspecific differences in relative fecundity between *L. annulata* and *I. cenchoa* may reflect body characteristics that would represent adaptations to the different reproductive strategies of the two species. Despite the conservative nature of some features of the life-cycle strategies of *L. annulata*, we demonstrate that reproductive strategies of the species may exhibit geographic variation based on the results of other studies approaching the same species in other areas of South America. Considering that larger conspecific females show higher fecundity, it is possible that natural selection favors sexual maturity of females to occur later.

Keywords. Ecology; Natural history; Neotropical.

INTRODUCTION

Studies of snake reproductive biology and feeding habits provide crucial information about their functional role in many ecosystems (Litvaitis, 2000; Shine, 2003; Shine and Bonnet, 2009; Brischoux et al., 2010). Some snake species undergo behavioral changes related to feeding habits and reproduction rate in response to the type and amount of food available (Marques and Puerto, 1994; Bonnet et al., 2001; Shine and Sun, 2003). For instance, gravid snakes may progressively decrease feeding rate as follicle size increases, thus reducing effects of physical activity (Brischoux et al., 2010). Beyond the factors related to feeding habits, environmental parameters affect the seasonality of the reproductive cycles, being more evident in regions where reproduction occurs during the warmest months of the year (Balestrin and Di-Bernardo, 2005; Tozetti and Martins, 2008; Hartmann et al., 2009; Ávila et al., 2010; Orofino et al., 2010).

According to Mathies (2011), snake reproductive cycles should be evaluated at the individual and population levels. At the individual level, one can find three different types: I) Discontinuous cyclical, in which the total regression of the gonads is observed at some period of the year;

II) continuous cyclical, in which complete regression does not occur but gamete production is reduced; and III) acyclical, in which production of gametes is continuous. At the population level, discontinuous and continuous cycles are seasonal synchronous (or semi-synchronous) if the observed synchrony between sexes is not markedly closed and aseasonal if there is a complete absence of synchrony between the sexes. With some exceptions, the snakes from tropical and subtropical regions present variable reproductive cycles (e.g., Maschio et al., 2007; Pizzatto et al., 2008; Turci et al., 2009; Albarelli and Santos-Costa, 2010). Although rare, reproductive modes can also vary intraspecifically among squamates, such as the brown-banded watersnake, *Helicops angulatus* (Linnaeus, 1758), whose populations may be oviparous or viviparous, depending on the region of occurrence (Braz et al., 2016).

Among Neotropical snakes, Imantodini (Myers, 2011) includes species with variable morphological patterns associated with different habits. For instance, the nocturnal, oviparous, and primarily anuran-eating blunthead tree snake, *Imantodes cenchoa* (Linnaeus, 1758), has a laterally compressed body and elongated tail, denoting its arboreal habits (Sousa et al., 2014a); in contrast, the banded cat-eyed snake, *Leptodeira annulata* (Linnaeus, 1758), is also

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nocturnal and feeds primarily on amphibians but has a relatively shorter body and tail, denoting predominantly terrestrial habits (Yanosky et al., 1996; Martins and Oliveira, 1998; Santos-Silva et al., 2014; Santos-Costa et al., 2015).

Morphological variations in some species of the genera *Leptodeira* Fitzinger, 1843 and *Imantodes* Duméril, 1853 can reflect differences in reproductive features such as fertility rate, reproductive cycle, and sexual dimorphism. Intraspecific sexual modifications have been reported for *I. cenchoa*, which comprises populations with continuous (Pizzatto et al., 2008) or biannual reproductive cycles (Sousa et al., 2014a), depending on the region of occurrence.

Herein, we describe the reproductive biology and feeding habits of a population of *Leptodeira annulata* from eastern Amazonia. Assuming the monophyly of *Imantodini* (sensu Myers, 2012), we compare the reproductive cycle and morphology of this species with that of *Imantodes cenchoa* (also part of *Imantodini*) and discuss the influence of environmental characteristics on the reproductive behavior of these species.

MATERIALS AND METHODS

Analyzed material

We examined 136 specimens of *Leptodeira annulata* (68 males, 68 females) from eastern Amazonia deposited in the Herpetological Collection of the Museu Paraense Emílio Goeldi (MPEG; Appendix). For comparisons, we used the data from Pizzatto et al. (2008) and Sousa et al. (2014a) for *Imantodes* and *Leptodeira* (Table 1).

Fieldwork was conducted in several localities in the state of Pará, Brazil, near densely populated areas and with landscapes drastically altered by human activities. Tropical rainforest climate or equatorial climate (designated Af by the Köppen climate classification; Köppen and Geiger 1928), characterized all sampling sites, with high rainfall, a well-marked rainy season between December and May, and average annual precipitation of 917.5–970.5 mm. The period from June to November (nearly 6 months) exhibits lower rates of rainfall, with average annual precipitation of

254–358 mm (Albuquerque et al., 2010). The average annual temperature approaches 27°C, while the annual average relative humidity approaches 90% (CPTEC/INPE, 2013).

Floristic formations comprise a variety of habitats briefly described as follows: (1) “Terra firme” (dryland) is the most typical vegetation of the region, represents a very uniform landscape and can be interrupted by non-arboreal vegetation. Originally, it covered about 90% of the Brazilian Amazon, but it has drastically decreased, mainly due to deforestation and the transformation of forests into monocultures and pastures. (2) “Campos rupestres” (rocky savannas) are composed of rupicolous (rocky habitat) vegetation that grows on a range of geologies, including quartzite-sandstone, granite-gneiss, and itabirite—an iron-rich metal sedimentary rock. Any open vegetation type associated with rocky outcrops (see Nunes et al., 2015). (3) “Campinarana” (white-sand savannas or “Amazon Caatinga”) are Amazonian ecosystems associated with poor, sandy soils often subjected to periodic flooding resulting from water table level variation. Compared to “terra firme” forests, the campinaranas present low parameters of productivity and diversity. They present relatively open understory with a scarcity of lianas and vines but with arboreal individuals reaching up to 30 m (Guimarães and Bueno, 2016). (4) “Várzea” forests (floodplain forest) are bordered by rivers and streams, being continuously flooded by tidal cycles. (5) “Igapó” forests are very common in the lowlands where water accumulation formed by winter rains continuously floods the rainforest between December and June (Milliken et al., 2010; Junk et al., 2012). And (6) “capoeira,” which is a complex of grasslands, sparse shrubs, and bushes, denoting secondary formations at different stages of regeneration. It is an expansion of secondary forest that develops in the abandoned areas after some years of intense use (Braga, 1979).

Reproduction

For all analyzed specimens, we measured snout–vent length (SVL) and tail length with the aid of a graduated ruler (to the nearest 1.0 mm) and body mass with the aid of a dynamometer (scale to the nearest 1.0 mg). We con-

Table 1. Comparison of the results from analyses of specimens from different areas (AC = State of Acre, AP = State of Amapá, AM = State of Amazonas, MA = State of Maranhão, PA = State of Pará, RO = State of Rondônia).

Species	Collection point	Sexual dimorphism (snout–vent length)	Sexual dimorphism (tail length)	Sexual bimaturism	Reproductive period	Reference
<i>Leptodeira annulata</i>	Eastern Amazonia	No	Yes	Males before females	Continuous	This study
<i>Leptodeira annulata</i>	A range of localities between 11°47'N, 23°35'S/39°43'E, 56°05'W (virtually the entire distribution of the species)	Females > Males	Yes	No	Continuous	Pizzatto et al., 2008
<i>Imantodes cenchoa</i>	Brazilian Amazonia (AC, AP, AM, MA, PA, RO)	Females > Males	No	Males before females	Two peaks	Sousa et al., 2014a
<i>Imantodes cenchoa</i>	A range of localities between 21°11'N, 26°55'S/45°24'E, 52°06'W (virtually the entire distribution of the species)	No	Yes	No	Continuous	Pizzatto et al., 2008

sidered all newborn specimens with SVL between 150–210 mm to be hatchling and all males presenting coiled ductus deferens and all females displaying vitellogenic follicles (secondary yolk stage) or oviducts carrying eggs to be sexually mature. On the basis of these parameters, even in the absence of data on the urogenital traits, we assumed that all specimens, males or females, with SVL equal to or longer than the shortest mature specimen of the corresponding sex were mature. We inferred the oviposition period on the basis of the seasonal distribution of gravid females and estimated the fecundity (reproductive rate) on the basis of the number of vitellogenic follicles (secondary yolk stage) or egg-bearing oviducts.

For analyses of the spermatogenic cycle and possible sperm storage, we collected the right testis and a portion of the efferent ducts from 24 males (2 per month). We followed Goldberg and Parker (1975) for the classification of the spermatogenic cycle, considering the stages of early spermiogenesis (metamorphosing spermatids, Stage 1) and spermiogenesis (mature sperm in lumen, Stage 2). We selected 30 vitellogenic follicles of 11 females of *Leptodeira annulata* for histological analyses and submitted them to routine histological processing for inclusion in paraffin (see Prophet et al., 1995). We stained the 5 μ m sections with Hematoxylin-Eosin (HE). We followed George and Castro (1998) in determining the maturity of the vesicular follicles based on the number of layers of ovarian follicular cells surrounding the oocyte (up to two layers = mature; three or more layers = immature).

Feeding habits

To assess feeding habits (i.e., composition and relative frequency of food items), we examined the stomach contents of 68 male and 68 female *Leptodeira annulata* from 24 localities in the state of Pará, Brazil and one locality in the state of Maranhão, Brazil. We performed a longitudinal incision on the venter to expose the stomach and intestines, allowing exploration of their contents. We measured SVL and total length of whole and partially digested prey with the aid of a caliper to the nearest 0.01 mm. We estimated mean relative body size (SVL and total length) of partially digested prey by comparing them with three conspecific specimens with similar size housed in the MPEG collection (Prudente et al., 2014).

We determined the direction of prey ingestion (prey-handling method) based on the relative position of each prey within the gastrointestinal tract of the specimens (anteroposterior = headfirst; posteroanterior = tail first). We did not include in our analyses of prey-handling method any prey in advanced stages of digestion or small prey found in a transverse position inside the *gastrointestinal tract*.

Statistical analyses

We performed statistical analyses to compare means among parameters of sexual dimorphism (SVL, tail length,

ventral and subcaudal counts) and number of follicles and/or eggs in the oviduct. We assessed assumptions of normality and homoscedasticity, respectively, by applying the Kolmogorov-Smirnov and Bartlett tests. When these tests confirmed both assumptions ($P > 0.05$), we used parametric tests to compare means [e.g., Student *t*-test, Analysis of Variance (ANOVA)]; otherwise, when any of the assumptions was violated ($P < 0.05$), we recurred to non-parametric tests to compare means (e.g., Mann-Whitney U test).

We used Pearson's Linear Regression to compare SVL with the number of vitellogenic follicles, eggs, and hatchlings. For these statistical analyses, we used the software BioEstat 5.0 (Ayres et al., 2007). To estimate the reproductive cycle, juvenile survival, and recruitment, we performed a circular statistical analysis (Zar, 2010) whereby we converted months into angles (30° intervals) and treated the number of follicles in secondary yolk stage, eggs, and hatchlings per month as the frequencies in each angle (Prado et al., 2005; Both et al., 2008; Prudente et al., 2014). On the basis of this method, we estimated (1) the mean vector, μ ; (2) the length, r , of the mean vector; and (3) the circular standard deviation, SD, related to μ , and (4) we performed Rayleigh's Uniformity Test (Zar, 2010) to assess dataset normality (null hypothesis, $P > 0.05$). For the circular statistical analysis, we used the Software Oriana 4.02 (Kovach, 2009). For the feeding habits, we analyzed the correlation between prey and predator sizes using Pearson's Linear Correlation Test in the software BioEstat 5.0 (Ayres et al., 2007).

RESULTS

Reproduction

The smallest mature male and female specimens, respectively, of *Leptodeira annulata* in our sample measured 312 mm (MPEG 718) and 301 mm (MPEG 772) SVL. Consequently, for each sex we considered all males of SVL ≥ 312 mm and all females of SVL ≥ 301 mm as mature. Thus, sexual bimaturism analysis revealed that 100% of males greater than 331 mm SVL were sexually mature, whereas for females, this only occurs when they reach 421 mm. Therefore, male specimens achieve sexual maturity at an earlier stage of development than females, characterizing bimaturism in this population of *L. annulata* (Fig. 1).

Mature male *Leptodeira annulata* presented longer tails (20.11–28.26%, $\bar{x} = 24.63\%$; $n = 48$) than mature females (21.55–33.33%, $\bar{x} = 27.16\%$; $n = 51$; $Z = 6.36$, $P < 0.05$). The ANOVA test detected no differences in the SVL of females and adult males ($Z = 1.16$, $P > 0.05$; Figs. 2 and 3).

Histological analyses of the follicles in the primary yolk stage showed the oocyte to be enveloped by a single layer of follicular cells or granulosa of simple pavement epithelium. The cytoplasm of this cell presented coarse granules of yolk arranged at the periphery of the cell, and the nucleus was not visible. These immature follicles (primary stage) had a thinner connective tissue layer and a diameter up to 7.0 mm. Follicles in secondary yolk stage

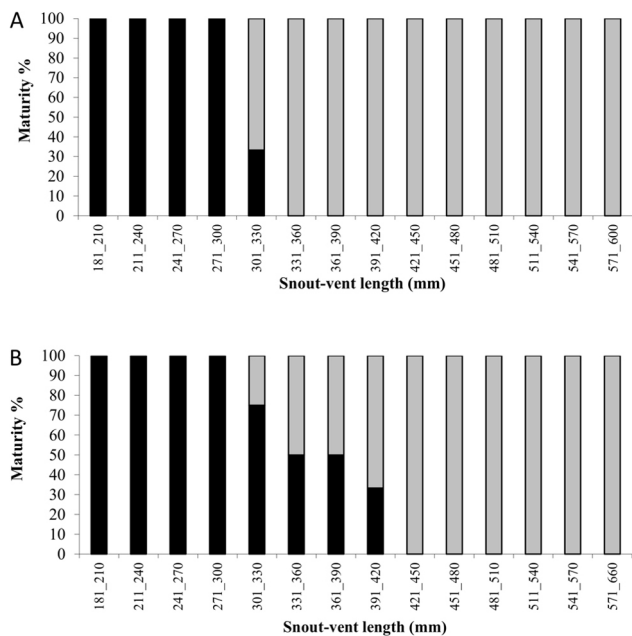


Figure 1. Percentage of sexually immature and mature males (A) and females (B) of *Leptodeira annulata* from eastern Amazonia, for the different size classes. Black bars = Immature; Gray bars = mature.

of *Leptodeira annulata* had more than two cell layers of ovarian follicular cells surrounding the oocyte, with a central nucleus and a cytoplasm filled with yolk. The follicles presented a thick layer of connective tissue adjacent to the ovarian follicular cell layer.

Macroscopically testes are asymmetric and paired, with a cylindrical and elongated shape. The testicular parenchyma is composed of numerous well-organized seminiferous tubules surrounded by a tunica albuginea of connective tissue. Histologically, in stage 1, early spermiogenesis of the seminiferous tubule is sealed in spermatogenic lineages at various stages of development: spermatogonia, spermatocytes, spermatids, and some spermatozoa in the center of the tubule. In stage 2, spermiogenesis, the seminiferous tubules is the open lumen and spermatogonia, spermatocytes, and numerous spermatids and spermatozoa are present in the lumen. Independent of the testicular stage, the efferent ducts were filled with spermatozoa (Fig. 4).

Leptodeira annulata undergoes asynchronous gonadal activity, presenting ovarian follicles of different sizes and stages of development. The macroscopic analysis revealed follicles in secondary yolk stage (> 7.0 mm) and eggs throughout the year (viz., January, February, March, May, June, July, August, October, and December). We recorded hatchlings along the year and in March, April, June, July, August, September, October, and December. The number of eggs was 2–10 ($\bar{x} = 4 \pm 1.79$; $n = 8$) and was significantly correlated with female SVL (Pearson's Linear Correlation Test, $t = 2.1063$; $r = 0.5746$; $P < 0.05$, $n = 8$; Table 2; Fig. 5).

Feeding habits

We observed a total of 51 food items prey in the stomach or intestines of 44 of the 136 examined snakes (32.35%; Table 3). Most specimens ($n = 32$; 72.73%) con-

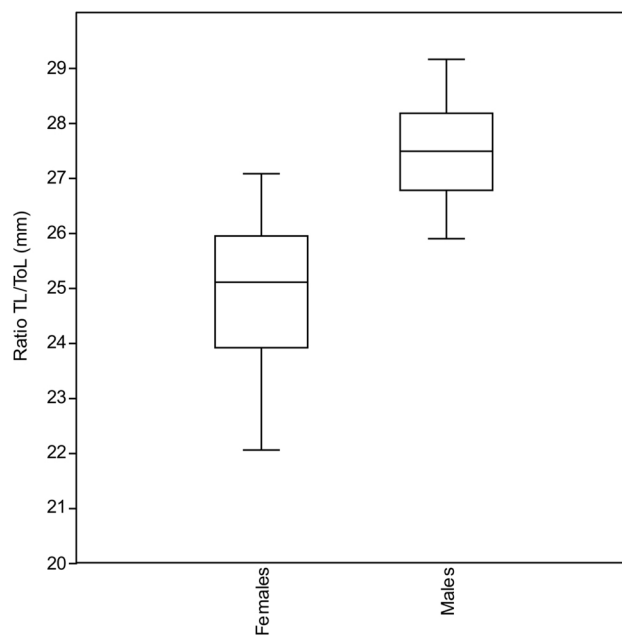


Figure 2. Difference between the means of the tail length (TL) proportions in relation to the total length (ToL) of the body of sexually mature female and male *Leptodeira annulata* from eastern Amazonia.

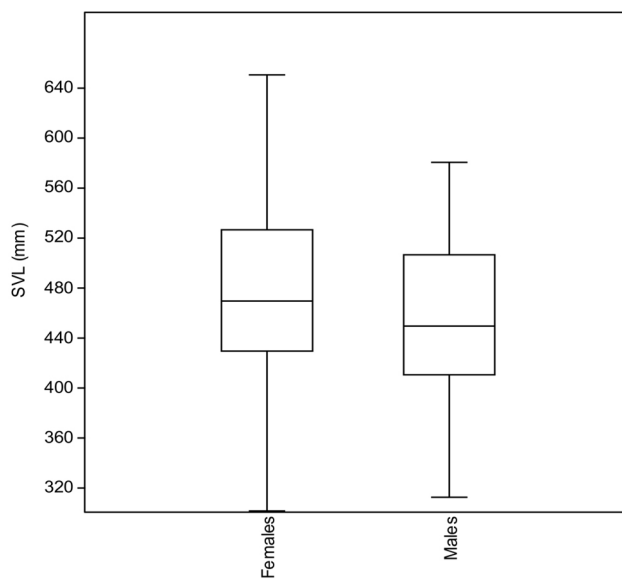


Figure 3. Difference between the snout-vent length (SVL) of adult female and male *Leptodeira annulata* from eastern Amazonia.

tained only one food item in the *gastrointestinal tract*, but four (9.09%) contained two items, and two (4.55%) contained three and seven items, respectively. The predominant food items were anurans ($n = 50$, 98.03%) observed in 43 snakes (97.73%), while a single gekkonid lizard identified as *Hemidactylus mabouia* (Moreau de Jonnès, 1818) ($n = 1$, 1.96%) was ingested by a single snake (2.27%). Among the ingested anurans, the most common prey was Hylidae ($n = 30$, 58.83%), followed by Leptodactylidae ($n = 16$, 31.37%), Bufonidae ($n = 50$, 98.03%), and Phyllomedusidae ($n = 2$, 3.92%). Five specimens fed on more than one prey category (Table 3). We also recorded arthropod remains in the guts of some specimens, which we attribute to secondary ingestion.

Among specimens with stomach contents, 43% of females ($n = 10$) and 53% of males ($n = 11$) were collected in the rainy season, whereas 57% females ($n = 13$) and 48%

of males ($n = 10$) were sampled in the dry season. We recorded stomach contents in both gravid and nongravid females in rainy season and dry season.

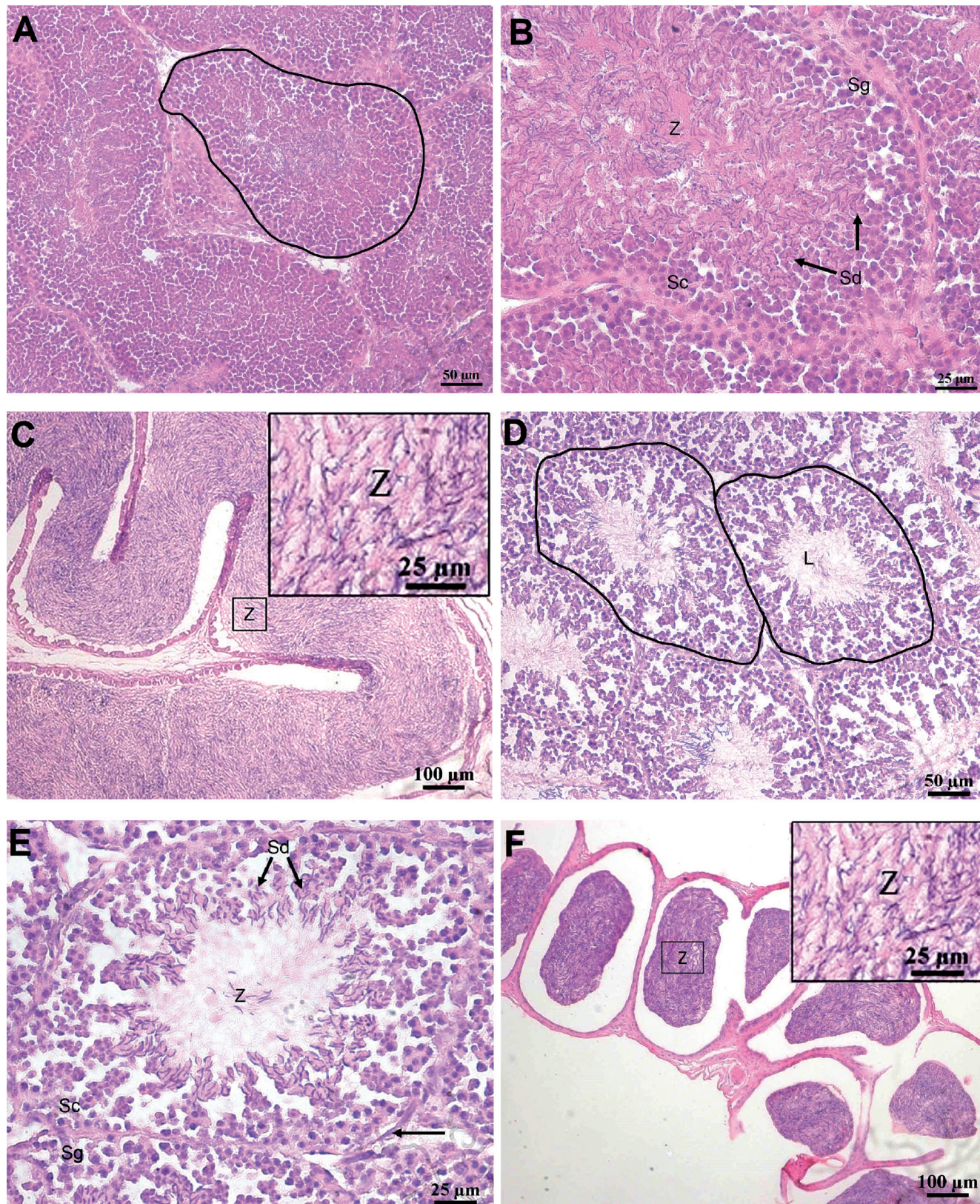


Figure 4. Sections of the testis of *Leptodeira annulata*. Stage 1, early spermiogenesis: **(A)** Seminiferous tubules in circle. **(B)** Magnification of A: Transverse section through a seminiferous tubule with population of developing germ cells. **(C)** Section of efferent ducts; detail filled with spermatozoa. **(D)** Stage 2, spermiogenesis (seminiferous tubules circled). **(E)** Magnification of D: Seminiferous tubule with spermatozoa in lumen; arrow indicates basal lamina. **(F)** Section of efferent ducts; detail filled with spermatozoa. Sg, spermatogonia; Sc, spermatocyte; Sd, spermatid; Z, spermatozoa.

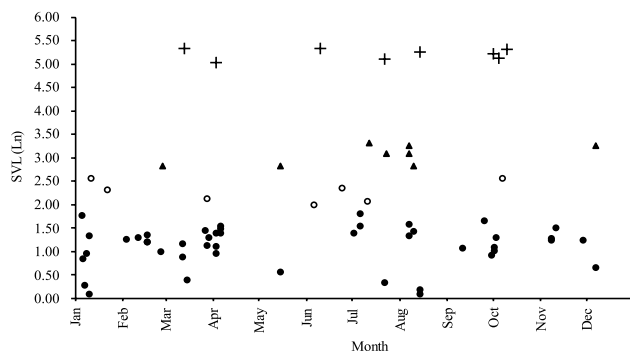


Figure 5. Seasonal distribution of follicles in primary yolk stage (black circles), follicles in secondary yolk stage (> 7 mm) (open circles), eggs (triangles), and hatchlings (crosses), in females of *Leptodeira annulata* from eastern Amazonia. The numbers represent the frequency of follicles, eggs, and hatchlings in each month; values transformed into natural logarithm (7 mm = 1.95 Ln).

Table 2. Results of the circular statistical analysis testing seasonality in the reproductive cycle of females of *Leptodeira annulata* from eastern Amazonia.

Variables	Follicles in secondary yolk stage and eggs	Hatchlings
Observations (n)	15	8
Mean vector (μ)	321.206°	97.278°
Length of mean vector (r)	0.298	0.252
Circular Standard Deviation (SD)	89.179°	95.11°
Rayleigh Test of Uniformity (P)	0.13	0.476

Considering the prey-handling method, we were able to identify the direction of intake of 30 food items. The results showed that 28 items (93.33%) were swallowed headfirst and two (6.67%) tail first.

We were able to measure the total length of only seven food items, but our data demonstrate that adult specimens of *Leptodeira annulata* do not exclude small prey from their diet. We found no correlation between the sizes of the snakes (SVL) and their prey (total length; $r = 0.1051$; $t = 0.2588$; $P > 0.05$).

DISCUSSION

Our results revealed differences in the reproductive parameters of *Leptodeira annulata* populations from different geographic regions. For example, we detected no sexual dimorphism in SVL and found sexual bimaturism, with males maturing earlier than females, in the eastern Amazonian populations, unlike what was observed by Pizzatto et al. (2008) in other populations of *L. annulata*. Our data corroborate the general trends of sexual dimorphism associated with the reproductive roles of males and females (e.g., longer tails in males resulting from the accommodation of hemipenes [Shine and Shetty, 2001; Lourdaís et al., 2006], and a larger body mass of females associated with fecundity [Shine, 1993]).

Given that larger conspecific females have higher fecundity (Vitt and Vangilder, 1983; Shine, 1994), it is possible that natural selection favors delayed female sexual

maturity (see our data and also the results of Marques [1996] for *Erythrolamprus aesculapi* [Linnaeus, 1766], Marques and Puerto [1998] and Santos-Costa et al. [2006] for *Tantilla melanocephala* [Linnaeus, 1758], Aguiar and Di-Bernardo [2005] for *Helicops infrataeniatus* Jan, 1865, Balestrin and Di-Bernardo [2005] for *Atractus reticulatus* [Boulenger, 1885], and Sousa et al. [2014a] for *Imantodes cenchoa*).

Contrary to the results of Pizzatto et al. (2008) for *Leptodeira annulata*, in which males may be significantly smaller than females, we did not detect sexual dimorphism in the SVL of this species. This corroborates parameters of reproductive physiology, as well as a strategy often present in species in which males fight during the breeding season (Shine, 1994). Male combat might occur in the populations of *L. annulata* analyzed here, but this hypothesis needs objective field observations.

Interspecific differences in fecundity between *Leptodeira annulata* (this study) and *Imantodes cenchoa* (see Pizzatto et al., 2008) might reflect body characteristics adapted to different habits. *Imantodes cenchoa* has a more strictly arboreal body plan, presenting a small ratio of body mass to body length. A laterally compressed body, long tail, and line of elongated vertebral scales result in a displaced center of gravity (Lillywhite and Henderson, 1993) and limit the size or number of eggs produced by this species (Sousa et al., 2014a; Sheehy et al., 2016). Those characteristics are not observed in *L. annulata*, which is terrestrial and a higher ratio of body mass/length, allowing the production of more eggs.

The characterization and classification of primary and secondary ovarian follicles from histological analyses provide crucial information to age of sexual maturation. In our sample, the absence of reproductive synchrony in the gonadal activity and presence of vitellogenic follicles (secondary yolk stage), eggs, and hatchlings throughout the year provide evidence of aseasonal reproduction in the analyzed population of *Leptodeira annulata*. Nonetheless, the rate of yolk deposition in the follicles can vary among individuals according to factors such as hormone levels and body condition (Mathies, 2011) such that extended vitellogenesis might not be a reliable indicator of reproductive seasonality when analyzing females individually.

The testes of *L. annulata* are similar to those of other reptiles in their testicular architecture and in arrangement of germ cells within the seminiferous tubules (Hernández-Gallegos et al., 2014; Souza et al., 2014b). We describe only two gonadal stages, early spermiogenesis and spermiogenesis, in contrast to colubrids (Goldberg and Parker, 1975), which present six stages in the spermatogenic cycle. Similarly, all male *L. annulata* were mature, with active spermiogenesis throughout the year, characterizing an aseasonal reproduction at the population level. We could detect all cell types of the spermatogenic lineage and the process of differentiation of spermatids into spermatozoa in stage 1.

We found females with and without stomach contents in both proportions in the same amount, both in gravid and non-gravid females, throughout the year,

Table 3. Types and proportion of occurrence of prey in the diet of 44 out of our 136 sampled specimens of *Leptodeira annulata* from eastern Amazonia. Some specimens fed on more than one prey category. Data on the habitats and habits of prey were obtained from the literature (Bartlett and Bartlett, 2003; Vitt et al., 2008; Rodrigues and Santos-Costa, 2014), as well as from AmphibiaWeb (2021).

Taxon	Habitat and habits of prey	Snakes with prey (n)	Snakes with prey (%)	Number of prey (n)	Number of prey (%)
Amphibia (Anura)					
BUFONIDAE					
Bufo not identified	No data	1	2.27	1	1.96
<i>Rhinella</i> sp.	No data	1	2.27	1	1.96
LEPTODACTYLIDAE					
Leptodactylidae not identified	No data	6	13.64	6	11.77
<i>Leptodactylus</i> sp.	No data	2	4.55	2	3.92
<i>Adenomera</i> sp.	Terrestrial, diurnal, and nocturnal, occur in forest areas.	2	4.55	2	3.92
<i>Leptodactylus bolivianus</i> Boulenger, 1898	Terrestrial, nocturnal. Typical of open areas associated with anthropic disturbances.	1	2.27	1	1.96
<i>Leptodactylus fuscus</i> (Schneider, 1799)	Terrestrial, nocturnal. Typical of open areas associated with anthropic disturbances.	1	2.27	1	1.96
<i>Leptodactylus macrosternum</i> Miranda-Ribeiro, 1926	Terrestrial, nocturnal. Typical of open areas associated with anthropic disturbances.	1	2.27	1	1.96
<i>Physalaemus ephippifer</i> (Steindachner, 1864)	Terrestrial, diurnal, and nocturnal. Typical of open areas associated with anthropic disturbances.	1	2.27	3	5.88
HYLIDAE					
Hylidae not identified	No data	12	27.28	14	27.46
<i>Dendropsophus melanargyreus</i> (Cope, 1887)	Arboreal and nocturnal. It occurs on the ground in reproductive sites with large clusters of specimens. Typical of edge of forest or open areas that still have shrub vegetation.	1	2.27	1	1.96
<i>Dendropsophus minutus</i> (Peters, 1872)	Arboreal and nocturnal. It occurs on the ground in reproductive sites with large clusters of specimens. Typical of edge of forest or open areas that still have shrub vegetation.	1	2.27	3	5.88
<i>Dendropsophus</i> sp.	No data	2	4.55	2	3.92
<i>Hypsiboas multifasciatus</i> (Günther, 1859)	Arboreal and nocturnal. It occurs on the ground in reproductive sites with large clusters of specimens. Typical of edge of forest or open areas that still have shrub vegetation.	1	2.27	1	1.96
<i>Osteocephalus taurinus</i> Steindachner, 1862	Arboreal and nocturnal	1	2.27	1	1.96
<i>Scinax</i> sp.	No data	6	13.64	6	11.77
<i>Scinax x-signatus</i> (Spix, 1824)	A typical arboreal species of forest edge or open areas that still have shrub vegetation. Typically associated with anthropic disturbances.	2	4.55	2	3.92
PHYLLOMEDUSIDAE					
<i>Pithecopus hypochondrialis</i> (Daudin, 1800)	Arboreal and nocturnal. Occurs on edge of forests.	1	2.27	2	3.92
Reptilia					
GEKKONIDAE					
<i>Hemidactylus mabouia</i> (Moreau de Jonnés, 1818)	Originally arboreal and nocturnal. Easily found in degraded habitats or human constructions.	1	2.27	1	1.96
TOTAL		44	100	51	100

strongly indicating that the reproductive period of *Leptodeira annulata* is not directly related to food consumption. Additionally, the fact that females contained food items during the reproductive period (females with secondary yolk and egg follicles) suggests that *L. annulata* does not reduce its food intake during the gestational period. In contrast, Shine (1987) suggested that in general female

snakes tend to reduce food consumption during this period, as observed in *Anilius scytale* (Linnaeus, 1758) (Maschio et al., 2010). Our results demonstrate that the reduction of food intake when females are gravid is not obligate. It can result from differences in activity patterns and especially reproductive strategies (e.g., viviparity versus oviparity; Lourdaís et al., 2002). However, the explanation for

such variations requires further experimental studies (see Gregory et al., 1999).

The aseasonal reproductive cycle is common in tropical snakes (Duellman, 1978), including *Dipsadini* Bonaparte, 1838 (Zug et al., 1979; Porto and Fernandes, 1996; Balestrin and Di-Bernardo, 2005) and *Xenodontini* Bonaparte, 1845 (Vitt, 1983; Vitt and Vangilder, 1983; Dixon and Soini, 1986). However, the reproductive seasonality recorded for some species in warm and rainy regions, such as *Anilius scytale* and *Drymarchon corais* Boie, 1827 (Maschio et al., 2007; Prudente et al., 2014), suggests variation in the reproductive strategies of some species. These differences occur among populations of *Imantodes cenchoa*, which has a broad geographic distribution (Sousa et al., 2004b; Pizzatto et al., 2008). In this species, some populations exhibit two seasonal peaks in reproductive activity, with juvenile survival and recruitment mainly occurring in the rainy season (Sousa et al., 2014a), while others reproduce throughout the year (Pizzatto et al., 2008). Differences in some reproductive traits, such as sexual dimorphism, bimaturism, and even reproductive cycle, as seen among the different populations of *Leptodeira annulata* and *I. cenchoa*, might result from environmental factors associated with geographic distribution.

Leptodeira annulata actively forages at night, both on the ground and in trees. These snakes feed on nocturnal prey (active at night) and also on diurnal prey found asleep under the vegetation or fallen trunks. Active foraging specimens also take advantage of explosive reproductive events of some amphibian species (Cunha and Nascimento, 1993; Yanosky et al., 1996). The habit and habitats of the prey of our sample corroborate the adaptability of *L. annulata* to altered habitats. The species often forages on the borders of primary or secondary forests, “capoeira” vegetation, and open areas such as the “campinarana” (white-sand savannas or Amazon Caatinga) and the “campos rupestres” (rocky savanna) or even in sparse housing areas (see Table 3).

Leptodeira annulata feeds indistinctly on proportionately large and small prey found both on the ground and in vegetation, behaving as an opportunistic feeder. This behavior can be a good example of how snakes’ interaction with the environment relates to the distribution and abundance of their prey, directly influencing their feeding behavior (Vitt and Vangilder, 1983; Ruffato et al., 2003).

Further studies involving ecological aspects should also take into account the geographic distribution of the analyzed specimens. Although many characteristics related to life history are relatively conservative (Pizzatto et al., 2008), this study demonstrates that different populations of the same species can present differentiated survival strategies (e.g., sexual dimorphism in SVL and TL, sexual bimaturism, and reproductive period) depending on their geographic distribution (as also observed in Pizzatto et al., 2008; Souza et al., 2014a). Granted that environmental pressure is a driving force on ecological characteristics in all species (Ayres and Scriber, 1994), results of studies involving species with a broad geographic distribution should analyze different populations separately to avoid

generalizing particular features of each population. Detailed knowledge of the reproductive cycle and feeding habits of eastern Amazonian snake populations is essential to understand the evolutionary history of these species, bringing new perspectives on reproduction and feeding behavior of Neotropical snakes.

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APPENDIX

Specimens examined, deposited in the Herpetological Collection of the Museu Paraense Emílio Goeldi:

Leptodeira annulata (n = 136): BRAZIL: **Maranhão**: Arari: MPEG 13501, 14300, 14542, 14543, 14544, 15029, 15030, 15031, 15629, 15630, 15631, 16062, 16063, 16083, 16160; **Pará**: Almerim: MPEG 16354, 16364, 16365, 20107; Benevides: MPEG 13313; Belém: MPEG 18918; Bragança: MPEG 11288; Chaves: MPEG 18865; Curionópolis: MPEG 20740, 20752, 20753; Dom Eliseu: MPEG 13389; Faro: MPEG 18356; Gurupá: MPEG 15161; Marabá: MPEG 7451, 7453, 7456, 7470, 9487, 10981, 10981, 15167, 15167, 16530, 16649, 16651, 16847, 16938, 16981, 17044, 17045, 17046, 17082, 17088, 17102; Melgaço: MPEG 18652, 18962, 19745, 20016, 20017, 20026, 20079, 20086, 20098, 20131, 20141, 20236, 20303, 20444; Mojú: MPEG 17600, 17601, 17710, 17711; Ourém: MPEG 4260; Ourilândia do Norte: MPEG 20789; Palestina do Pará: MPEG 1555, 11778, 11779, 11780, 15554; Paragominas: MPEG 18848; Peixe Boi: MPEG 3229; Portel: MPEG 696, 717, 718, 772, 914, 917, 921, 924, 929, 930; Salvaterra: MPEG 18338, 18339, 16393, 19050, 19055, 19074, 19077, 19080, 19095, 19104, 19105; São Félix do Xingú: MPEG 19557; Soure: MPEG 17724, 17785, 19263; Tomé-Açu: MPEG 11738, 11739, 11740, 11741, 11742; Tucuruí: MPEG 16646; Viseu: MPEG 2075, 4317, 4329, 4432, 4437, 5982, 5996, 6124, 6364, 7294, 7323, 7337, 7679, 8200, 8456, 9185, 9186, 9187, 9188, 9189, 14181, 14942, 15957; Uninformed location: MPEG 10815, 20757, 20758, 20769, 20912.