ACTA
AMAZONICA

http://dx.doi.org/10.1590/1809-4392201802371

ORIGINAL ARTICLE

Reproductive and feeding biology of the common lancehead *Bothrops atrox* (Serpentes, Viperidae) from central and southwestern Brazilian Amazonia

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ABSTRACT

The pitviper *Bothrops atrox* is a widely distributed and medically important snake in Amazonia. Given that the reproductive and feeding biology of snakes varies geographically, we aimed to characterize the natural history of individuals from the central and southwestern portions of the biome. We analyzed museum-preserved specimens collected in the region between the metropolitan areas of the Brazilian cities of Manaus and Porto Velho. We took morphometric measurements and performed the analysis of gonads and digestive tracts of 109 individuals. Females attain sexual maturity with larger body sizes. Adults of the species show pronounced sexual dimorphism in body size, with females being larger. The reproductive cycle, especially in males, appears to be synchronized with regional rainfall, which markedly differed across the biome. The pitvipers had a generalist diet, consuming a wide range of prey such as centipedes, frogs, lizards, snakes and mammals. We provide the first record of predation of the snake *Imantodes cenchoa* (Dipsadidae) by *B. atrox*. There was an ontogenetic shift in the diet: smaller individuals fed mainly on ectothermic prey (centipedes, frogs, lizards and snakes), while adults tended to incorporate endothermic prey (mammals) to their food repertoire.

KEYWORDS: diet; natural history; Neotropics; reproduction

Biologia reprodutiva e alimentar da jararaca *Bothrops atrox* (Serpentes, Viperidae) do centro e sudoeste da Amazônia brasileira

RESUMO

A jararaca *Bothrops atrox* é uma serpente de ampla distribuição e de importância médica na Amazônia. Visto que a biologia reprodutiva e alimentar de serpentes varia geograficamente, nosso objetivo foi o de caracterizar a história natural de indivíduos provenientes das porções central e sudoeste do bioma no Brasil. Analisamos espécimes preservados coletados na área compreendida entre as regiões metropolitanas dos municípios brasileiros de Manaus e Porto Velho. Realizamos medidas morfométricas e analisamos as gônadas e o trato digestivo de 109 exemplares. Fêmeas apresentaram maturação sexual com tamanhos corporais maiores que os machos. Adultos apresentaram marcado dimorfismo sexual em tamanho, sendo que as fêmeas foram, em média, maiores que os machos. O ciclo reprodutivo, especialmente em machos, pareceu estar sincronizado com o regime regional de chuvas, que difere de outras partes do bioma. As serpentes apresentaram dieta generalista, tendo ingerido uma ampla gama de presas, como lacraias, anuros, lagartos, serpentes e mamíferos. Registramos, pela primeira vez, a predação da serpente *Imantodes cenchoa* (Dipsadidae) por *B. atrox*. Houve mudança ontogenética na dieta: indivíduos menores se alimentaram principalmente de presas ectotérmicas (lacraias, anuros, lagartos e serpentes) e adultos tenderam a incorporar itens endotérmicos (mamíferos) ao repertório alimentar.

PALAVRAS-CHAVE: dieta; história natural; Neotrópico; reprodução

INTRODUCTION

The genus *Bothrops* currently has 45 Neotropical species, distributed from Mexico to Argentina (Uetz and Hošek 2016), that occupy a range of habitats from forests to open areas, including anthropized areas (Martins *et al.* 2002; Melgarejo 2009). Recent studies with *Bothrops* have resulted in more accurate information on the natural history of several species, which has allowed broad ecological patterns for the genus to be understood (Martins *et al.* 2001; Almeida-Santos and Salomão 2002; Martins *et al.* 2002). In the case of venomous snakes like *Bothrops*, information on natural history may be particularly relevant to devise strategies to minimize the frequency of snakebite cases (Santos *et al.* 1995; Bernarde 2014).

CITE AS: Bisneto, P.F.; Kaefer, I.L. 2019. Reproductive and feeding biology of the common lancehead *Bothrops atrox* (Serpentes, Viperidae) from central and southwestern Brazilian Amazonia. *Acta Amazonica* 49: 105-113.

Of the 26 species occurring in Brazil, the few for which data on reproductive biology are available include *Bothrops jararaca* (Almeida-Santos and Orsi 2002), *B. moojeni* (Nogueira *et al.* 2003), *B. neuwiedi* (Valdujo *et al.* 2002; Hartmann *et al.* 2004), *B. mattogrossensis* (Monteiro *et al.* 2006), *B. alternatus* (Nunes *et al.* 2010), *B. insularis* (Marques *et al.* 2013), *B. leucurus* (Lira-da-Silva 2009; Barros *et al.* 2014) and *B. atrox* (Hoge and Federsoni 1976/1977; Cunha and Nascimento 1981; Oliveira 2003; Santos-Costa *et al.* 2015; Silva 2015). These studies show that aspects of reproduction, such as viviparity and the existence of a seasonal reproductive cycle, are conserved in the group. Reproductive cycles are strongly influenced by regional variations in climatic seasons, which can generate differences in reproductive timing among populations of different regions (Almeida-Santos and Salomão 2002), and, possibly, reproductive isolation (Sanders *et al.* 2014).

Juvenile recruitment in *Bothrops* appears to coincide with the hottest and rainiest periods of the year (Almeida-Santos and Salomão 2002; Barros *et al.* 2014). *Bothrops* in southeastern Brazil (*B. alternatus, B. cotiara, B. fonsecai, B. itapetiningae, B. jararaca, B. jararacussu, B. leucurus, B. moojeni* and *B. neuwiedi*) appear to have a unimodal annual peak of juvenile activity between the end of February and the beginning of May, resulting from a summer and fall recruitment phase (Almeida-Santos and Salomão 2002). Most studies on reproduction in *Bothrops* have been carried out in southern and southeastern Brazil (Almeida-Santos and Orsi 2002; Hartmann *et al.* 2004; Sawaya *et al.* 2008; Marques *et al.* 2013), where climatic seasonal patterns differ from the Amazon region. In southern Brazil, summer coincides with the rainy season, and the conditions of temperature, humidity and rainfall, as well as the abundance of food (mainly anurans, which comprise much of the diet of juvenile *Bothrops*), greatly favor the survival of young reptiles (Fitch 1987), the accumulation of energy for the production of eggs and young by females, and mate-seeking activities of males (Lillywhite 2014). In Amazonia, temperature is constant throughout the year, while precipitation is concentrated in a rainy season that lasts about six months (Forti and Moreira-Nordemann 1991).

Regarding feeding behavior, it is known that ontogenetic changes in diet occur in *Bothrops* (Martins *et al.* 2002). Since they are generalists, items such as other snakes, fish, birds and carrion were also recorded in the diet of many species (Sazima and Strüssman 1990; Martins *et al.* 2002; Oliveira and Martins 2003). Few species have a different pattern, indicating that a generalist diet may be a synapomorphy in this group (Martins *et al.* 2002).

The common lancehead, *Bothrops atrox* (Linnaeus 1758), is a widely distributed species in the Amazonian biome, and is a generalist in habitat use (Martins and Oliveira 1998; Fraga *et al.* 2013b). These characteristics, in addition to the ability to use both sit-and-wait and active hunting strategies, result in a widely diversified diet (Martins *et al.* 2002; Oliveira 2003). Information on the diet of *B. atrox*, mainly from anecdotal field observations (e.g., Duellman 1978; Duellman and Mendelson 1995; Martins and Oliveira 1998), but also from larger sample sizes (Oliveira 2003; Santos-Costa *et al.* 2015), suggests that individuals of this species undergo ontogenetic changes in diet.

Since there are relatively few studies on diet and reproduction of snakes in the Neotropical region, and most existing studies were conducted primarily in southern South America, there is uncertainty as to whether known patterns apply to species or populations in Amazonia. As already mentioned, the geographical coverage of studies on *Bothrops* in the Amazon is incomplete, with most studies having been carried out in the eastern region, an area which has a seasonal rainfall pattern different from that occurring in the central and western regions (Santos-Costa 2003; Maschio 2008; Santos-Costa *et al.* 2015). Considering that dietary and reproductive patterns may differ among populations in different areas, the general objective of this study was to describe the diet and reproductive biology of *Bothrops atrox*, the common lancehead, in the central and southwestern regions of the Brazilian Amazon. More specifically, we aimed to: (1) identify the stage of development at which sexual maturation occurs in males and females; (2) test the existence of sexual dimorphism in morphological characters; (3) describe the annual reproductive cycle; (4) identify food items consumed; and (5) test for the occurrence of ontogenetic changes in the diet.

MATERIAL AND METHODS

Sampling of specimens and study area

The specimens analyzed in this study were collected along a transect of about 1000 km along the interfluve between the Purus and Madeira rivers, in the region between the cities of Manaus, in Amazonas state, and Porto Velho, in Rondônia state (Brazil). The climate of the region is tropical rainy, with average annual temperature between 24 and 28 °C, and annual precipitation occurring in a period of heavy rain, usually between December and May, and a drier period between June and November (Leopoldo *et al.* 1987; Forti and Moreira-Nordemann 1991). The mean annual rainfall varies between 2075 mm in the Manaus region to 1733 mm in the Porto Velho region, while the annual mean relative air humidity ranges between 75 and 90% (DNPM 1978).

The vegetation of the region is dominated by *terra-firme* (never flooded) forests of variable species composition and structure, also including floodplain forests that are seasonally inundated by muddy and black (nearly silt-free) water, as well as *campinaranas* (white-sand forests) and white-sand seasonally-flooded open scrub vegetation (*campinas*) (Prance 1987). To the north, the vegetation is characterized by dense ombrophylous forests, while in the south forests are more open (IBGE 1997). The topography of the region is flat, low (27–122 m) and lacks elevated areas to impede wind circulation. Within areas covered by forest, there is little change in temperature during the day (Cortez 2004).

A total of 109 specimens were analyzed, all deposited in the Amphibian and Reptile Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA) and in the collection of the Fundação de Medicina Tropical Dr. Heitor Vieira Dourado (FMT-HVD), both in Manaus, Amazonas, Brazil (Supplementary Material, Appendix S1). This sample excluded individuals from captivity and/or which were captured by means of pitfall traps. Specimens were analyzed regardless of sex, size, stage of maturation and the perceived presence of food items.

Morphometric measures

The following measurements were taken of each specimen (in millimeters): snout-vent length (SVL), tail length (TaL) and total length (ToL). Head measurements were not made due to physical damage often observed in that portion of the body in preserved specimens. These measures were chosen because they are generally considered to represent body size and shape in snakes (Monteiro *et al.* 2006).

Sexual maturity

Whenever possible, the following reproductive data were analyzed: sex; number of ovarian follicles in secondary vitellogenesis, oocytes or embryos; diameter of the largest ovarian follicle or oviductal embryo; height, width and length (in millimeters) of the right testicle. Females were considered mature when follicles in secondary vitellogenesis were present and had a diameter ≥ 8 mm, or oviduct embryos; for males, those with SVL ≥ 470 mm were considered mature, following the literature (Oliveira 2003, Silva *et al.* 2017b). All individuals larger than the youngest mature specimen of each sex were considered potentially mature (Nunes *et al.* 2010), and included in analyzes of sexual dimorphism.

Sexual dimorphism

The existence of sexual dimorphism in SVL was analyzed with a Mann-Whitney U test. Degree of sexual size dimorphism (SSD) was calculated according to Gibbons and Lovich (1990): [SSD = (SVL of the largest sex/SVL of the smaller sex)-1]. This index reflects differences in size between both sexes. The higher the value, the greater is the difference in body size. The existence of sexual dimorphism in TaL was tested with covariance analysis (ANCOVA), using SVL as a covariate. Any individual showing any form of caudal loss or damage was excluded from the TaL dimorphism calculations.

Reproductive cycle

We measured the follicle diameter of females, while in males we calculated the ratio between width and height of the right testicle. The gonadosomatic index (GSI = [gonad length/SVL] x100), which describes the proportion of the whole animals represented by gonads, was also used to estimate gamete production in males and females separately (adapted from Shine 1977). We compared these four measurements between the rainy (November to April) and dry (May to October) seasons to test seasonal variation in these parameters through a Mann-Whitney U test.

Diet

Food items were observed through the dissection of the digestive tract (stomach and intestine) of the specimens. The number of food items and the type of prey (ectothermic or endothermic) were recorded. Prey items were identified to the lowest possible taxonomic level through morphological analysis, with the help of identification keys and taxonomic and systematic studies (e.g., Martins and Oliveira 1998; Adis 2002; Vitt *et al.* 2008; Fraga *et al.* 2013a). The occurrence of ontogenetic changes in the diet was assessed by comparing the SVL of individuals with endothermic and ectothermic prey content using a Mann-Whitney U test.

RESULTS

Body size, reproductive maturity and sexual dimorphism

The SVL of mature females significantly exceeded that of mature males (Mann-Whitney U = 243.0, $p < 0.001$, df = 1, n = 34), as did total length (Mann-Whitney U = 224.5, $p < 0.001$; Df = 1; n = 31) (Table 1). Considering body size as a covariate, there was no significant difference in TaL between the sexes (ANCOVA, F = 21.23, p = 0.34, n = 31). The SSD value was 0.49.

Table 1. Morphometric measures of *Bothrops atrox* from central and southwestern Amazonia. All measures are in millimeters. F: females; F*: mature females; M: males; M*: mature males; N: number; SD: standard deviation; SVL: snout-vent length; TaL: tail length; ToL: total length.

Measurement	Sex	Min	Max	Mean	SD	N
SVL	F	229	1265	560.4	237.8	74
	M	282	823	568.6	135.7	25
	F*	795	1265	919.7	148.6	14
	M*	480	823	615.1	103.9	20
ToL	F	274	1415	643.9	261.8	69
	M	330	954	673.3	163.9	23
	F*	906	1415	1038.6	153.2	13
	M*	565	954	734.7	121.2	18
TaL	F	40	155	87.3	31.6	69
	M	48	140	103.9	26.3	23
	F*	106	155	133.5	16.2	13
	M*	79	140	113.3	19.3	18

Reproductive cycle

The gonadosomatic index varied slightly along the year and did not differ between seasons for males (Mann-Whitney U = 46.5, p = 0.08, n = 25) nor females (Mann-Whitney U = 179.5, p = 0.83; n = 39) (Figure 1A). Vitellogenic follicles were at their largest between February and July, but did not differ between seasons (Mann-Whitney U = 193, p = 0.67, n = 41) (Figure 1B). The testis width/height ratio peaked between January and May and differed between seasons (Mann-Whitney U = 37.5, p = 0.02, n = 25) (Figure 1C). Newborns (SVL < 300 mm, according to Hoge and Federsoni, 1976/77; Oliveira 2003; and Silva *et al.* 2017b) were found in January (n = 3), February (n = 4), March (n = 1), April (n = 1), May (n = 2), June (n = 2) and November (n = 4).

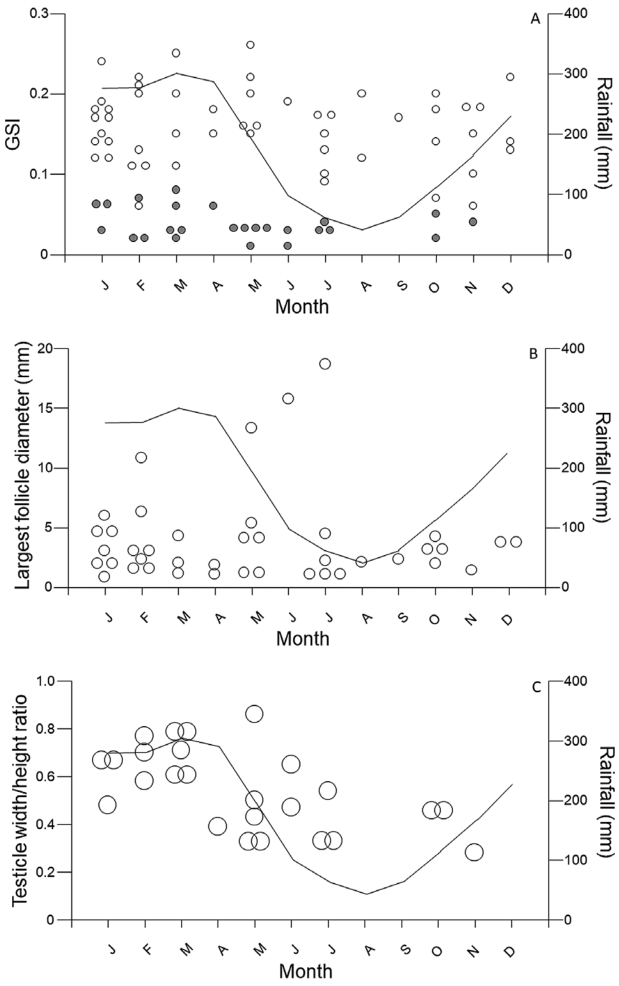

Figure 1. Reproductive cycle of *Bothrops atrox* from the central and southwestern Amazon. The lines in each graph indicate mean accumulated monthly rainfall in the region A: seasonal distribution of the gonadosomatic index (GSI) in individuals of *B. atrox*. White circles = females (n = 54), and gray circles = males (n = 25); B: seasonal distribution in the diameter of the vitelogenic follicles in females (n = 41). C: seasonal distribution in the ratio between testicular width and height in males (n = 25).

Diet

Among the 109 specimens analyzed, 33 (35%) contained food items in the digestive tract. Of these, 24 (73%) contained exclusively ectothermic prey (centipedes, anurans, lizards or snakes); eight (24%) had ingested exclusively endothermic prey (mammals); one (3%) had ingested both prey categories; and 10 (30%) ingested more than one food item (n = 2 - 4). The SVL of snakes containing ectotherm prey ranged from 240 to 865 mm (mean = 486.04, SD = 205.21), while the SVL of snakes containing endotherm prey ranged from 390 to 1110 mm (mean = 671.22, SD = 232.52) (Figure 2). Predators of endotherms were significantly larger than those of ectotherms (Mann-Whitney U = 60.5; p = 0.04, df = 1). Prey belonged to the orders Scolopendromorpha, Anura, Squamata, Didelphimorphia and Rodentia, as well as an unidentified species of Chilopoda and an unidentified vertebrate (Table 2). Most abundant food items were, in descending order of frequency, anurans (38%), lizards (19.5%), mammals (19.5%), centipedes (15.2%) and snakes (4.3%). Fragments of insects found in the gut of some snakes were considered to be secondary digestion (i.e., prey of an anuran subsequently ingested by a *B. atrox*).

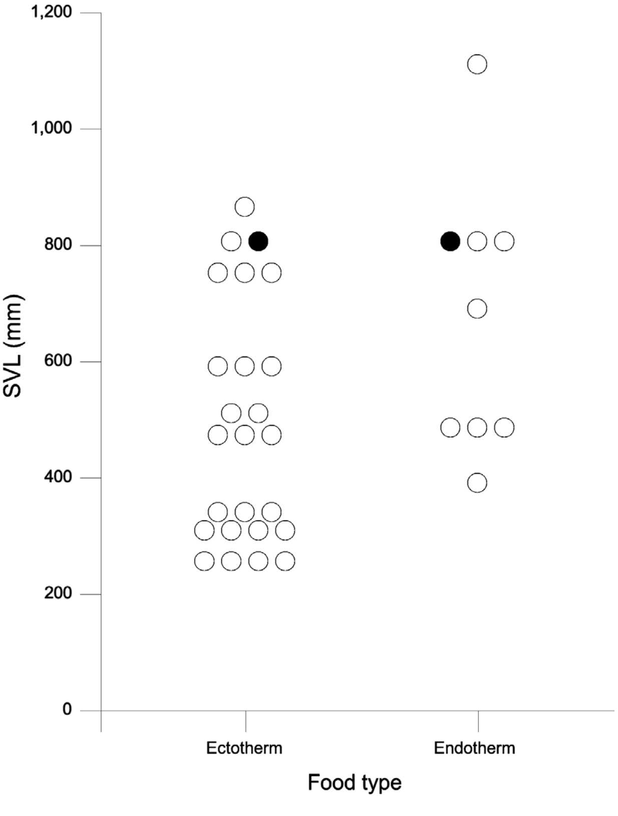

Figure 2. Relationship between body length (SVL, in mm) and type of prey (endothermic or ectothermic) ingested by *Bothrops atrox*. The black circles represent the same individual (SVL: 790 mm) that fed on both types of prey.

Table 2. Prey consumed by 109 specimens of *Bothrops atrox* from central and southwestern Amazonia analyzed in this study. Frequency refers only to snakes that contained food itens in their digestive tract. The insects found in the digestive system were considered as secondary digestive tract residue (see results for diet). NI: not identified.

Identification	Number of items	Frequency (%)
CENTIPEDES	7	15.21
Scolopendromorpha	6	
Scolopendra sp.	6	
NI	1	
AMPHIBIANS	5	10.8
Craugastoridae	1	
Pristimantis fenestratus	1	
Hylidae	1	
Osteocephalus sp.	1	
Leptodactylidae	3	
Adenomera andreae	1	
Adenomera sp.	1	
Leptodactylus sp.	1	
SNAKES	2	4.34
Colubridae	1	
Tantilla melanocephala	1	
Dipsadidae	1	
Imantodes cenchoa	1	
LIZARDS	9	19.56
Gymnophtalmidae	2	
Leposoma sp.	1	
NI	1	
Teiidae	2	
Kentropyx calcarata	1	
NI	1	
NI	5	
MAMMALS	9	19.56
Didelphimorphia	1	
Rodentia	2	
Cricetidae	1	
NI	1	
NI	6	
INSECTS	13	28.26
NI VERTEBRATE	1	2.17
TOTAL	46	

DISCUSSION

Body size, reproductive maturity and sexual dimorphism

As in the present study, larger females have been recorded in other *Bothrops* species, including: *B. moojeni* (Leloup 1975; Nogueira *et al.* 2003), *B. asper* (Solórzano and Cerdas 1989), *B. jararaca* (Sazima 1992), *B. fonsecai* (Sazima and Manzani 1998), *B. neuwiedi* (Valdujo *et al.* 2002), *B. pubescens* (Hartmann *et al.* 2004), *B. alternatus* (Nunes *et al.* 2010), *B. itapetiningae* (Leão *et al.* 2014), and *B. atrox* (Oliveira 2003; Silva *et al.* 2017b). Sexual size dimorphism is a common phenomenon in snakes (Shine 1978), and may reflect size-based fecundity, where larger females produce greater numbers of offspring (Martins *et al.* 2001). In males, the smaller body size is related to greater mobility, increasing the ability of smaller individuals to actively seek available mates and to be less detectable to predators during the mate search (Shine 1978).

Males reached reproductive maturity at a smaller size than females. This has also been observed in other *Bothrops* species, including *B. asper* (Solórzano and Cerdas 1989), *B. jararaca* (Sazima 1992), *B. pubescens* (Hartmann *et al.* 2004), *B. alternatus* (Nunes, *et al.* 2010). Beaupre *et al.* (1998) suggested that males and females have similar growth rates, in which case males reach maturity before females of the same species (Shine *et al.* 1998). Maturity in females may be delayed due to the energetic costs involved in reaching the larger sizes required to generate greater volumes of eggs and/or young (Shine 1978; Seigel and Ford 1987).

In some species of *Bothrops*, males engage in ritual combat, which establishes dominance and subordinate roles, and priority status for access to mates (Schuett 1996, 1997). In *Bothrops* from southernmost regions of Brazil, male combats usually occur in autumn and early winter. In species that display ritual combat, the ratio of size-based sexual dimorphism is smaller, because selection favors larger males, which are more competitive in combat and gain access to females (Shine 1978). SSD for *B. neuwiedi* was 0.39, which was interpreted as evidence for absence of ritual combat in this species (Hartmann *et al.* 2004), The value for SSD was similar for *B. atrox* in our study (0.49), although ritual combat behavior has been observed between *B. atrox* males in eastern Amazonia (Fernandes *et al.* 1993). Differently, Oliveira (2003) argued that throughout many years of studies on snakes in the region of Manaus no ritual combats were ever observed between males of this species, suggesting that in populations of this area, ritual combat is rare or does not exist.

The larger body size of females is probably positively related to fecundity, providing more space for reproductive organs and embryos inside the body cavity (Shine 1993). Another commonly reported pattern is a relatively larger tail in males, as this body part bears the hemipenis and their retracting muscles (King 1989). However, male TaL was not significantly greater than that of females in our sample, which disagrees with other reports for *B. atrox* and other species of the genus (Oliveira 2003; Silva *et al.* 2017b). We believe that this variation may be due to the small number of mature individuals available for analyzes after exclusion of specimens with any form of tail damage (14 females and 20 males).

Reproductive cycle

Reproduction seems to be seasonal in *Bothrops* species, with births synchronized with warmer seasons of the year in subtropical regions, as is the case with *B. neuwiedi* (Hartmann *et al.* 2004), and *B. alternatus* (Nunes *et al.* 2010), and with the rainy season in tropical regions, for example, in *B. jararaca* (Sazima 1992), *B. neuwiedi* (Valdujo *et al.* 2002), *B. moojeni* (Nogueira *et al.* 2003), *B. mattogrossensis* (Monteiro *et al.* 2006), *B. asper* (Solórzano and Cerdas 1989; Sasa *et al.* 2009), and *B. leucurus* (Lira-da-Silva 2009). In our sample, only males showed signs of reproductive seasonality, having greater testicular volume in the rainy season. Unusually, the distribution of the gonadosomatic index varied little throughout the year. This occurred for both sexes, suggesting that this method is not effective for determining the reproductive cycle of *B. atrox* in central Amazonia. Females had follicles in vitellogenesis (> 5 mm) throughout the year, but the largest follicles (> 10 mm) occurred only between February and July, from the end of the rainy season and into the dry season. For males, testicular volume peaked between January and May, the height of the rainy season, gradually decreasing during the dry season. These observations agree with previous studies (Martins and Oliveira 1998; Oliveira and Martins 2001), which suggests that mating occurs in the first months of the year, between February and May, when males have more swollen testicles (indicating sperm production), whereas in subsequent months the embryos develop so that births are mainly concentrated in the rainy season, when the greatest number of juveniles are found in nature.

In eastern Amazonia, Maschio (2008) found females with follicles developed in October and November. In the same area, pregnant females ocurred between September and January, with perfectly developed young (already bearing the species characteristic coloration pattern) in November and January (Cunha and Nascimento 1981), while very young individuals were recorded in January, February, March, June, July, September, October, November and December (Santos-Costa 2003; Santos-Costa *et al.* 2015). These findings suggest that, in eastern Amazonia, recruitment of newborns occurs throughout the year. In the region of Manaus, in central Amazonia, copulations have been observed in April (Oliveira and Martins 2001), with well-developed embryos recorded from August to December (Oliveira 2003), and newborns between December and February, indicating that births occur at the beginning of the rainy season (Martins and Oliveira 1998; Oliveira and Martins 2001). Although the size of follicles did not vary between seasons in our sample, the temporal distribution of newborns suggests a synchronization with the period of the year when prey, mostly anurans, are most available (Fitch 1987; Sazima 1992; Sasa *et al.* 2009). It is suggested that, in *Bothrops*, reproductive regulation is facilitated by delayed egg fertilization through long-term sperm storage via uterine muscular twisting (Almeida-Santos and Salomão 2002). Such an evolutionary strategy could allow females the post-copulatory control of offspring paternity (Almeida-Santos and Salomão 2002).

Diet

Most *Bothrops* species have a generalist diet, which includes a wide variety of prey (Martins *et al.* 2002). Ontogenetic dietary shifts were also reported in most species of the genus (Martins *et al.* 2002). Other studies on *Bothrops* diet, including the current investigation, have corroborated both ideas (Nogueira *et al.* 2003; Oliveira 2003; Monteiro *et al.* 2006; Santos-Costa *et al.* 2015; Rodrigues *et al.* 2016; Silva *et al.* 2017a). The most important items in *Bothrops* diets (considering only known generalist species) are mammals, lizards and anurans (Martins *et al.* 2002). Our results agree with this generalization, as these were the three prey groups most frequently found. Martins *et al.* (2002) considered centipedes to be of lesser importance in *Bothrops* diet (< 10%). In our sample centipedes represented about 15% of identified items, present in the digestive tract of individuals considered to be reproductively immature. It is likely that, as the animals grow and become able to prey on endothermic animals that yield higher amounts of calories, they cease feeding on low-energy-yield prey, like centipedes. Insular species have diets that differ from those of continental species, due to isolation and different prey availability, and in these cases the consumption of ectothermic prey, such as centipedes, remains important throughout life (Martins *et al.* 2002).

It is known that diet studies based on museum specimens can lead to underestimates of certain prey due to the differential digestion of prey types made up of fragile tissues such as amphibians (Glaudas *et al.* 2017). However, the large proportion of frogs detected as prey in our sample suggests that this might not be a concern in our study.

Ophiophagy in *Bothrops*, and particularly in *B. atrox*, has been reported in the literature, although it is considered to be of little importance in the overall diet of generalist species (Martins *et al.* 2002). Snake species known to have been preyed upon by *B. atrox* include the colubrid *Tantilla melanocephala* (also recorded in the current study), and another unidentified colubrid (Martins and Gordo 1993), the dipsadids *Atractus torquatus* (Oliveira and Martins 1996) and *Oxyrhopus melanogenys* (Gavira and Loebmann 2011), and the viperid *Porthidium lansbergii* (Roldan and Lucero 2011). Bernarde and Abe (2006) also recorded ophiophagy in *B. atrox*, but did not specify the prey species, whereas Rodrigues *et al.* (2016) observed the occurrence of cannibalism in this species. We recorded a specimen of *Imantodes cenchoa* (Serpentes, Dipsadidae) among the prey items of *B. atrox*, which represents, to our knowledge, the first record of this snake in the diet of the common lancehead. Although *I. cenchoa* is considered a primarily arboreal snake (Martins and Oliveira 1998), it is sometimes found on the ground, and *B. atrox* has been observed foraging actively on the ground in search of prey (Oliveira and Martins, 1996). Therefore, it is possible that the individual of *I. cenchoa* was preyed by *B. atrox* on the ground while moving from one tree to another.

CONCLUSIONS

Our results allow the following conclusions about the reproduction and diet of *Bothrops atrox* in central and southwestern Amazonia: 1) females reach sexual maturity at a greater body size than males, which probably take less time to reach adulthood; 2) there is marked sexual dimorphism in size between the sexes, with females larger than males; 3) the reproductive cycle, especially in males, seems to be synchronized with the regional rainfall regime, which differs from that found in other parts of the biome; 4) the snakes have a generalist diet, with the ingestion of a wide range of prey such as centipedes, anurans, lizards, snakes and mammals; and 5) there is an ontogenetic change in the diet, with smaller individuals feeding exclusively on ectothermic prey (centipedes, anurans, lizards and snakes), and adults also feeding on endothermic prey (mammals).

ACKNOWLEDGMENTS

We thank Claudia Keller and the two anonymous reviewers for relevant suggestions on an earlier version of this manuscript; Rafael de Fraga, Marcelo Gordo, Cristina Bührnheim, Marcelo Menin and Adrian Barnett for valuable suggestions during the course of this study; Fernanda Werneck and Maria das Graças Costa Alecrim for allowing access to the scientific collections from Instituto Nacional de Pesquisas da Amazônia and Fundação de Medicina Tropical Doutor Heitor Vieira Dourado, respectively; Marcelo Menin for identifying the frogs eaten by the snakes. Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) provided a master's scholarship to PFB. Financial support for this study was received from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) via Edital Universal 461573/2014-8 and a productivity grant to ILK.

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RECEIVED: 20/07/2018
ACCEPTED: 22/10/2018
ASSOCIATE EDITOR: Claudia Keller

SUPPLEMENTARY MATERIAL

(only avaliable in the electronic version)

BISNETO & KAEFER. Reproductive and feeding biology of the common lancehead *Bothrops atrox* (Serpentes, Viperidae) from central and southwestern Brazilian Amazonia.

Appendix S1. Analyzed specimens of *Bothrops atrox*.

Fundação de Medicina Tropical Dr. Heitor Vieira Dourado: BRAZIL: AMAZONAS: Careiro da Várzea: FMT 3544, FMT 3881; **Manaus:** FMT 3498, FMT 3510, FMT 3574, FMT 3580, FMT 3589, FMT 3598, FMT 3612, FMT 3618, FMT 3670, FMT 3707, FMT 3786, FMT 3794, FMT 3817, FMT 3845, FMT 3860, FMT 3867, FMT 3879, FMT 3887, FMT 3888, FMT 3891, FMT 3892, FMT 4111, FMT 4112, FMT 4113, FMT 4115, FMT 4117, FMT 4119, FMT 4123, FMT 4126, FMT 4128, FMT 4129, FMT 4132, FMT 4133, FMT 4134, FMT 4135, FMT 4137, FMT 4141, FMT 4145, FMT 4146, FMT 4147, FMT 4148, FMT 4164; **Presidente Figueiredo:** FMT 3874.

Instituto Nacional de Pesquisas da Amazônia: BRAZIL: AMAZONAS: Careiro: INPA-H 019808, INPA-H 032193, INPA-H 032213; **Iranduba:** INPA-H 023358; **Manaus:** INPA-H 008565, INPA-H 010933, INPA-H 011906, INPA-H 012010, INPA-H 012601, INPA-H 012602, INPA-H 018232, INPA-H 029490, INPA-H 030412, INPA-H 030447, INPA-H 031484, INPA-H 031485, INPA-H 032189, INPA-H 032192, INPA-H 032217, INPA-H 034949; **Rio Preto da Eva:** INPA-H 031472, INPA-H 031486; **RONDÔNIA: Porto Velho:** INPA-H 027842, INPA-H 027843, INPA-H 027844, INPA-H 027845, INPA-H 027846, INPA-H 027847, INPA-H 027848, INPA-H 031992, INPA-H 032178, INPA-H 032179, INPA-H 032180, INPA-H 032181, INPA-H 032182, INPA-H 032184, INPA-H 032185, INPA-H 032187, INPA-H 032188, INPA-H 032190, INPA-H 032191, INPA-H 032194, INPA-H 032195, INPA-H 032196, INPA-H 032197. INPA-H 032198, INPA-H 032199, INPA-H 032200, INPA-H 032201, INPA-H 032202, INPA-H 032203, INPA-H 032204, INPA-H 032205, INPA-H 032206, INPA-H 032208, INPA-H 032209, INPA-H 032210, INPA-H 032211, INPA-H 032214, INPA-H 032215, INPA-H 032216, INPA-H 032218, INPA-H 032219.