
**REPRODUCTIVE AND TROPHIC ECOLOGY OF
ERYTHROLAMPRUS TAENIOGASTER (SERPENTES: DIPSADIDAE)
IN THE BRAZILIAN EASTERN AMAZON**

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Abstract.—Despite the increasing number of studies on reproduction and diet of neotropical snakes, reproductive and feeding patterns of several species are poorly known, especially in the Amazon. Herein, we present results of a study on reproductive and trophic ecology of the Common Coral Grass Snake (*Erythrolamprus taeniogaster*) from different localities in Brazilian Eastern Amazon that are deposited in the Herpetological Collection of Museu Paraense Emílio Goeldi. We found sexual dimorphism, with significantly larger head and body sizes in adult females than in adult males. We also found sexual bimaturation, with females reaching sexual maturity at a larger snout-vent length than males. We did not observe any correlation between body size and number of vitellogenic follicles and eggs in females. Males are able to mate throughout the year, characterizing an acyclic (at individual level) and aseasonal (at population level) reproductive cycle. Females with eggs and recruitment occur throughout the year, characterizing a cyclic discontinuous reproductive cycle in females, with seasonal (at individual level) and aseasonal patterns (at population level). Regarding the diet, *E. taeniogaster* is predominantly piscivorous, actively foraging during the day, when they catch both inactive (nocturnal) and active (diurnal) prey.

Key Words.—feeding; reproduction; semiaquatic; squamata; South American swampsnakes

INTRODUCTION

Deeper knowledge about reproductive and feeding biology of neotropical snakes has been achieved in the last two decades, providing information making it possible to delimit new trends and patterns among snakes (e.g., Maschio et al. 2010; Marques et al. 2014; Sousa et al. 2014; Stender-Oliveira et al. 2016; Teixeira et al. 2017). A substantial number of studies with Brazilian snakes focus on reproductive aspects based on macroscopic analyses of the reproductive tract, which has led to some criticism because this method does not consider histological analyses of both males and females (see Mathies 2011). Most of these studies also do not consider the distribution of populations, risking erroneous results on reproductive patterns of species.

According to Mathies (2011), reproductive cycles of snakes must be analyzed at the individual level,

classifying the reproductive cycle as cyclic discontinuous, cyclic continuous, or acyclic; and at the population level, in which discontinuous and continuous cycles may be divided into synchronic seasonal, semi-synchronic, or aseasonal. In tropical regions, snake populations tend to have continuous and aseasonal reproductive cycles because of the relatively stable climate (Duellman 1978; Fitch 1982; Vitt and Vangilder 1983), although only males of some species seem to have continuous or acyclic reproductive cycles (Mathies 2011). Invariably, however, because females have a high energetic cost (Callard and Kleis 1987; Mathies 2011), their reproductive cycle is discontinuous with seasonal pattern. In some species, reproduction may not be defined as synchronic seasonal or definitely aseasonal, and therefore, they are classified as extended (Scartozzoni et al. 2009). The extended reproduction occurs when the period of secondary vitellogenesis is long, between 6–10 mo, and females

are pregnant between 4–7 mo (Mathies 2011). Trophic ecology may influence the reproductive cycle of snakes through foraging strategy, seasonal variation in prey availability, and ability to accumulate energy reserves (see Seigel and Ford 1987). Thus, understanding the reproductive ecology of snakes will only be possible if researchers take into account studies on trophic ecology.

The genus *Erythrolamprus* with 55 known species, is distributed from Central America throughout South America (<http://www.reptile-database.org>). Most species within this genus are terrestrial, although a few species are semi-fossorial or semi-aquatic. These snakes are found in humid environments in primary and secondary forest, floodplains, and wetlands (e.g., *igapó* and *várzea*), as well as in other very distinct biomes, such as Caatinga and Cerrado in Brazil (Dixon 1980). The diet of *Erythrolamprus* species is composed of worms, insects, fishes, salamanders, anurans (including tadpoles), lizards, amphisbaenians, birds, mammals, other snakes, and eggs of reptiles (e.g., Maschio et al. 2010; Siqueira et al. 2012; Nascimento et al. 2013; Sousa et al. 2014; Teixeira et al. 2017).

The Common Coral Grass Snake (*Erythrolamprus taeniogaster*) is distributed from Peru through south of Boa Vista in Bolivia, Mato Grosso do Sul, Pará and Pernambuco, southern Ceará, and the coast of Bahia, in Brazil (Ferreira et al. 2017; <http://www.reptile-database.org>). This species is widely distributed in the Amazon, and

information on natural history indicates that it occupies the humid ground of forests, brushlands, grasslands, and environments under strong anthropogenic pressure close to water bodies (see Cunha and Nascimento 1978). As with other snakes within the genus, *Erythrolamprus taeniogaster* is oviparous, and there is a lack of information on its reproductive ecology (Cunha and Nascimento 1993; Martins and Oliveira 1998). Information on the diet is scarce, indicating this species feeds primarily on fishes (see Cunha and Nascimento 1978, 1993; Sousa and Costa-Campos 2016). Therefore, our main goal was to understand the reproductive and trophic ecology of *Erythrolamprus taeniogaster* in Brazilian Eastern Amazon, using macro and microscopic analyses of the gonads, and quantitative and qualitative analyses of the diet.

MATERIALS AND METHODS

Study site and analyzed material.—We analyzed 585 *Erythrolamprus taeniogaster*: 198 males, 278 females, and 109 juveniles of indeterminate sex. Various individuals collected this species over several years, in several localities within the states of Maranhão (n = 80) and Pará (n = 505; Supplemental Information Table S1), in a region known as Brazilian Eastern Amazon (Fig. 1) and specimens were deposited in the Herpetological Collection of Museu Paraense Emílio Goeldi (MPEG).

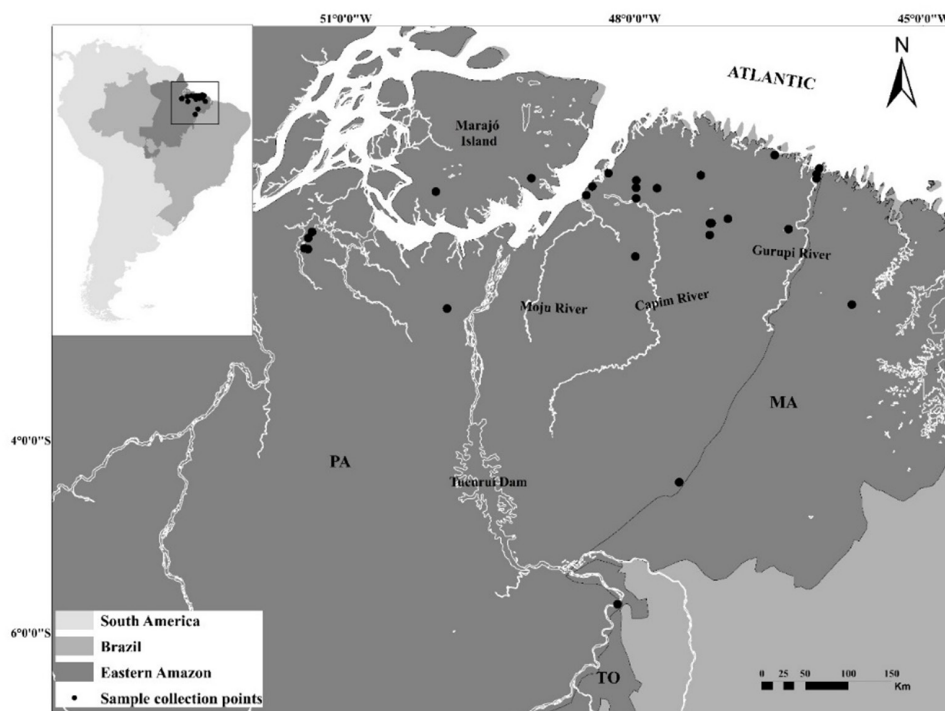


FIGURE 1. Geographic distribution of individual (black dots) Common Coral Grass Snake (*Erythrolamprus taeniogaster*) analyzed from the Brazilian Eastern Amazon.

The Eastern Amazon is a mosaic of preserved and disturbed habitats, with floodplain and upland forests (*Terra-firme*), savannas (*Cerrado*), and sub-humid forests (Ab'Saber 2002). Climate is Af (A = Tropical; f = humid) rainy tropical (Köppen and Geiger 1928), with mean annual rainfall of 1,000–3,000 mm and mean monthly temperature of about 26° C (<http://www.cptec.inpe.br/>). Rainfall is the most variable climatic factor in the region, resulting in a division between dry season (June–November), with a mean monthly rainfall level over the period of 88 mm, and rainy season (between December and May), with a mean monthly rainfall level over the period of 300 mm (<http://www.cptec.inpe.br/>).

For each specimen analyzed, we recorded: (1) snout-vent length (SVL); (2) tail length (TL) using a millimeter metric tape; (3) head length (HL); (4) head width (HW); (5) head height (HH); (6) distance between the eyes (DE) with a 0.01 mm precision caliper; and (7) sex, by a direct examination of the gonads of males and females. We classified snakes as sexually mature males those with a SVL equal to or greater than the smallest male with entangled deferent ducts (adapted from Shine 1977). We classified as sexually mature females all those with SVL equal to or greater than the smallest female with vitellogenic follicles longer than 10 mm (characteristic of a secondary vitellogenic follicle, as observed in histological analysis), carrying eggs in the oviducts, or those with pleated oviducts (as in Maschio et al. 2021). We considered as juveniles all those individuals with evident umbilical scars (as in Santos-Costa et al. 2006).

Analyses of reproductive characteristics.—To characterize the reproductive cycle, we used only sexually mature individuals. For females, we analyzed the relationship between the number of macroscopically

observed vitellogenic follicles and/or eggs in the oviduct. For males, we used length, width, and thickness of both testicles to calculate testicular volume (TV), which has been used as an indicator of spermatogenic activity (Shine 1977). We used the following formula for ellipsoid volume:

$$TV = \frac{4}{3} (a \times b \times c)$$

where a = half the length, b = half the width, and c = half the thickness (Pleguezuelos and Feriche 1999; Rojas et al. 2013).

We also analyzed the appearance of deferent ducts (i.e., opaque, smooth, or tangled); the diameter of right and left deferent ducts in their larger portion, the distal region close to the cloaca; and total length and width of the right kidney to determine the hypertrophy of the renal sexual segment (RSS). We inferred testicular morphometry (diameter of seminiferous tubules and height of seminiferous epithelium; Fig. 2) and kidneys (measurements of renal sexual segment: diameter of renal tubules and height of renal epithelium; Fig. 2) using an Olympus BX53 microscope with a CellSens Standard (Olympus, Tokyo, Japan) image capture system.

For analyses of spermatogenesis and vitellogenesis, we collected gonads of males and females of *E. taeniogaster*, respectively, fixed in 10% formalin and preserved in 70% alcohol, for light microscopy analyses. After obtaining gonads, we removed fragments of the right testicle, deferent duct, and kidney (n = 10) to describe the spermatogenic cycle (Table 1), sperm storage, and hypertrophy of the RSS. Classification of the spermatogenic cycle was described according to Loebens et al. (2016), divided into three stages: (1) recrudescence: presence of primary spermatocytes

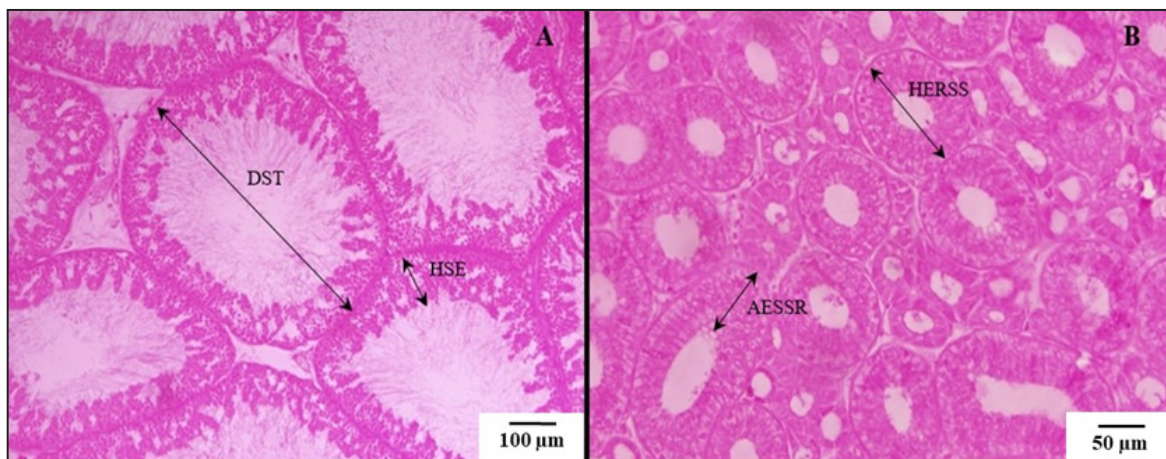


FIGURE 2. Measurements recorded in histological sections of male Common Coral Grass Snake (*Erythrolamprus taeniogaster*). (A) Seminiferous tubules of the testes with DST = diameter of seminiferous tubule, and HSE = height of seminiferous epithelium. (B) Renal sexual segment with HERSS = tubular diameter of renal sexual segment and AERSS = height of the epithelium of renal sexual segment. Staining was done with basic fuchsin.

TABLE 1. Snout-vent length (SVL), tail length (TL), head length (HL), head width (HW), head height (HH) and distance between the eyes (DE) with the number of individuals analyzed (n), mean \pm standard deviation (SD) and range of values of the Common Coral Grass Snake (*Erythrolamprus taeniogaster*) from Brazilian Eastern Amazon. All measurements are in millimeters.

Morphological characteristic	Mature males			Mature females		
	n	mean \pm SD	range	n	mean \pm SD	range
SVL	138	419.2 \pm 63.5	232–653	189	499.5 \pm 70.3	260–738
TL	125	96.4 \pm 17.7	51–160	164	106.1 \pm 17.7	12–60
HL	134	20.9 \pm 3.0	11.7–32.1	178	24.2 \pm 3.2	15.4–32.3
HW	134	12.3 \pm 1.9	6.6–19.7	178	14.7 \pm 2.3	7.3–20.0
HH	95	9.5 \pm 1.9	5.3–18.3	139	10.9 \pm 1.4	6.9–13.2
DE	95	6.4 \pm 1.0	4.5–12.6	139	7.0 \pm 0.8	5.0–9.4

and spermatids; (2) early spermiogenesis: presence of spermatids in metamorphosis; and (3) spermiogenesis: presence of mature spermatozooids in lumen (maximum level of spermiogenesis).

In females, we analyzed ovarian follicles ($n = 10$), which we classified as non-vitellogenic and vitellogenic according to the number of follicular layers on their distal portion. We determined the maturity of vesicular follicles according to George and Castro (1998), based on the number of layers of follicular ovarian cells surrounding oocytes (up to two layers = mature; three or more layers = immature). With this analysis, we observed that follicles must be considered in the secondary stage when they are at least 10 mm long.

All material was dehydrated in a graded ethanol series (30% to 100%) for one hour in each concentration. Methacrylate resin (Leica Historesin-Leica, Wetzlar, Germany) was infiltrated by passing the samples in different proportions of Ethanol-Historesin solutions (5:1, 4:1, 3:1, 2:1, 1:1), for 24 h in each solution, followed by inclusion in plastic molds. After that, we made 3 μ m thick cross-sectional cuts on a Leica RM2235 microtome (Leica, Nussloch, Germany) with glass knives. We arranged the sections in order on slides to be stained with 1% toluidine and basic fuchsin. After staining, we washed the slides with xylol for 15 min and fixed with EntellanTM synthetic resin (Merck, Darmstadt, Germany). We photographed all material using a BX53 Olympus microscope with a CellSens Standard image capture system (version 1.16; Tokyo, Japan) to identify different stages of follicle maturation and analyze and identify different stages of testicular maturation.

Diet analysis.—We described the diet via direct observation of consumed food items in the digestive tract. We conducted a quantitative analysis by counting the number of prey items in the stomach or intestine, and a qualitative analysis by identifying the items consumed to the lowest taxonomic level possible, with the help of experts. For prey items partially digested, we compared them with three other specimens (of the same species), with similar size, deposited in herpetological and

ichthyological scientific collections of Museu Paraense Emílio Goeldi, which allowed us to estimate mass and snout-vent length of each item consumed.

To infer the direction of prey ingestion, we analyzed its position in the digestive tract in relation to the head of the predator, classifying direction as anteroposterior (head ingested first) or posteroanterior (posterior region ingested first). We used measurements of snake length and prey length to analyze the relationship between prey and snake size. To analyze ontogenetic variation or sexual dimorphism in diet, we compared the types and sizes of the prey in digestive tracts of sexually mature males and females with each other and with immatures. We used information on prey habits and habitat use available in the literature to analyze habitat and microhabitat use compared to diet composition.

Data analysis.—We tested normality and homogeneity in the distribution of all data, then used parametric tests or similar non-parametric tests, depending on normality and homogeneity in the distribution of our data. To test whether there is sexual dimorphism between SVL and TL, HL, HW, HH, and DE, we used Student's *t*-test with data for sexually mature males and females only. We performed an Analysis of Covariance (ANCOVA) using SVL as a covariate to determine if there was sexual dimorphism in head measurements using dependent variables HL, HW, HH, DE, and sex as fixed factors. To analyze sexual bimaturism, we calculated the percentage of sexually mature males and females in different size classes. We also analyzed the relationship between number of eggs and vitellogenic follicles and SVL of females using Pearson's Product Moment Correlation. In addition, we inferred the reproductive cycle of females by considering the presence of characteristics typical of reproductive period (presence of follicles larger than 10 mm and eggs) in relation to the period of the year that the individual was caught.

To analyze the reproductive cycle of males, we used Linear Regression to test whether relative volume of testicles; relative diameter of deferent ducts; and length, relative length, and width of kidneys are related to SVL.

We used residuals to eliminate the influence of body size on the variables of interest (Marques et al. 2006). Residuals were used only to illustrate the reproductive cycle. We tested the variables (differences in volume of testicles, diameter of deferent ducts, and length and width of the right kidney during the months of the year) using ANCOVA due to the relationship between these variables and SVL: volume of testicles ($r^2 = 0.517$, $n = 76$, $P < 0.001$), diameter of deferent ducts ($r^2 = 0.522$, $n = 76$, $P < 0.001$), and length ($r^2 = 0.788$, $n = 76$, $P < 0.001$) and width ($r^2 = 0.704$, $n = 76$, $P < 0.001$) of right kidney, with the months of the year as a categorical predictor variable. We tested measurements of the diameter of tubules and the height of testicular epithelium using Analysis of Variance (ANOVA) or a Kruskal-Wallis test to determine if there was a difference both in the diameter of the tubules and in the height of the testis and kidney epithelium between seasons (dry and rainy). We determined if there were significant differences using the *post-hoc* Tukey Honestly Significant Difference (Tukey HSD) test.

Because data were non-normal and $n < 30$, we analyzed the relationship between prey size and predator size with Spearman's Rank Correlation between ingested prey TL and snake SVL, prey TL and snake HL, and prey TL/SVL ratio and snake SVL. We inferred the feeding behavior of females based on the proportion of adult females with prey in their stomachs (Pizzato and Marques 2006). We used the free software PAST 3.19 (Hammer et al. 2001) for all analyses. We used a significance level (α) of 0.05 in all tests.

RESULTS

The mean SVL of *Erythrolamprus taeniogaster* females was 79.4 ± 7.44 (standard error) mm longer than the mean SVL of males, and the difference was significant ($t_{\text{separate variances}} = 10.81$, $df = 321$, $P < 0.001$). Furthermore, all other traits were likewise shown to be greater in females than in males (TL: mean difference = 9.42 ± 2.10 mm [$t = 4.49$, $df = 298$, $P < 0.001$], HL: mean difference = 3.31 ± 0.35 mm [$t_{\text{separate variances}} = 9.72$, $df = 313$, $P < 0.001$], HW: mean difference = 2.44 ± 0.25 mm [$t_{\text{separate variances}} = 10.16$, $df = 325$, $P < 0.001$], HH: mean difference = 1.61 ± 0.25 mm [$t_{\text{separate variances}} = 6.35$, $df = 206$, $P < 0.001$], and DE: mean difference = 0.58 ± 0.12 mm [$t = 4.71$, $df = 236$, $P < 0.001$]; Table 1). The results obtained through ANCOVA (HH [$F_{131,8}$, $P < 0.001$], HL [$F_{430,3}$, $P < 0.001$], TL [$F_{430,3}$, $P < 0.001$], HW [$F_{342,3}$, $P < 0.001$], DE [$F_{163,3}$, $P < 0.001$]), however, showed that these differences are primarily because females have a significantly larger SVL than that of males ($P < 0.001$ for all measures).

Males become sexually mature at a smaller SVL than females. All males with SVL ≥ 380 mm were sexually mature (although 70% of them were mature at 305 mm),

whereas in females complete sexual maturity was reached only in individuals with SVL ≥ 405 mm. Females of *E. taeniogaster* had follicles in primary vitellogenesis throughout the year. We found follicles in secondary vitellogenesis (> 10 mm) in individuals collected in all months except March and September. We recorded females with eggs during the rainy season (between December and May, $n = 4$) and dry season (between June and November, $n = 16$). We recorded juveniles in every month except December. In sexually mature females, we recorded between one and nine follicles ($n = 26$, mean = 4.8 follicles) and eggs ($n = 17$, mean = 3.6 eggs). The number of secondary vitellogenic follicles and eggs were not correlated with female SVL ($P = 0.730$; $n = 42$). We did not observe secondary vitellogenic follicles and eggs simultaneously in any female. These results show that the reproductive cycle of females is cyclic discontinuous, with a seasonal pattern at the individual level and aseasonal at the population level.

Testicles consist of interstitial tissue; conjunctive tissue; blood vessels; interstitial or Leydig cells, producers of testosterone; and seminiferous tubules with small groups of endocrine cells, the Sertoli cells. We recorded eight types of germinative cells in the seminiferous tubules of *E. taeniogaster*, according to the chromatin condensation: spermatogones A; spermatogones B; primary spermatocytes; secondary spermatocytes; spermatids I, II and III; and spermatozoids. The spermatogenic cycle of *E. taeniogaster* is acyclic at the individual level, and as in females, aseasonal at population level. Different testicular stages were observed throughout the year: Recrudescence, stage 1, observed during the late dry season and early rainy season (November and December); Early Spermiogenesis, stage 2, observed during the rainy season (February and March); and Spermiogenesis, stage 3, observed during the late rainy season and early dry season (May and June; Fig. 3). We did not observe any seasonal variation (rainy or dry season) in diameter of seminiferous tubule ($H = 0.534$, $df = 1$, $P = 0.465$) or height of seminiferous epithelium ($F_{1,8} < 0.001$, $P = 0.985$). Testicular volume differed significantly between seasons ($F_{1,74} = 52.77$, $P < 0.001$), with higher volume during the rainy season (Fig. 4). The diameter of deferent ducts varied seasonally ($F_{1,74} = 0.118$, $P < 0.001$), with higher diameter during the rainy season, and spermatozoids stored throughout the year. We found differences in length ($F_{1,74} = 4.06$, $P < 0.001$) and diameter ($F_{1,74} = 0.532$, $P < 0.001$) of the right kidney, which were larger during the rainy season. We did not observe any seasonal difference in tubular diameter of the RSS ($F_{1,8} = 0.443$; $P = 0.524$), as well as in the height of the RSS epithelium ($H = 0.109$, $df = 9$, $P = 0.917$; Fig. 5). Thus, the RSS of *E. taeniogaster* has an aseasonal cycle, with hypertrophy of distal distorted tubules in both seasons (rainy and dry; Fig. 6).

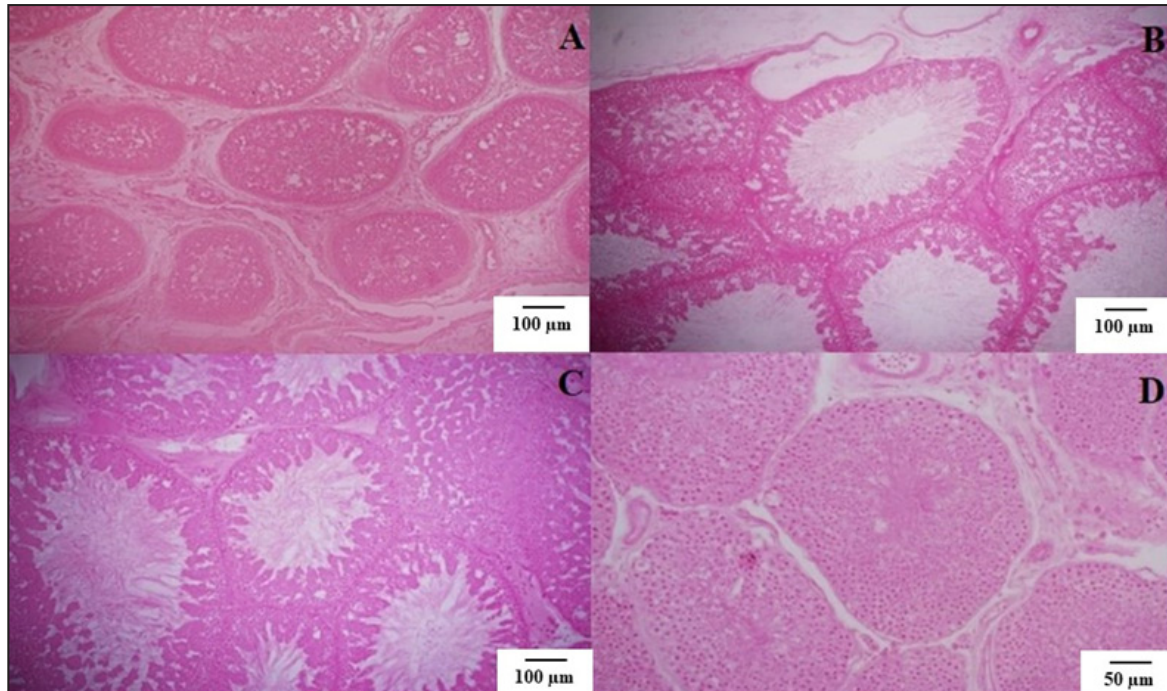


FIGURE 3. Testicular cross-sectional histology of the Common Coral Grass Snake (*Erythrolamprus taeniogaster*). (A) Recrudescence during late dry season and early rainy season, stage 1 (MPEG 209, November). (B) Early spermiogenesis during rainy season, stage 2 (MPEG 10940, February). (C) Spermiogenesis during late rainy season and early dry season, stage 3 (MPEG 9895, June). (D) Maximum height of seminiferous epithelium during rainy season, stage 3 (MPEG 18105, May). Staining was done with basic fuchsin.

We could identify items in stomachs of 45 individuals (20%, $n = 226$), resulting in 64 food items, composed primarily of fishes ($n = 47$, 73% of the items) and anurans ($n = 17$, 27%). In six individuals, there was more than one food item in the stomach (Table 2). The most frequent families of prey were Callichthyidae and Synbranchidae (both found in eight snakes). The Cascarudo (*Callichthys callichthys*; $n = 8$) and *Anablepsoides* sp. ($n = 8$) were the most frequent prey items, followed by *Synbranchus* sp. (five snakes). Among snakes with food items in stomachs, 57% were collected during the dry season (between June and November) and 43% were collected during rainy season (between December and May). The direction of prey ingestion most observed was the anteroposterior (77%, $n = 49$), while the posteroanterior direction was observed only in five individuals (8%), and in 10 individuals (16%) it was not possible to determine the direction of prey ingestion because of small sizes or advanced stage of digestion (Supplemental Information Table S2). Correlations between snake SVL and total prey length (TPL; $r_s = 0.629$, $P < 0.001$; $n = 34$), and between snake HH and TPL ($r_s = 0.596$, $P < 0.001$; $n = 34$) were significantly positive. Correlation between TPL/SVL ratio and snake SVL was also significantly positive ($r_s = 0.539$, $P < 0.001$; $n = 34$). Larger snakes tended to ingest larger prey, but also ingested some small ones (Fig. 7). Most fish species consumed by *E. taeniogaster* (68%) are nocturnal (Supplemental Information Table S3). We

found five anurans in the stomachs of *E. taeniogaster*: (1) the terrestrial Miranda's White-lipped Frog (*Leptodactylus macrosternum*); (2) *Leptodactylus* gr. *melanonotus* (no common name); (3) the Steindachner's Dwarf Frog (*Physalaemus ephippifer*); (4) the arboreal Many-banded Treefrog (*Boana multifasciata*); and (5) the Venezuela Snouted Treefrog (*Scinax x-signatus*).

DISCUSSION

In most snake species, larger females tend to produce larger offspring or clutches, or have a higher reproductive frequency (Shine 1988, 1994). In *Erythrolamprus taeniogaster*, females are larger than males, although there was not a relationship between body size of females and number of vitellogenic follicles and eggs, which indicates that size is not directly related to fecundity in this species. Body size comes at a cost, since mobility of egg-bearing females is reduced and they are more susceptible to predation: the larger the number of eggs, the greater the cost (see Shine 1980). Each sex adopts a different strategy: males are subject to sexual selection and tend to spend time and energy searching for potential mates, fighting other males, and in sperm competition, whereas females tend to increase their fecundity spending time and energy in reproductive strategies that allow them to increase clutch size and frequency of reproduction and accumulate energetic reserves (Madsen and Shine 1994; Bonnet et al. 1998).

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TABLE 2. Food items with sample sizes (n) and frequencies (%) in the diet of the Common Coral Grass Snake (*Erythrolamprus taeniogaster*) in the Brazilian Eastern Amazon.

Taxon	Snakes with food items		Food items	
	n	%	n	%
Fishes				
Callichthyidae				
<i>Callichthys callichthys</i>	7	15.5%	8	12.5%
<i>Corydoras</i> sp.	1	2.2%	2	3.1%
Erythrinidae				
<i>Hoplias malabaricus</i>	1	2.2%	1	1.6%
<i>Hoplias</i> sp.	3	6.7%	3	4.7%
Unidentified species	1	2.2%	1	1.6%
Gymnotidae				
<i>Gymnotus carapo</i>	2	4.5%	2	3.1%
Hypopomidae				
Unidentified species	3	6.7%	3	4.7%
Pimelodidae				
Unidentified species	1	2.2%	1	1.6%
Rivulidae				
<i>Anablepsoides micropus</i>	1	2.2%	1	1.6%
<i>Anablepsoides</i> sp.	3	6.7%	8	12.5%
Sternopygidae				
<i>Sternopygus macrurus</i>	1	2.2%	1	1.6%
<i>Sternopygus</i> sp.	1	2.2%	1	1.6%
Synbranchidae				
<i>Synbranchus marmoratus</i>	3	6.7%	3	4.7%
<i>Synbranchus</i> sp.	5	11.1%	5	7.8%
Trichomycteridae				
<i>Ituglanis amazonicus</i>	1	2.2%	3	4.7%
Unknown Family	4	9.0%	4	6.0%
Subtotal (Fish)	38		47	
Amphibians				
Hylidae				
<i>Boana multifasciata</i>	1	2.2%	1	1.6%
<i>Scinax x-signatus</i>	1	2.2%	1	1.6%
Leptodactylidae				
Tadpoles	1	2.2%	10	15.6%
<i>Leptodactylus macrosternum</i>	2	4.5%	2	3.1%
<i>Leptodactylus</i> gr. <i>melanonotus</i>	1	2.2%	1	1.6%
<i>Physalaemus ephippifer</i>	1	2.2%	2	3.1%
Subtotal (Amphibians)	7		17	
Total	45	100%	64	100%

Longer tails in females than in males differs from the pattern commonly observed in non-arboreal snakes, in which males have relatively longer tails than females to accommodate hemipenes and sexual glands (King 1989). Spermatogenesis in *E. taeniogaster* occurs throughout

the year, which is possible only in regions with relatively high and constant temperature (Barros et al. 2012). We also observed a relation between hypertrophy of the renal sexual segment and spermiogenesis, as well as variation of the renal sexual segment, which is also not common

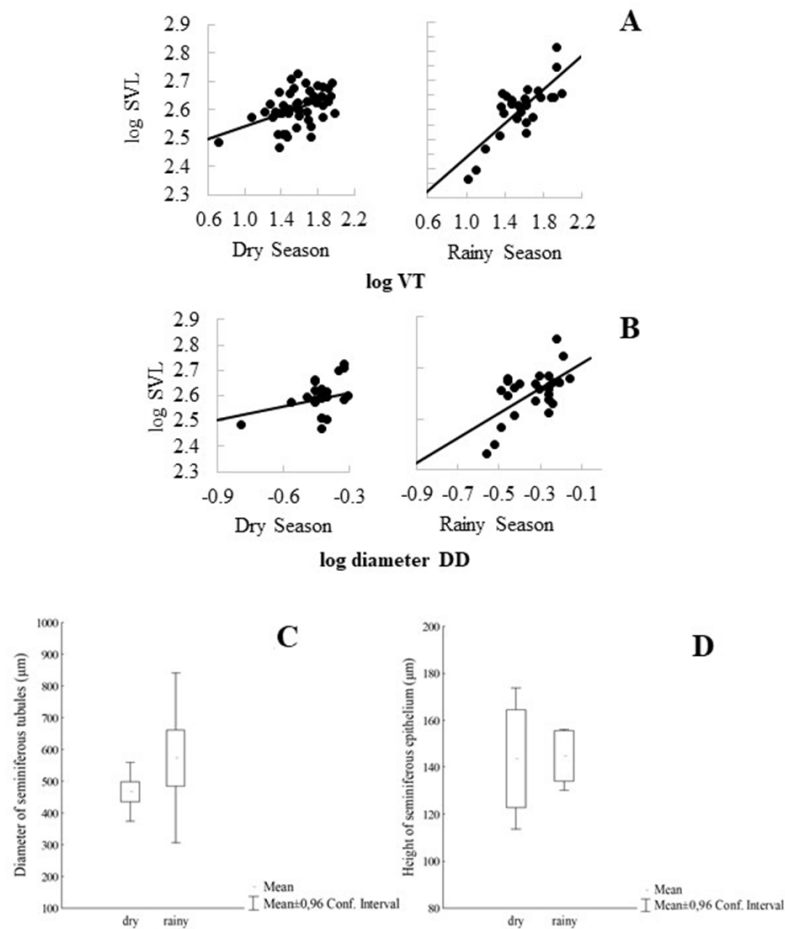


FIGURE 4. Reproductive cycle of male Common Coral Grass Snake (*Erythrolamprus taeniogaster*) in the Brazilian Eastern Amazon. (A) Testicular relative volume - VT; (B) Relative volume of deferent ducts - VT; (C) Median diameter (dot) of seminiferous tubules; (D) Median height (dot) of seminiferous epithelium. Boxes are quartiles and vertical lines show range of values.

in snakes because the length and diameter of the kidneys rarely vary between breeding, active, and resting periods (Fox 1977; Sever et al. 2007). These characteristics show that the smaller tail length in males of *E. taeniogaster* may be related to a higher investment in sexual maturity because the high mobility and reduced metabolic costs provide advantages to males with smaller tails (see Madsen et al. 1993).

Although sexual maturity in females was later than in males and occurred at a larger body size, the number of eggs and ovarian follicles in secondary vitellogenesis was not correlated with body size. Males that reach sexual maturity with smaller body size are more favored than those that invest their energy in growth (Madsen et al. 1993), indicating that *E. taeniogaster* males are probably spending more energy in reproduction than in growth, which allows them to start reproducing with a smaller body size. Additionally, Shine (1988) observed that in aquatic snakes, clutch size influences swimming ability of females, increasing predation intensity and affecting

foraging efficiency, which may explain the lack of correlation and low fecundity (mean of 3.59 eggs) in *E. taeniogaster* females.

The reproductive cycle of *E. taeniogaster* females was characterized as cyclic discontinuous, with seasonal pattern and aseasonal vitellogenesis, with females containing eggs throughout the year in both rainy and dry seasons, and with recruitment all year except December. This pattern is not observed in all other *Erythrolamprus* species because there are records of reproductive aseasonality (the Gold-bellied Bunt Adder, *Erythrolamprus p. poecilogyrus*, and the Crown Ground Snake, *Erythrolamprus viridis*) and seasonality (*Erythrolamprus p. sublineatus*, no common name; Vitt 1983; Quintela et al. 2017). We believe that the variation in the reproductive cycle of *E. taeniogaster* is related to biotic factors, such as prey abundance and availability, and abiotic factors, such as high levels of rainfall, with low annual variation in temperature and air humidity. This variation may be observed in the diet of this species,

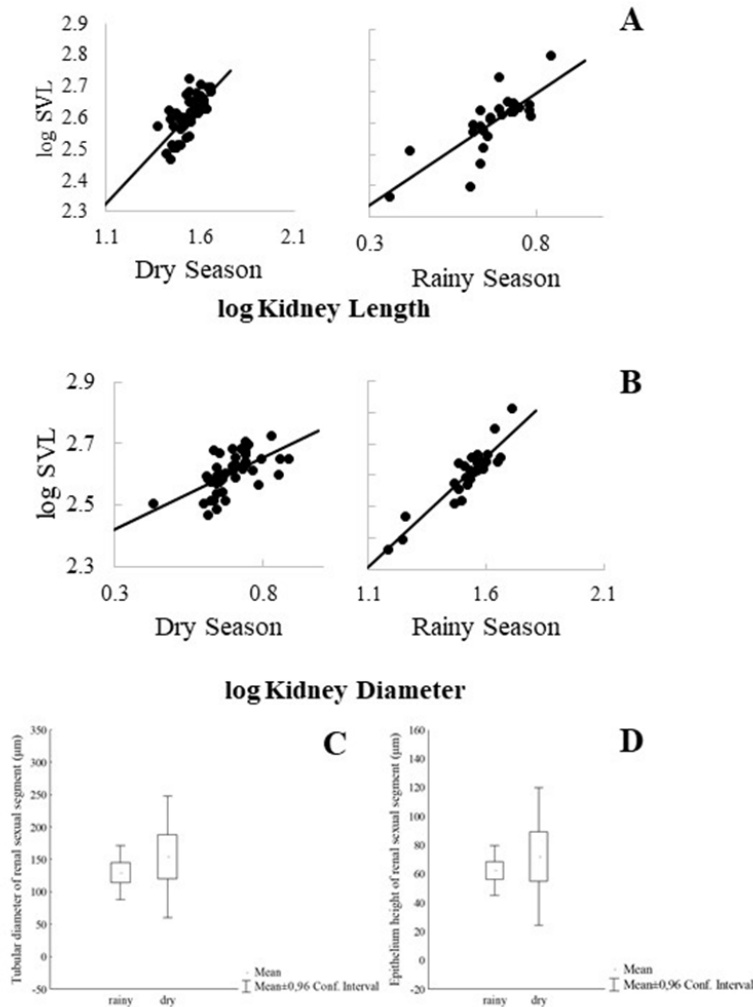


FIGURE 5. Macroscopic measurements of right kidney and microscopic measurements of the renal sexual segment of male Common Coral Grass Snake (*Erythrolamprus taeniogaster*), at different periods of the year, in the Brazilian Eastern Amazon. (A) Kidney length; (B) Kidney diameter; (C) Median tubular diameter (dot) of renal sexual segment; (D) Median epithelium height (dot) of renal sexual segment. Boxes are quartiles and vertical lines show range of values.

consisting of anurans and fishes, both of which are abundant during the rainy season.

Snail-eaters (*Sibynomorphus mikanii*) in southeastern Brazil, a region with four well-defined seasons, has non-continuous spermiogenesis throughout the year and that the epithelium of deferent ducts is adapted to store spermatozooids (Rojas et al. 2013). Morphological and structural characteristics of germinative cells of *E. taeniogaster* males are similar to those described in mammals. The histological analysis showed seminiferous tubules with germinative cells in every stage of maturation and spermatozooids throughout the year, characterizing an aseasonal reproductive cycle. We observed, however, variation in the diameter of deferent ducts, especially during the rainy season, differing from previous observations in *S. mikanii*.

Our results showed that *Erythrolamprus taeniogaster* is sexually dimorphic in body length, with females larger than males, and in measured characteristics of the head, even though these features of the head are related to the greater length of the body. In aquatic and semiaquatic snakes, the pattern observed is that females are always larger than males in all measurable characteristics (see Vincent and Herrel 2007), which would be explained by differential selection between males and females related to prey management and ingestion (as in Shine 1991). Although *E. taeniogaster* is sexually dimorphic in SVL, the size difference is not related to prey size selectivity because prey size for males and females differed only in relation to SVL, not head length. Therefore, we suggest that in *E. taeniogaster* in the Eastern Amazon, neither males nor females are size selective with regard to their prey; rather, *E. taeniogaster* is an opportunistic predator

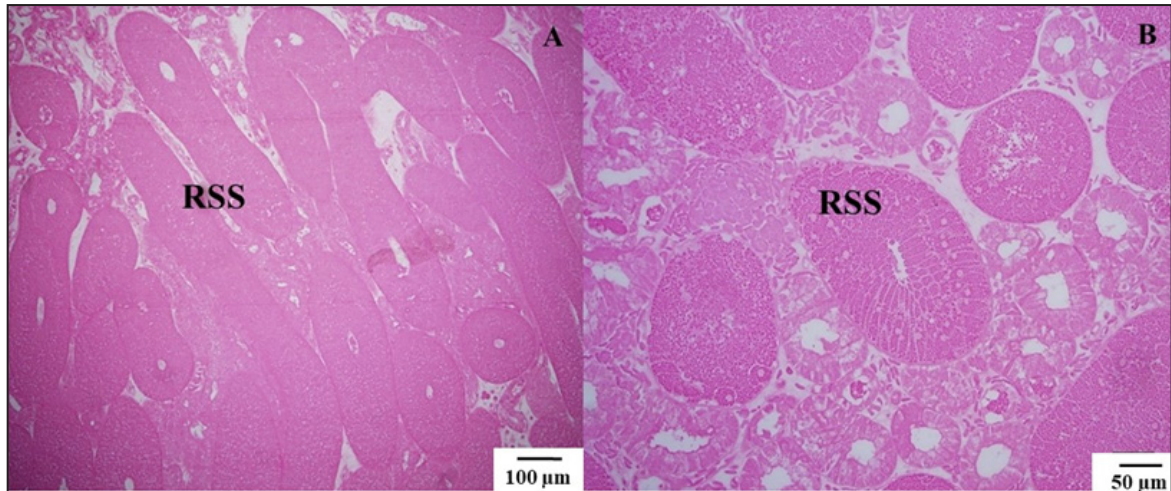


FIGURE 6. Cross-transsectional histology of the kidney of the Common Coral Grass Snake (*Erythrolamprus taeniogaster*). (A) Distal tubules hypertrophied during rainy season (MPEG 10940 collected in February, maximum hypertrophy). (B) Distal tubules hypertrophied during dry season (MPEG 9895 collected in June). The abbreviation RSS = renal sexual segment. Staining was done with basic fuchsin.

that consumes both large and small prey in its foraging environment throughout its development. Thus, we suggest that prey size selectivity by *E. taeniogaster* is not related to head characteristics or sexual dimorphism in relation to SVL but is a conservative characteristic of the group.

Reproductive success in snakes is related to feeding conditions, and any environmental change may negatively affect species, especially those with specific ecological requirements. Some species, however, such as *E. taeniogaster*, have a wide environmental plasticity. This snake tolerates environments with high levels of anthropogenic disturbances and is always near water bodies because they prey on fishes found in permanent ponds, lakes, and streams. We found *E. taeniogaster* feeds primarily on fishes, but also on anurans. Such characteristics are shared by other *Erythrolamprus* species, such as Jaeger's Ground Snake (*E. j. jaegeri*; Vidal 2002; Sawaya et al. 2008), Military Ground Snake (*E. m. miliaris*; Lema et al. 1983; Vitt and Vangilder 1983; Sazima and Haddad 1992; Marques and Souza 1993), and Water Snake (*E. semiaureus*; Achaval and Olmos 2007). Differing from *E. taeniogaster*, however, these species prey primarily on anurans and secondarily on fishes (Vitt 1983; Michaud and Dixon 1989; Pinto and Fernandes 2004).

The presence of fishes in the diet of *E. taeniogaster* has been previously observed by Cunha and Nascimento (1993) in *Synbranchus marmoratus* and the Banded Knifefish (*Gymnotus carapo*). We identified new prey species of the Families Callichthyidae, Erythrinidae, Rivulidae, Hypopomidae, Sternopygidae, Trichtomycteridae, and anurans of the families Leptodactylidae and Hylidae. The fishes consumed by *E. taeniogaster* explore backwater and low-flow environments, living among floating vegetation

near the water surface. In addition, environmental characteristics favor the presence of sites for shelter and prey capture because the Amazon is rich in hydric resources, such as ponds, streams, lakes, and rivers (pers. obs.). Most fish species consumed by *E. taeniogaster* in the Brazilian Eastern Amazon are nocturnal and use a backwater environment with low water flow typical of lake and stream shores, among floating vegetation, and characterized by low depth. *Callichthys callichthys*, *Corydoras* sp., *Hoplias malabaricus* (commonly known as Trahira), *Hoplias* sp., *Synbranchus marmoratus* (commonly known as the Marbled Swamp Eel), and *Synbranchus* sp. tolerate low levels of oxygen in the water, and may occasionally breathe atmospheric air, which makes them highly resistant to temporarily dry environments, allowing them to occupy highly disturbed

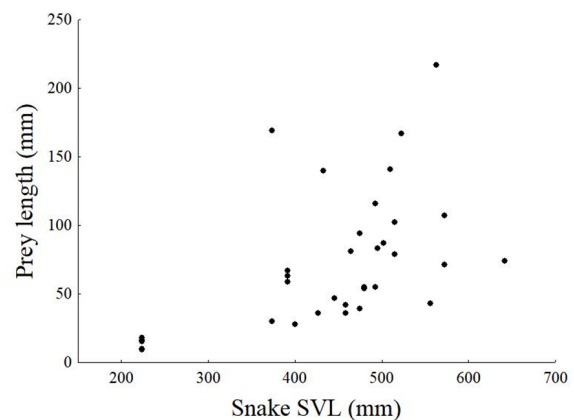


FIGURE 7. Relationship between snout-vent length (SVL) and total prey length (TPL) of the Common Coral Grass Snake (*Erythrolamprus taeniogaster*) in the Brazilian Eastern Amazon.

areas (Ferreira et al. 1998; Cabalzar 2005; Soares 2005; Oyakawa et al. 2006; Oliveira-Raiol et al. 2012). These characteristics make these fishes more vulnerable to predators, including *E. taeniogaster*, offering an explanation to the high frequency of these prey items in the stomachs of *E. taeniogaster*.

The prey catching behavior of *E. taeniogaster* is similar to the pattern observed in other snakes, with prey being ingested headfirst (Mushinsky 1987). This behavior reduces time and effort in swallowing, minimizing energy expenditure, the vulnerable period, and injury risk because of resistant rays and spines in the fins of some fishes (Silvano et al. 2001; Pinto and Lema 2002; Cabalzar 2005; Oyakawa et al. 2006). This risk is reduced, or null, when body characteristics of the prey do not bring any risk to predator, as small prey, or an elongated body without spines in the fins.

Snakes tend to feed on relatively large prey, which are more difficult to catch and digest but provide a high amount of energy after digestion (Arnold 1993). In other words, the amount of energy obtained by eating large prey is high, reducing the frequency of prey searching and, therefore, decreasing the risk of predation, which seems to be consistent with the pattern observed in *E. taeniogaster*. This result was also observed in our study, showing that larger individuals of this species tend to feed on larger prey, although they do not reject small prey.

We observed that seven of 24 females with prey items in the stomachs had eggs in their oviducts (five females with one egg and two females with five eggs). The other mature females with prey items had only primary and secondary vitellogenic follicles, some of them at the final stage of development, in addition to egg marks in the oviducts. These results indicate that *E. taeniogaster* does not reduce food consumption during the reproductive period, as observed in the Grass Snake (*Natrix natrix*; Reading and Davies 1996) and the Coral Cylinder Snake (*Anilius scytale*; Maschio et al. 2010).

The presence of arboreal (*Scinax* ×-*signatus* and *Boana multifasciata*) and terrestrial (*Leptodactylus macrosternum*, *Leptodactylus* gr. *melanonotus* and *Physalaemus ephippifer*) anurans (Duellman 1978; Lima et al. 2006; Oliveira-Raiol et al. 2012; IUCN 2021) in the diet indicates *E. taeniogaster* may also forage close to the shores of water bodies and low vegetation (Supplemental Information Table S3). Most consumed species (anurans: *Leptodactylus macrosternum*, *Leptodactylus* gr. *melanonotus* and *Physalaemus ephippifer*; and fishes: *Callichthys callichthys*, *Anablepsoides* sp. and *Synbranchus* sp.) are usually found in anthropogenic environments (Buhnrheim and Fernandes 2003; Melo et al. 2005; Soares 2005; Oyakawa et al. 2006; Oliveira-Raiol et al. 2012) and favor the occurrence of *E. taeniogaster* in this habitat type, as observed by Cunha and Nascimento (1993) in eastern Pará, an area under

strong anthropogenic disturbance.

The difference between the activity period of *Erythrolamprus taeniogaster* (diurnal) and most of their prey (68%) indicates that *E. taeniogaster* forages actively, searching for prey resting and in shelters. The diurnal prey eaten by *E. taeniogaster* are, in most cases, sedentary and bottom foragers that occasionally swim close to the surface (Silvano et al. 2001; Cabalzar 2005; Soares 2005; Oyakawa et al. 2006; Oliveira-Raiol et al. 2012), which also explains the capture of these prey by *E. taeniogaster*. *Erythrolamprus taeniogaster* is a piscivorous snake, commonly found in the Eastern Amazon, in anthropogenic habitats, close to backwater environments. Description of the reproductive cycle and diet of this species, together with other findings in different neotropical species are important tools that help us elucidate feeding and reproductive patterns of this and other species in this region.

Acknowledgments.—We thank Jeannie Nascimento dos Santos, for the space provided in the Cell Biology and Helminthology Laboratory “Profa. Dra. Reinalda Marisa Lanfred,” in addition to allowing the use of the necessary equipment for assembly and analysis of histological slides. We also thank Ana Lúcia da Costa Prudente, curator of the Herpetology Collection at the Museu Paraense Emílio Goeldi, for borrowing the specimens analyzed in this study. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001.

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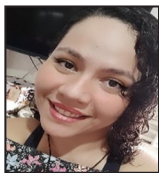
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