

ORIGINAL ARTICLE

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

Pedro Ferreira BISNETO, Igor Luis KAEFER*

Universidade Federal do Amazonas – UFAM, Instituto de Ciências Biológicas, Programa de Pós-Graduação em Zoologia, Av. General Rodrigo Octavio 1200, Coroado I, 69067-005 Manaus, AM, Brasil.

* Corresponding author: kaefer@ufam.edu.br**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. fonsceai*, *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 interfluvium 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 ($n = 4$).

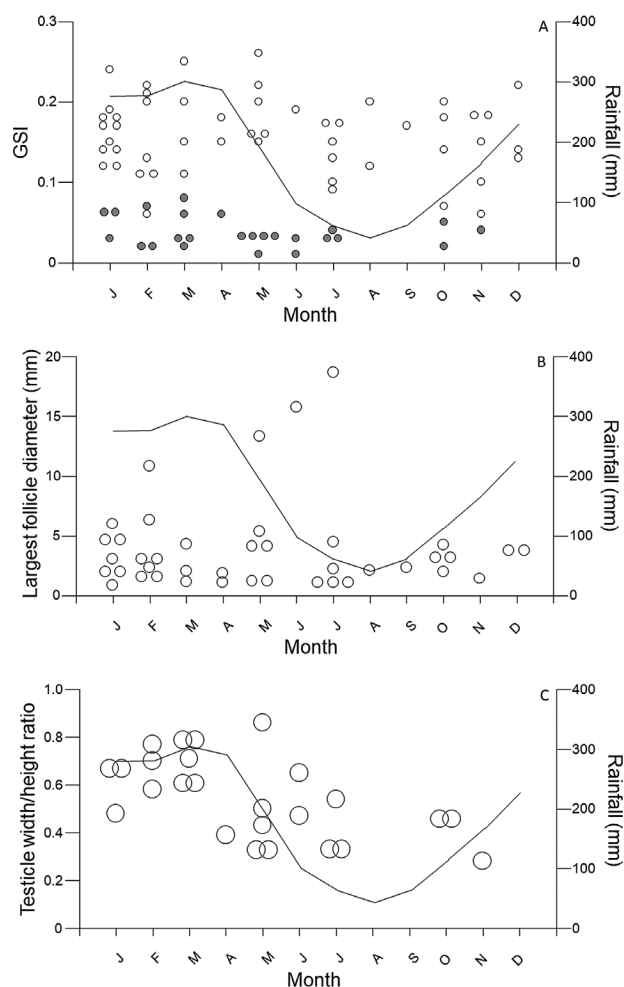


Figure 1. Reproductive cycle of *Bothrops atrox* from the central and southwestern Amazon. The lines in each graph indicate mean accumulated monthly rainfall in the region A: seasonal distribution of the gonadosomatic index (GSI) in individuals of *B. atrox*. White circles = females ($n = 54$), and gray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

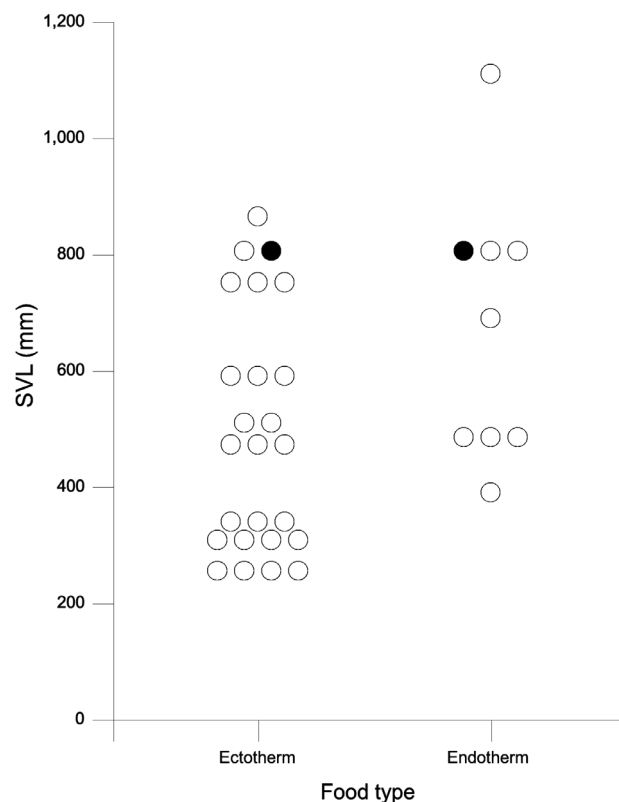


Figure 2. Relationship between body length (SVL, in mm) and type of prey (endothermic or ectothermic) ingested by *Bothrops atrox*. The black circles represent the same individual (SVL: 790 mm) that fed on both types of prey.

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 items 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	
<i>Scolopendra</i> sp.	6	
NI	1	
AMPHIBIANS	5	10.8
Craugastoridae	1	
<i>Pristimantis fenestratus</i>	1	
Hylidae	1	
<i>Osteocephalus</i> sp.	1	
Leptodactylidae	3	
<i>Adenomera andreae</i>	1	
<i>Adenomera</i> sp.	1	
<i>Leptodactylus</i> sp.	1	
SNAKES	2	4.34
Colubridae	1	
<i>Tantilla melanocephala</i>	1	
Dipsadidae	1	
<i>Imantodes cenchoa</i>	1	
LIZARDS	9	19.56
Gymnophthalmidae	2	
<i>Leposoma</i> sp.	1	
NI	1	
Teiidae	2	
<i>Kentropyx calcarata</i>	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. fonscai* (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 occurred 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.

REFERENCES

- Adis, J. (Ed.). 2002. *Amazonian Arachnida & Myriapoda*. Pensoft Pub, Sofia, 589p.
- Almeida-Santos, S.M.; Orsi, A.M. 2002. Ciclo reprodutivo de *Crotalus durissus* e *Bothrops jararaca* (Serpentes, Viperidae): morfologia e função do oviduto. *Revista Brasileira de Reprodução Animal*, 26: 109–112.
- Almeida-Santos, S.M.; Salomão, M.G. 2002. Reproduction in Neotropical pitvipers, with emphasis on species of the genus *Bothrops*. In: Schuett, G.W.; Höggren, M.; Douglas, M.E.; Greene, H.W. (Ed.). *Biology of the Vipers*. Eagle Mountain Publishing, Eagle Mountain, p.445–462.
- Barros, V.A.; Rojas, C.A.; Almeida-Santos, S.M. 2014. Is rainfall seasonality important for reproductive strategies in viviparous Neotropical pit vipers? A case study with *Bothrops leucurus* from the Brazilian Atlantic Forest. *Herpetological Journal*, 24: 67–75.
- Bernarde, P.S.; Abe, A.S. 2006. A snake community at Espigão do Oeste, Rondônia, southwestern Amazon, Brazil. *South American Journal of Herpetology*, 1: 102–113.
- Bernarde, P.S. 2014. *Serpentes Peçonhentas e Acidentes Ofídicos no Brasil*. Anolisbooks, São Paulo, 223p.
- Carpenter, C.C. 1977. Communication and displays of snakes. *American Zoologist*, 17: 217–223.
- Cortez, M. 2004. Climatologia de Rondônia. *Primeira Versão*, Ano II, 11 (171): 79–98.
- Cunha, O.R.; Nascimento, F.P. 1981. Ofídios da Amazônia. XII - Observações sobre a viviparidade em ofídios do Pará e Maranhão (Ophidia, Aniliidae, Boidae, Colubridae e Viperidae). *Boletim do Museu Paraense Emílio Goeldi, Zoologia*, 109: 1–20.
- DNPM. 1978. Departamento Nacional de Produção Mineral. *Radambrasil, Levantamento de Recursos Naturais*. v.18. Manaus. Ministério de Minas e Energia. Rio de Janeiro, 746p.
- Duellman, W.E.; Mendelson III, J.R. 1995. Amphibians and reptiles from northern Departamento Loreto, Peru: taxonomy and biogeography. *University of Kansas Science Bulletin*, 55: 329–376.
- Duellman, W.E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. *Miscellaneous Publication of the University of Kansas Museum of Natural History*, Lawrence, 65: 1–352.
- Fernandes, W.; Cardoso, S.R.; Chaves, M.M.; Miyaji, C.K.; Sant'ana, S.S.; Lula, L.A. 1993. Aspectos reprodutivos de *Bothrops atrox*: período de cópula e dados sobre a ninhada (Serpentes, Viperidae). *Proceedings of the III Congresso Latino-Americano de Herpetologia*, Universidade Estadual de Campinas, Campinas, p.68.
- Fitch, H.S. 1987. Collecting and life-history techniques. In: Seigel, S.A.; Collins, J.T.; Novak, S.S. (Ed.). *Snakes, Ecology and Evolutionary Biology*. Macmillan, New York, p.143–164.
- Forti, M.C.; Moreira-Nordemann, L.M. 1991. Rainwater and throughfall chemistry in a "terra firme" rain forest: Central Amazonia. *Journal of Geophysical Research*, 96: 7415–7421.
- Fraga, R.; Lima, A.P.; Prudente, A.L.; Magnusson, W.E. 2013a. *Guia de cobras da região de Manaus – Amazônia Central*. Editora INPA, Manaus, 303p.
- Fraga, R.; Magnusson, W.E.; Abrahão, C.R.; Sanaiotti, T.; Lima, A.P. 2013b. Habitat Selection by *Bothrops atrox* (Serpentes: Viperidae) in Central Amazonia, Brazil. *Copeia*, 2013: 684–690.
- Gavira, R.S.; Loebmann, D. 2011. *Bothrops* sp. (gr. *atrox*) (jararaca/lancehead) diet. *Herpetological Review*, 42: 436.
- Gibbons, J.W.; Lovich, J.E. 1990. Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). *Herpetological Monographs*, 4: 1–29.
- Glaudas, X.; Kearney, T.C.; Alexander, G.J. 2017. Museum specimens bias measures of snake diet: a case study using the ambush-foraging puff adder (*Bitis arietans*). *Herpetologica*, 73: 121–128.
- Hartmann, M.T.; Marques O.A.; Almeida-Santos S.M. 2004. Reproductive biology of the southern Brazilian pitviper *Bothrops neuwiedi pubescens* (Serpentes, Viperidae). *Amphibia-Reptilia*, 25: 77–85.
- Hoge, A.R.; Federsoni Jr., P.A. 1976/1977. Observações sobre uma ninhada de *Bothrops atrox* (Linnaeus, 1758) (Serpentes: Viperidae: Crotalinae). *Memórias do Instituto Butantan*, 40/41: 19–36.

- IBGE. 1997. Instituto Brasileiro de Geografia e Estatística. *Recursos naturais e meio ambiente: uma visão do Brasil*. 2nd ed. Instituto Brasileiro de Geografia e Estatística. Rio de Janeiro. 208p.
- Leão, S.M.; Pelegrin, N.; Nogueira, C.C.; Brandão, R.A. 2014. Natural history of *Bothrops itapetiningae* Boulenger, 1907 (Serpentes: Viperidae: Crotalinae), an endemic species of the Brazilian Cerrado. *Journal of Herpetology*, 48: 324–331.
- Leopoldo, P.R.; Franken, W.; Salati, E.; Ribeiro, M.N. 1987. Towards a water balance in the central Amazonian region. *Experientia*, 43: 222–233.
- Lillywhite, H.B. 2014. *How Snakes Work*. Oxford University Press. New York. 256p.
- Lira-da-Silva, R.M. 2009. *Bothrops leucurus* Wagler, 1824 (Serpentes; Viperidae): Natural History, Venom and Envenomation. *Gazeta Médica da Bahia*, 79: 56–65.
- Marques, O.A.; Kasperoviczus, K.; Almeida-Santos, S.M. 2013. Reproductive Ecology of the Threatened Pitviper *Bothrops insularis* from Queimada Grande Island, Southeast Brazil. *Journal of Herpetology*, 47: 393–399.
- Martins, M.; Gordo, M. 1993. *Bothrops atrox* (Common Lancehead). Diet. *Herpetological Review*, 24: 151–152.
- Martins, M.; Oliveira, M. E. 1998. Natural history of snakes in forest of the Manaus region, Central Amazonia, Brazil. *Herpetological Natural History*, 6: 78–150.
- Martins, M.; Araújo, M.S.; Sawaya, R.J.; Nunes, R. 2001. Diversity and evolution of macrohabitat use, body size and morphology in a monophyletic group of Neotropical pitvipers (*Bothrops*). *Journal of Zoology*, 254: 529–538.
- Martins, M.; Marques, O.A.V.; Sazima, I. 2002. Ecological and phylogenetic correlates of feeding habits in Neotropical pitvipers (genus *Bothrops*). In: Schuett, G.W.; Höggren, M.; Douglas, M. E.; Greene, H. W. (Ed.). *Biology of the Vipers*. Eagle Mountain Publishing, Utah, p.307–328.
- Maschio, G.F. 2008. *História natural e ecologia das serpentes da Floresta Nacional de Caxinauã e áreas adjacentes, Pará, Brasil*. Doctoral Thesis, Universidade Federal do Pará/Museu Nacional Emílio Goeldi, Belém. 214p.
- Melgarejo, A.R. 2009. Serpentes peçonhentas do Brasil. In: Cardoso, J.L.; França, F.O.; Wen, F.H.; Málaque, C.M.; Haddad Jr., V. (Ed.). *Animais Peçonhentos no Brasil: Biologia, Clínica e Terapêutica dos Acidentados*. 2nd ed. Sarvier, São Paulo, p.42–70.
- Monteiro, C.; Montgomery, C.E.; Spina, F.; Sawaya, R.J.; Martins, M. 2006. Feeding, reproduction, and morphology of *Bothrops mattogrossensis* (Serpentes, Viperidae, Crotalinae) in the Brazilian Pantanal. *Journal of Herpetology*, 40: 408–413.
- Nogueira, C.C.; Sawaya, R.J.; Martins, M. 2003. Ecology of the pitviper, *Bothrops moojeni*, in the Brazilian Cerrado. *Journal of Herpetology*, 37: 653–659.
- Nunes, S.F.; Kaefer, I.L.; Leite, P.T.; Cechin, S.Z. 2010. Reproductive and feeding biology of the pitviper *Rhinocerophis alternatus* from subtropical Brazil. *Herpetological Journal*, 20: 31–39.
- Oliveira, M.E.; Martins, M. 1996. *Bothrops atrox* (Common Lancehead). Foraging Behaviour and Ophiophagy. *Herpetological Review*, 27: 22–23.
- Oliveira, M.E.; Martins, M. 2001. When and where to find a Pitviper: Activity patterns and habitat use of the Lancehead, *Bothrops atrox*, in central Amazonia, Brazil. *Herpetological Natural History*, 8: 101–110.
- Oliveira, M.E. 2003. *História Natural de Jararacas Brasileiras do grupo Bothrops atrox (Serpentes, Viperidae)*. Doctoral Thesis. Universidade do Estado de São Paulo, Programa de Pós-Graduação em Ciências Biológicas (Área de Zoologia). 123p.
- Oliveira, M.E.; Martins, M. 2003. *Bothrops atrox* (Common Lancehead). Prey. *Herpetological Review*, 31: 123–124.
- Prance, G.T. 1987. Vegetation. In: Whitmore, T.C.; Prance, G.T. (Ed.). *Biogeography and Quaternary history in tropical America*. Clarendon Press, Oxford, p.28–45.
- Rodrigues, G.M.; Maschio, G.F.; Prudente, A.L. 2016. Snake assemblages of Marajó Island, Pará state, Brazil. *Zoologia*, 33: 1–13.
- Roldan, J.S.; Lucero, M.F. 2011. A prey item not previously recorded for *Bothrops asper*: a case of ophiophagy involving two sympatric pit viper species. *Herpetotropicalos*, 5: 107–109.
- Sanders, K.L.; Rasmussen, A.R.; Guinea, M.L. 2014. High rates of hybridization reveal fragile reproductive barriers between endangered Australian sea snakes. *Biological Conservation*, 171: 200–208.
- Santos, M.C.; Martins, M.; Boechat, A.L.; Neto, A.P.; Oliveira, M.E. 1995. *Serpentes de Interesse Médico da Amazônia*. UAL/ SESU, Manaus, 64p.
- Santos-Costa, M.C. 2003. *História natural das serpentes da Estação Científica Ferreira Penna, Floresta Nacional de Caxinauã, Melgaço, Pará*. Doctoral Thesis. Pontifícia Universidade Católica de Porto Alegre, Porto Alegre. 87p.
- Santos-Costa, M.C.; Maschio, G.F.; Prudente, A.L. 2015. Natural history of snakes from Floresta Nacional de Caxinauã, Amazônia Oriental, Brasil. *Herpetology Notes*, 8: 69–98.
- Sasa, M.; Wasko, D.K.; Lamar, W.W. 2009. Natural history of the terciopelo *Bothrops asper* (Serpentes: Viperidae) in Costa Rica. *Toxicon*, 54: 904–922.
- Sawaya, R.J.; Marques, O.A.; Martins, M. 2008. Composição e história natural das serpentes de Cerrado de Itirapina, São Paulo, sudeste do Brasil. *Biota Neotropica*, 8: 127–149.
- Sazima, I.; Manzani, P.R. 1998. *Bothrops fonsecai* (Fonseca's lancehead). Reproduction and size. *Herpetological Review*, 29: 102–103.
- Sazima, I.; Strüßmann, C. 1990. Necrofagia em serpentes brasileiras: exemplos e previsões. *Revista Brasileira de Biologia*, 50: 461–468.
- Sazima, I. 1992. Natural history of the jararaca pitviper, *Bothrops jararaca*, in southeastern Brasil. In: Campbell, J.A.; Brodie, E.D. (Ed.). *Biology of the pitvipers*. Tyler, Texas, p.199–216.
- Schuett, G.W. 1996. Fighting dynamics of male copperheads *Agkistrodon contortrix* (Serpentes, Viperidae): stress-induced inhibition of sexual behavior in losers. *Zoo Biology*, 15: 209–221.
- Schuett, G.W. 1997. Body size and agonistic experience affect dominance and mating success in male copperheads. *Animal Behaviour*, 54: 213–224.

- Seigel, R.A.; Ford, N.B. 1987. Reproductive ecology. In: Seigel, R.A.; Collins, J.T.; Novak, S.S. (Ed.). *Snakes: Ecology and Evolutionary Biology*. McGraw-Hill Publishing Company, New York, p.210–252.
- Shine, R. 1977. Reproduction in Australian elapid snakes II. Female reproductive cycles. *Australian Journal of Zoology*, 25: 655–666.
- Shine, R. 1978. Sexual size dimorphism and male combat in snakes. *Oecologia*, 33: 269–277.
- Shine, R. 1993. Sexual dimorphism in snakes. In: Seigel, R.A.; Collins, J.T. (Ed.). *Snakes: Ecology and Behavior*. McGraw-Hill, Inc., New York, p.49–86.
- Shine, R.; Harlow, P.S.; Keogh, J.S.; Boeadi. 1998. The influence of sex and body size on food habits of a giant tropical snake, *Python reticulatus*. *Functional Ecology*, 12: 248–258.
- Silva, K.M. 2015. *Biologia reprodutiva da jararaca da Amazônia, Bothrops atrox (Serpentes: Viperidae)*. Master Dissertation. Universidade de São Paulo, Programa de Pós-Graduação em Anatomia dos Animais Domésticos e Silvestres, 81p.
- Silva, K.M.; Almeida-Santos, S.M.; Bertani, R. 2017a. Hundred legs good, two fangs better: adult centipede (Scolopendridae) devoured by a juvenile Amazon lancehead, *Bothrops atrox* (Viperidae). *Acta Amazonica*, 47: 171–174.
- Silva, F.M.; Oliveira, L.S.; Nascimento, L.R.; Machado, F.A.; Prudente, A.L. 2017b. Sexual dimorphism and ontogenetic changes of Amazonian pit vipers (*Bothrops atrox*). *Zoologischer Anzeiger - A Journal of Comparative Zoology*, 271: 15–24.
- Solórzano, A.; Cerdas, L. 1989. Reproductive biology and distribution of the terciopelo, *Bothrops asper* Garman (Serpentes: Viperidae), in Costa Rica. *Herpetologica*, 45: 195–207.
- Uetz, P. & Hošek, J. (Ed.). The Reptile Database. (<http://www.reptile-database.org>). Accessed on 15/06/2016.
- Valdujo, P.H.; Nogueira, C.C.; Martins, M. 2002. Ecology of *Bothrops neuwiedi pauloensis* (Serpentes: Viperidae: Crotalinae) in the Brazilian Cerrado. *Journal of Herpetology*, 36: 169–176.
- Vitt, L.J.; Magnusson, W.E.; Pires, T.A.; Lima, A.P. 2008. *Guia de Lagartos da Reserva Adolpho Ducke, Amazônia Central*. Áttema Design Editorial, Manaus, 175p.

RECEIVED: 20/07/2018

ACCEPTED: 22/10/2018

ASSOCIATE EDITOR: Claudia Keller

SUPPLEMENTARY MATERIAL

(only available 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: AMZNAS: 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: AMZNAS: 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.



This is an Open Access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.