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SEXUAL DIMORPHISM, REPRODUCTION AND FEEDING BIOLOGY OF *Helicops angulatus* (LINNAEUS, 1758) (COLUBRIDAE: HYDROPSINI) IN EASTERN AMAZON, BRAZIL

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ABSTRACT

We described natural history traits of the brown-banded water snake *Helicops angulatus* from Eastern Brazilian Amazon, one of the most threatened areas in Amazonia. We recorded morphometric information, feeding habits, and reproductive strategies from 97 mature females, 58 mature males, and 40 juveniles. Females are larger than males, although males have longer tail length. Females and males mature at different sizes, with males becoming mature at smaller sizes. We observed the presence of follicles and secondary eggs throughout the year. However, we found two reproductive peaks, in July and October, corresponding to the dry season in the Amazon region. Diet consists mainly of fishes, followed by frogs that use water bodies for reproduction. Most prey were ingested headfirst (82.35%), possibly to decrease risk of injuries during the capture and ingestion. We found a positive relationship between total length of the prey and snout-vent length of snakes. Compared to other species, *H. angulatus* ingests proportionally larger prey (22-44% of the snout-vent length of snakes), probably optimizing energy gain.

Keywords: Biology, Diet, Neotropical, Water snake, Oviparity, Reproduction.

RESUMEN

Dimorfismo sexual, reproducción y biología alimentaria de *Helicops angulatus* (Linnaeus, 1758) (Colubridae: Hydropsini) en la Amazonia Oriental, Brasil. Describimos los rasgos de la historia natural de la serpiente de agua de bandas marrones *Helicops angulatus* de la Amazonia oriental brasilera, una de las áreas más amenazadas de la Amazonia. Registramos información morfométrica, hábitos de alimentación y estrategias reproductivas de 97 hembras maduras, 58 machos maduros y 40 juveniles. Las hembras son más grandes que los machos, aunque los machos tienen mayor largo de cola. Hembras y machos maduran con diferentes tamaños, los machos maduran con tamaños más pequeños. Observamos la presencia de folículos y huevos secundarios durante todo el año. Sin embargo, encontramos dos picos reproductivos, en julio y octubre, correspondientes a la estación seca en la región amazónica. La dieta consiste principalmente en peces, seguida de ranas que utilizan cuerpos de agua para reproducirse. La mayoría de las presas fueron ingeridas de cabeza (82.35%), posiblemente para disminuir el riesgo de lesiones durante la captura e ingestión. Encontramos una relación positiva entre la longitud total de la presa y la longitud hocico-respiradero de las serpientes. En comparación con otras especies, *H.*

angulatus ingiere presas proporcionalmente más grandes (22-44% de la longitud del hocico-respiradero de las serpientes), probablemente optimizando la ganancia de energía.

Palabras clave: Biología, Dieta, Neotropical, Serpiente de agua, Oviparidad, Reproducción.

INTRODUCTION

A key factor to understand evolutionary processes, ecological adaptations, and furthermore conservation status of snakes lays on the knowledge of their natural history (Greene and Losos, 1988; McCallum and McCallum, 2006). Breeding and feeding behavior are the most investigated aspects of natural history in snakes, which may be used in different studies such as functional traits, phylogeny, biogeography, etc. Although the number of studies focused on natural history has grown in recent years, the Amazon region still has many gaps in knowledge related to different organisms, including snakes. This gap is mainly related to difficulties in accessing areas farther from urban centers, lack of investment in basic research and few human resources. Thus, it is common to carry out studies with animals that are already available in scientific collections, and thus carry out studies with the information that is added to each collected animal (Marinoni and Peixoto, 2010).

Snakes show morphological and behavioral adaptations that allowed, over time, their irradiation in different environments, both terrestrial and aquatic. The elongated body and the absence of limbs make the snakes agile and capable of occupying a great diversity of microhabitats, being able to prey on a wide variety of items. In addition, the kinetic head allows the ingestion of relatively large prey (Greene, 1983; Cundall and Greene, 2000; Santos et al., 2016; Silva et al., 2017a). Some taxa differ in their habits, especially when it comes to breeding and feeding activity (Pizzatto, Jordão and Marques, 2008; Alencar, Gaiarsa and Martins, 2013; Silva, Oliveira, Nascimento, Machado and Prudente, 2017b). This information may be important to understand, for example, how those behaviors vary and how they affect the species distribution (Santos-Costa, Prudente and Di-Bernardo, 2006; Albarelli and Santos-Costa, 2010; Siqueira, Nascimento and Santos-Costa, 2012; Nascimento, Siqueira and Santos-Costa, 2013; Siqueira, Nascimento, Montingelli and Santos-Costa, 2013).

The South American aquatic snake genus *Helicops* (Wagler, 1830), has nineteen species and is distributed almost everywhere found in South America, being recorded in Venezuela, Colombia, Bolivia, Peru, Guyana, Suriname, French Guiana, Trinidad, Ecuador, Uruguay, Argentina, Paraguay, and Brazil (Duellman, 1978; Cunha and Nascimento, 1993; Uetz, Freed and Hosek, 2021). Most species prey on fishes, frogs (adults and tadpoles) and semi-aquatic lizards (Martins and Oliveira, 1998; Ford and Ford, 2002, Aguiar and Di-Bernardo, 2004, Ávila and Arruda, 2006, Sturaro and Gomes, 2008, Santos-Costa, Maschio and Prudente, 2015; Teixeira, Montag and Santos-Costa, 2017).

There are thirteen viviparous species of *Helicops*, with continuous or seasonal reproductive cycles (Ford and Ford, 2002; Aguiar and Di-Bernardo, 2005; Ávila, Ferreira and Arruda, 2006; Costa, Santana, Leal, Koroiva and Garcia, 2016), three oviparous species (*H. hagmanni* Roux, 1910, *H. pastazae* Shreve, 1934, and *H. gomesi* Amaral, 1921), and a single species (*H. angulatus*) with a bimodal reproductive pattern.

Specimens of *Helicops angulatus* are found in Amazon Basin, Chititano Dry Forest, Cerrado, Caatinga and in the northern portion of the Atlantic Forest, mostly at low elevations (Nogueira et al., 2019). They can be found in aquatic environments, as ponds, rivers, streams and dams, in both forested and open areas (Cunha and Nascimento, 1993; Martins and Oliveira, 1998; Ford and Ford, 2002; Santos-Costa et al., 2015). Oviparous populations of this species occur from northern to northeastern and eastern South America, while viviparous populations are found from northwestern to mid-western South America (Cunha and Nascimento, 1981; Dixon and Soini, 1983; Rossman, 1984; Braz, Scartozzoni and Almeida-Santos, 2016).

Herein, we describe some natural history traits of *Helicops angulatus* from different locations in the eastern Brazilian Amazon, providing information on their reproduction (sexual dimorphism, reproductive maturity, and reproductive seasonality) and feeding habits (diet composition, frequency of food items, relationship between predator and prey sizes).

MATERIALS AND METHODS

We analyzed 195 *Helicops angulatus* preserved specimens (97 mature females, 58 mature males, and 40 juveniles) from the Herpetological Collection of Museu Paraense Emílio Goeldi (Appendix I). Specimens were collected in Eastern Amazon (Brazilian State of Pará) in 15 sites located between 5°00” and 0°00” S and 55° 00” and 44°00” W (Fig. 1). Local climate is hot-humid throughout the year in all 15 sampled sites (AFi – according to Köppen classification), with a marked dry season between June and November (mean rainfall: 88 mm) and a marked rainy season between December and May (mean rainfall: 300 mm) (Albuquerque, Souza, Oliveira and Jr. Souza, 2010). Mean annual temperature varies between 23 and 27 °C, and the mean air relative humidity is around 85% (CPTEC / INPE, 2013). All localities here addressed were originally covered by tropical rainforest, but, currently, many of them exhibit high deforestation rates, driven by the expansion of agricultural frontiers, road construction, among others

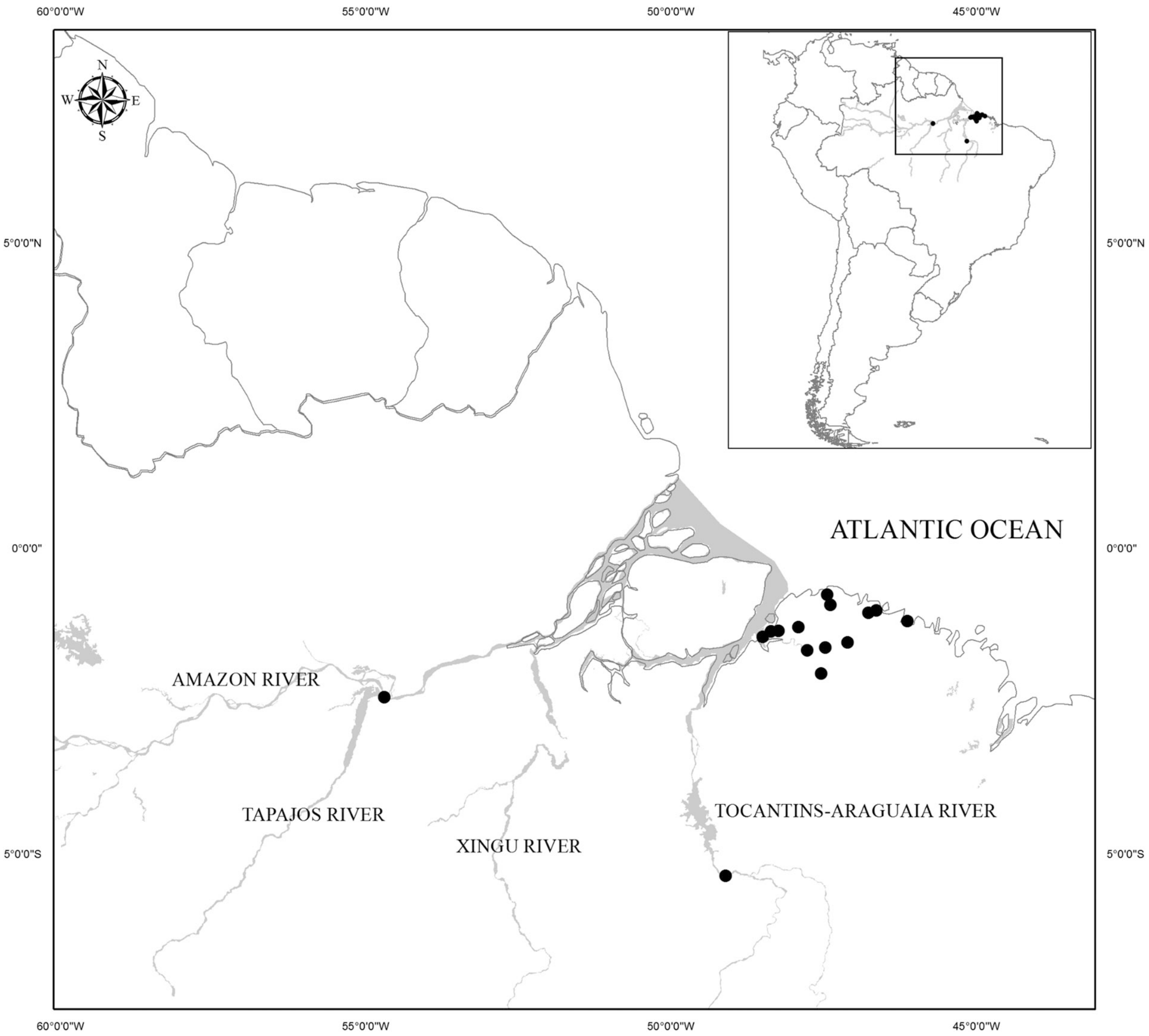

Fig. 1. Collection localities of the specimens of *Helicops angulatus* examined for this study (black dots), Eastern Amazon, Pará, Brazil.

human interventions (Peres et al., 2010; Vieira and Almeida, 2013). Climate changes caused by deforestation have increased the dry periods in the Amazon Basin, affecting organisms associated with aquatic environments, including aquatic snakes such as *H. angulatus* (Ruiz-Vásquez, Arias, Martínez and Espinoza, 2020).

For each specimen, we collected the following measurements (in millimeters): snout–vent length (SVL), tail length (TL), number of ventral scales (VS) and number of subcaudal scales (ScS). The data was log-transformed in order to deal with the assumptions of normality and homogeneity of variance beyond the homogeneity of inclination (parallelism) and to test the interaction between the factor (sex) and covariates (SVL). We tested normal distribution using the Kolmogorov-Smirnov test, and tested the homogeneity of variance using F test (Fisher). This data was used to test sexual dimorphism in body and tail size of *H. angulatus*. We used one-way analysis of covariance (ANCOVA), with sex as factor and SVL as a covariate to analyze sexual dimorphism in TL measures (see Maschio et al., 2021). We analyzed sexual dimorphism in the VS and ScS using Bartlett test (Bartlett, 1937). For samples with normal and homogeneous distribution, we used Student's T test, while for samples with normal distribution, but no homogeneity of variances, we used Welch's T test (Welch, 1958; Zimmerman and Zumbo, 1993). All analyses were ran using statistical R package version 2.15.1 (R

Table 1. Measures of mature females and males of *H. angulatus* in Eastern Amazon, Pará, Brazil, showing the number of specimens examined (n), mean, standard deviation (SD) and minimum (MIN) and maximum (MAX) sizes. Legend: SVL = snout–vent length; TL = tail length; VS= number of ventral scales and ScS = number of subcaudal scales. *specimens with damaged tail were excluded.

	Mature females					**Mature males**				
	n	**Mean**	**SD**	**MIN**	**MAX**	***n***	**Mean**	**SD**	**MIN**	**MAX**
SVL (mm)	97	474.0	75.7	336	676	58	343.0	44.0	228	442
TL (mm)*	85	217.6	37.4	136	344	44	213.0	43.0	111	319
VS	79	112.2	3.4	101	123	35	107.1	3.8	99	115
ScS*	79	74.5	5.7	56	89	35	87.1	6.0	73	101

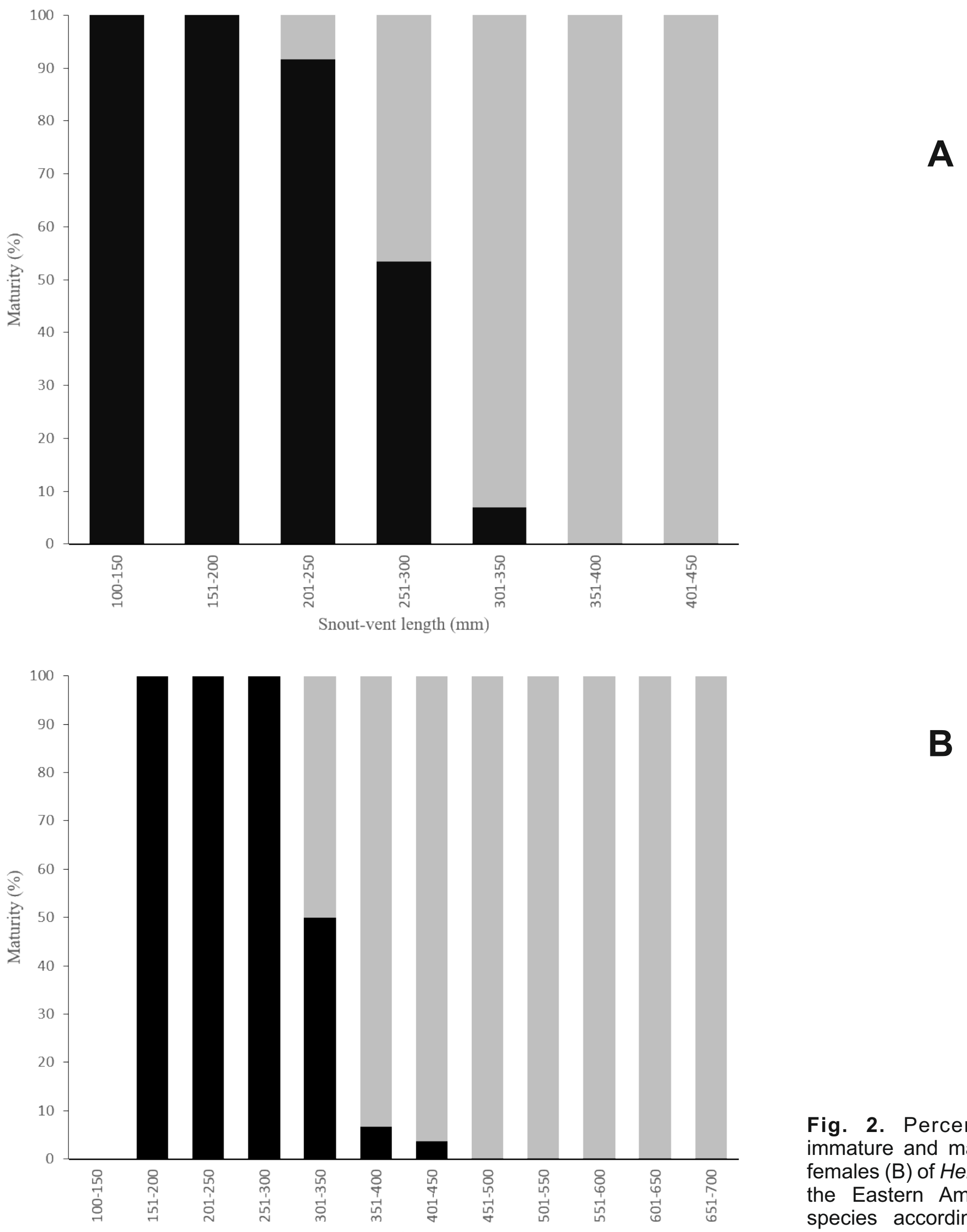

Fig. 2. Percentage of sexually immature and mature males (A) and females (B) of *Helicops angulatus* from the Eastern Amazon, Pará, Brazil, species according to size classes. Black = immature, grey = mature.

Table 2. Prey frequencies of *Helicops angulatus* from Eastern Amazon, State of Pará, Brazil.

	Snakes with prey items		**Prey frequency**	
Prey taxa	**n**	**%**	**n**	**%**
FISHES				
Cichlidae				
Crenicichla sp.	1	5.9	2	8
Apistogramma sp.	2	11.7	3	12
Aequidens sp.	1	5.9	1	4
Callichthyidae				
Corydoras sp.	1	5.9	1	4
Species unknow	1	5.9	1	4
Curimatidae				
Cyphocharax sp.	1	5.9	2	8
Erythrinidae				
Hoplias malabaricus	1	5.9	1	4
Species unknow	1	5.9	1	4
Gymnotidae				
Gymnotus sp.	3	17.6	3	12
Lebiasinidae				
Copella sp.	1	5.9	4	16
Pyrrhulina sp.	1	5.9	3	12
FROGS				
Bufonidae				
Rhinella gr. *margaritifera*	1	5.9	1	4
Hylidae				
Boana boans	1	5.9	1	4
Leptodactylidae				
Adenomera sp.	1	5.9	1	4
TOTAL	**1**	**7**	**2**	**5**

Development Core Team; http:// www.R-project.org), with 0.05 significance level (α).

We analyzed sexually mature individuals from every month of the year to unveil if reproduction occurs throughout the year (no seasonality) or if it is restricted to a specific period (seasonally adjusted). Furthermore, we used the following data to determine in which size males and females become mature: size of the largest ovarian follicle or oviductal egg; number of vitellogenic follicles (> 10 mm) or oviductal eggs to estimate fecundity; maximum diameter of a deferent duct at its distal end close to the cloaca (Almeida-Santos et al., 2006); and testicle length and width (all to the nearest 0.1 mm). Size at sexual maturity for females was Welch's based on the smallest (SVL) female with vitellogenic follicles or oviductal eggs and oviducts enlarged (Shine, 1977). Males were considered mature when they had enlarged and turgid testicles, and thickened convoluted deferent ducts (Shine, 1988; Almeida-Santos, Pizzatto and Marques, 2006). Specimens with umbilical scar were considered newborn (Santos-Costa et al., 2006). We performed an analysis of the reproductive cycle from adult specimens, observing the temporal distribution of eggs in the oviduct using circular analysis. For this analysis, we used software ORIANA version 4 (Kovach, 2016).

To analyze prey consumption by *H. angulatus*, we made an abdominal incision in 170 specimens and removed all prey items in the stomach and/or intestine (if present). We obtained information on ecological prey through literature. We recorded how prey were ingested according to the position of the head in the stomach of the snake (headfirst or tail first). Whenever possible, we measured all the prey ingested by *H. angulatus*. When prey was fish, we measured the distance from rostrum to tail fin, while for frogs and lizards we measured snout-cloaca distance. We tested the correlation between prey and snakes' length with a

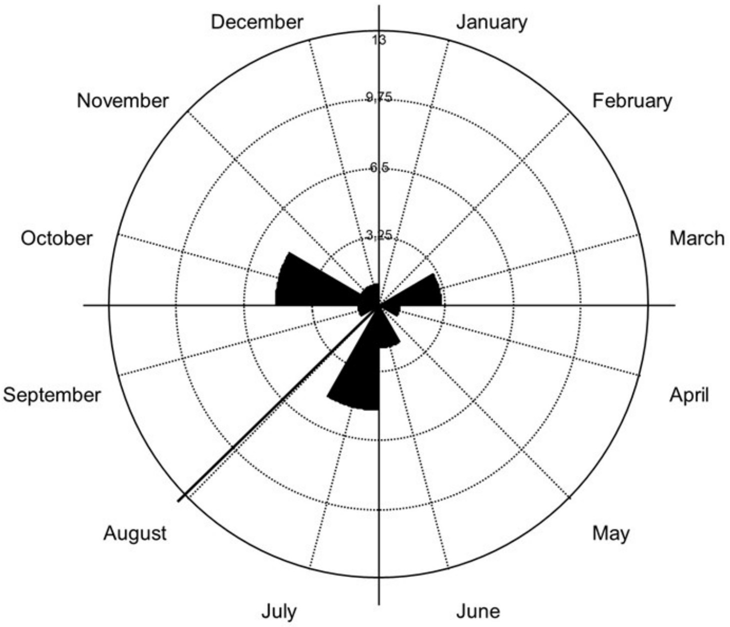

Fig. 3. Egg distribution over the seasonal period of *Helicops angulatus*, Eastern Amazon, Pará, Brazil.

Pearson's correlation test. For prey in advanced stage of decomposition, we compared with three similar-sized specimens from the same species deposited in the herpetological collection of Museu Paraense Emílio Goeldi (see Prudente, Menks, Silva and Maschio, 2014).

RESULTS

The smallest mature female was 336 mm SVL, whereas the smallest mature male was 228 mm SVL (Table 1). Males (SVL mean = 343 mm) became sexually mature with SVL smaller than females (SVL mean = 474 mm) (*t* = 12.015, F = 2.9684, *P* <0.0001, *N* female = 97; *N* male = 58). In addition, mature males had significantly higher tail sizes than mature females (Parallelism 1.125 *f* = 3.053 and *P* = 0.083, ANCOVA $f_{1,126}$ = 46.133 and *P* <0.001).

We observed that 97% of males became sexually mature with SVL greater than 301 mm (Fig. 2A), while 93% of females became sexually mature with SVL greater than 351 mm (Fig. 2B). We also observed that approximately 50% of males were already sexually mature at length class ranging between 251 and 300 mm, while no females were mature at that same range size (Fig. 2A–B). Larger mature male SVL was 442 mm, while larger mature female SVL was 676 mm, supporting the existence of sexual bi-maturity in *H. angulatus*.

We recorded 19 females with eggs throughout the year (March: *N* = 3; April: *N* = 1, June: *N* = 2; July: *N* = 5; September: *N* = 1, October: *N* = 5; November: *N* = 1; December: *N*= 1). Two females found in March had embryos at early development stage. We found two reproductive peaks: in July and October, during dry season in Amazon (Fig 3). Juveniles were observed in almost every month of the year: March (*N* = 5), April (*N* = 2), May (*N* = 2), June (*N* = 1), July (*N* = 5), September (*N* = 3), October (*N* = 11), November (*N* = 5) and December (*N* = 6). In addition, we did not observe any difference between number of vitellogenic follicles and number of eggs (Mann-Whitney U = 107.0, Z = 1.5, *P* = 0.29, *N* = 40).

From the 170 *Helicops angulatus* specimens, 17 (10%) had any prey item in the stomach, with fishes representing 82.4% and frogs representing 17.7% (Table 2). We identified nine fish species, distributed in six families. From the 25 prey identified, most were ingested headfirst (*N* = 14; 56%), while only 12% were ingested tail first (*N* = 3). In eight cases (32%), we were not able to identify if the head or tail was ingested first due to advanced stage of decomposition. Prey total length corresponded to 22% to 44% of the snout-vent length of the snakes, suggesting that *H. angulatus* tends to feed on proportionately large prey. In addition, we found a positive relationship between prey total length and snakes snout-vent length, Pearson Correlation, *r* = 0.61, *P* = 0.02 (Fig. 4).

DISCUSSION

Our results confirm the oviparity in *Helicops angulatus* populations of the eastern Amazon, as suggested by Braz et al. (2016), who found

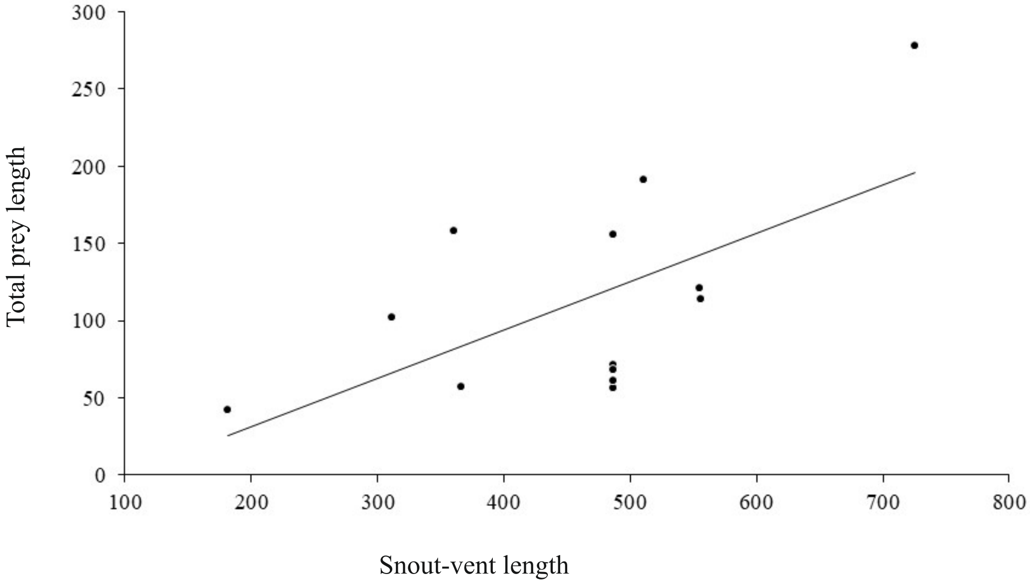

Fig. 4. Relationship between snout-vent length (SVL in mm) and total prey length (in mm) found in *Helicops angulatus*, Eastern Amazon, Pará, Brazil. ($R^2 = 0.3775$).

Total prey length

reproductive bimodality, a rare phenomenon in snakes. Populations from North, Mid-East and Northeast regions of South America are oviparous, while populations from Northwest to Mid-West of South America are viviparous (Braz et al., 2016). Some hypotheses suggest that viviparous condition may have arisen during unfavorable environmental scenarios, leading to the retention of embryos in periods of low temperatures, lack of resources and large predatory pressure (Seigel and Ford, 1987; Shine, 1995).

Unlike other biomes, climate seasonality is not observed in most of the Amazon, with little variation in air temperature and humidity throughout the year, and a wide availability of aquatic environments, supporting a wide supply of prey (Duellman, 1978; Santos-Costa et al., 2015). In aquatic environments, seasonal variation in food availability is low when compared to terrestrial environments (Junk, Bayley and Sparks, 1989). With the rise of the water level during rainy seasons, there is a natural expansion in the area of water bodies, increasing habitat availability for fishes and reducing their density because of their dispersion. However, with the decrease of water level during dry season, there occurs a reduction in the area of water bodies, reducing habitat availability for fishes and increasing their density (see Okada, Agostinho, Petrere and Penczak, 2003; Luz-Agostinho et al., 2009). Such variation on water level probably affects aquatic snakes that consume mainly fishes (Starace, 1998; Lopez and Giraudo, 2003; Ávila et al., 2006), as *Eunectes murinus* (Linnaeus, 1758), *Hydrodynastes gigas* (Duméril, Bibron and Duméril, 1854), *Helicops leopardinus* (Schlegel, 1837), and *Helicops angulatus*. One explanation to the absence of a well-defined reproductive season is the continuous availability of food throughout the year. Aquatic environments and their surroundings, where *H. angulatus* mainly inhabits, provide higher fish availability during dry season (Montag, Freitas, Wosiacki and Barthem, 2008; Castello, Isaac and Thapa, 2015) and greater frog availability during rainy season (Duellman, 1978; Hödl, 1990).

We observed that *H. angulatus* mature females are larger than males (snout-vent length), although males become mature at smaller sizes, confirming what seems to be a common condition for the Tribe Hydropsini (Ford and Ford, 2002; Aguiar and Di-Bernardo, 2005; Ávila et al., 2006). This pattern may be considered an evolutionary advantage for some groups of snakes, because with a larger internal space, individuals may store more energy reserves (Bonnet, Shine, Naulleau and Vacher-Vallas, 1998), which is considered essential for the viability and larger storage of eggs and/or embryos (Shine, 1978; King, 2000).

In fact, high fecundity was observed in *H. angulatus*, as well as in other *Helicops*, as *H. infrataeniatus* Jan, 1875 (Aguiar and Di-Bernardo, 2005) and *H. leopardinus* (Schlegel, 1837) (Ávila et al., 2006). Although *H. angulatus* females are larger, males have a proportionally larger tail, as in many other species of snakes, which is a relatively common pattern in Serpentes (Shine, 1993; Shine et al., 1999). Greater length of the tail in males may also provide greater ability of movement, decreasing the metabolic costs to maintain their body (Anderson, 1994).

We observed a higher number of females with eggs during the dry season (11 eggs from July to October), and identified two reproductive peaks: one in early dry season (June and July) and other in late dry season (October). Some studies indicate that continuous reproductive cycle is a common pattern for tropical snakes (Santos-Costa et al., 2006; Siqueira et al., 2012; Nascimento et al., 2013). However, recent studies show that some species may present seasonal reproduction, as *Anilius scytale* (Linnaeus, 1758) (Maschio, Prudente, Lima and Feitosa, 2007) and *Drymarchon corais* Boie, 1827 (Prudente et al., 2014) or two annual reproductive cycles, as observed in *Imantodes cenchoa* Linnaeus, 1758 (Souza, Prudente and Maschio, 2014). These findings suggest that, in addition to historical factors, also contemporary factors, such as environmental conditions and behavioral traits may play an important role on the snake's reproductive strategies (Cadle and Greene, 1993). *Helicops angulatus* feeds primarily on fishes that forage at the bottom of lentic water bodies (Godoy, 1975; Isaac, Guidelly, França and Pavanelli, 2004; Teixeira et al., 2017), as *Gymnotus*, *Copella*, *Apistogramma*, *Cyphocharax*, *Aequidens*, *Crenicichla*, *Corydoras* and *Hoplias* juveniles. However, *H. angulatus* shows a wider diet range, capturing terrestrial frogs that build foam nests in leaf litter, as *Adenomera* sp., or frogs that lay eggs directly into the water, as *Rhinella* gr. *margaritifera* (Laurenti, 1768) (terrestrial) and even the tree frog *Boana boans* (Linnaeus, 1758) that lay eggs in temporary ponds (Duellman, 1978; Kwet and Di-Bernardo, 1999; Bartlett and Bartlett, 2003). Based on the behavior of anurans and studies on foraging habitats, it is probable that *Helicops angulatus* forages primarily into the water and eventually on the ground (Teixeira et al., 2017). Similar behavior was observed for *H. infrataeniatus* and *H. leopardinus*, which also capture terrestrial frogs (Aguiar and Di-Bernardo, 2004; Ávila et al., 2006).

H. angulatus captured relatively large prey (22–44% of the snake's size), in contrast to what is observed in *H. infrataeniatus*, which ingests smaller prey (5–15% of its length) (Aguiar and Di-Bernardo, 2004). This feeding behavior can vary within the genus *Helicops*, indicating that it is not a conservative characteristic for the group. In our study, we observed that the environments where *H. angulatus* was found present a diversity of prey (fish and frogs) with different sizes, and that capturing larger prey would be more advantageous to maximize foraging efficiency (see Mushinsky, 1987; Ávila et al., 2006). This pattern also explains why *H. angulatus* captures their prey mainly headfirst, since it reduces the risk of injury caused especially by fishes with lateral and dorsal fins. Pinto and Lema (2002) observed two species of captive snakes and concluded that capturing prey headfirst reduces time and effort during swallowing, the amount of energy spent, vulnerability period and risk of injuries caused by their prey (Maschio, Prudente, Rodrigues and Hoogmoed, 2010; Prudente et al., 2014; Souza et al., 2014).

Detailed investigation on feeding habits and reproductive characteristics of *Helicops angulatus*, as well as information on the biology of other snakes, may support studies on the functioning of populations and communities in tropical environments. In addition, this information may be useful to support co-evolutionary studies, since food preferences and reproductive strategies of a given species may be either related to the environment where it lives (environmental response, e.g., environmental filtering, niche divergence) or to a shared evolutionary history, especially in the case of phylogenetically related species, e.g., Hydropsini (evolutionary response, e.g., niche conservation). Finally, data on the reproduction of *Helicops angulatus* may be supplemented with the analysis of gonads through techniques of scanning electron microscopy, providing more detailed information on the reproductive cycle of this species that we could not observe in this study.

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Appendix I.

Accession numbers of Herpetological Collection of Museu Paraense Emílio Goeldi. – *Helicops angulatus*.

Brazil: Pará: Ananindeua: MPEG 18942, MPEG 19830 **Augusto Correa:** MPEG 548, MPEG 567, MPEG 651, MPEG 669, MPEG 2355, MPEG 3895, MPEG 4592, MPEG 5333, MPEG 5334, MPEG 5347, MPEG 5352, MPEG 5353, MPEG 6455, MPEG 6538, MPEG 6675, MPEG 67311, MPEG 10003, MPEG 10731, MPEG 12470, MPEG 10739, MPEG 10741 **Belém:** MPEG 17313, MPEG 18557, MPEG 18758, MPEG 19586, MPEG 19718, MPEG 19594 **Benevides:** MPEG 20155 **Bragança:** MPEG 3007, MPEG 7861, MPEG 8329, MPEG 8331, MPEG 8332, MPEG 8361, MPEG 8363, MPEG 9968, MPEG 11335, MPEG 11386, MPEG 11387, MPEG 12998, MPEG 17311. **Castanhal:** MPEG 1536, MPEG 4038, MPEG 4039, MPEG 4040, MPEG 4400, MPEG 4410, MPEG 4773, MPEG 7170, MPEG 8651, MPEG 10775, MPEG 11791, MPEG 12470, MPEG 12608, MPEG 12999. **Mãe do Rio:** MPEG 18677. **Marabá:** MPEG 17053, MPEG 17081, MPEG 18880, MPEG 19365, MPEG 19366, MPEG 19367, MPEG 19368, MPEG 19369 **Maracanã:** MPEG 1583, MPEG 1584, MPEG 1885, MPEG 1886, MPEG 2091, MPEG 2408, MPEG 2409, MPEG 2557, MPEG 2558, MPEG 2783, MPEG 2784, MPEG 2785, MPEG 2786, MPEG 2787, MPEG 2789, MPEG 2803, MPEG 3336, MPEG 3396, MPEG 4076, MPEG 4079, MPEG 4843, MPEG 4854, MPEG 5796. **Ourém:** MPEG 4220, MPEG 4993, MPEG 4996, MPEG 5007, MPEG 5010, MPEG 5011, MPEG 7000, MPEG 7002, MPEG 7025, MPEG 7026. **Santarém:** MPEG 19052. **Santarém Novo:** MPEG 1842, MPEG 1843, MPEG 3244, MPEG 3245, MPEG 4139, MPEG 4140, MPEG 4148, MPEG 4150, MPEG 4152, MPEG 7054, MPEG 7073. **São Domingos do Capim:** MPEG 8062. **São Miguel do Guamá:** MPEG 20987, MPEG 20988, MPEG 21006, MPEG 21007.**Viseu:** MPEG 1030, MPEG 1043, MPEG 1049, MPEG 1050, MPEG 1051, MPEG 1052, MPEG 1060, MPEG 1352, MPEG 2308, MPEG 2309, MPEG 2310, MPEG 2311, MPEG 2312, MPEG 2314, MPEG 2315, MPEG 3077, MPEG 3079, MPEG 3080, MPEG 3081, MPEG 3082, MPEG 3084, MPEG 3086, MPEG 3088, MPEG 3754, MPEG 3755, MPEG 4500, MPEG 4502, MPEG 5285, MPEG 5286, MPEG 5291, MPEG 5302, MPEG 6570, MPEG 6576, MPEG 6577, MPEG 6578, MPEG 8873, MPEG 8872, MPEG 8875, MPEG 8876, MPEG 10013, MPEG 10018, MPEG 10071, MPEG 10073, MPEG 10078, MPEG 10888, MPEG 13247, MPEG 13248, MPEG 13249, MPEG 13250, MPEG 13251, MPEG 13252, MPEG 13340, MPEG 13899, MPEG 13900, MPEG 13901, MPEG 13903, MPEG 13904, MPEG 14009, MPEG 14010, MPEG 14011, MPEG 14012, MPEG 14013, MPEG 14457, MPEG 14459, MPEG 14461, MPEG 15070, MPEG 15071, MPEG 15072, MPEG 15073, MPEG 15074, MPEG 15075, MPEG 15076, MPEG 15338, MPEG 15711, MPEG 15787, MPEG 15858, MPEG 16010, MPEG 16310, MPEG 16311.