Trabajo

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Composition and natural history of the snake community in a preserved forest in Central Amazonia, Pará, Brazil

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ABSTRACT
We present information about a snake community in a preserved forest in central Amazonia and describe the composition, habitat use, daily activity, diet, and reproduction. The study area is mainly in the municipality of Itaituba in Parque Nacional da Amazônia, state of Pará, Brazil. We set up 26 plots along of a 135 km on a stretch of the BR-230 highway. We used three quantifiable capture methods: Time Constrained Visual Search (TCS), Road Search by Car (RS) and Pitfall Traps with drift fence (PTS). We also recorded all snakes eventually found by the team outside the collection protocol (occasional encounters) and those obtained by other people (third-party encounters). Reproductive (sexual dimorphism, reproductive maturity, recruitment, and fecundity), and feeding biology (diet composition and frequency of food items) are presented. We recorded 61 species from 38 genera and seven families. *Imantodes cenchoa*, *Helicops angulatus*, and *Bothrops atrox* were the most abundant species. Most species have terrestrial habits and nocturnal activity. The most consumed prey was lizards and frogs. Observing the number of specimens distributed monthly, we noted that most specimens with eggs and embryos were recorded in the dry season, while births occurred throughout the year. Compared to some snake communities located south and north of the Amazon River, the snake community of Parque Nacional da Amazônia has high species diversity, resulting from the presence of different lineages as well as different functional groups, which reflect past and present events that have occurred in this region.

Key Words: Amazon rainforest; Diet; Reproduction; Tapajós River; Activity.

Introduction

The complexity of ecological relationships and species richness of snakes distinguish the Neotropical region from other regions of the world (Henderson *et al.*, 1979; Vitt, 1987). Species richness patterns in this region have recently been described, and appear to follow the same trends as other vertebrates, suggesting that similar factors may determine the diversity of ectothermic and endothermic animals (Roll *et al.*, 2017; Guedes *et al.*, 2018). This high diversity of snakes in the neotropics is the result of a complex history of origin, colonization and diversification of distinct clades, which has resulted in irregular diversity patterns (Cadle and Greene, 1993; Head *et al.*, 2009; Fenker *et al.*, 2014; Zaher *et al.*, 2019). High phylogenetic endemism of snakes in this region has been attributed to the combination

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of recent and past events (Harrison, 2013; Thornhill *et al.*, 2017). In particular, topography and certain characteristics related to climate have been invoked to explain the historical and recent diversity of Neotropical snakes (Azevedo *et al.*, 2019). Some studies suggest that the topography acts as a climatic barrier in the distribution of snakes in the Brazilian Atlantic Forest, indicating that the physiological restrictions determine the patterns of biogeographic distribution in this ectothermic group (Moura *et al.*, 2016). Likewise, thermal conditions would better explain the compositional and phylogenetic beta-diversity of snakes in the Atlantic Forest, while factors related to water would better explain the structure of assemblies within the same climatological regime (Moura *et al.*, 2016).

There is considerable heterogeneity among climatically-similar sites in the Amazon basin. Faunal surveys for the southwestern Amazon, for example, reveal lower species diversity than sites in northwestern and central Amazonia (Rabosky *et al.*, 2019). An interesting pattern of variation was observed along a north-south gradient, with localities north of the main Amazon channel showing 30% higher richness and diversity of snakes compared to the lowlands of southwestern Amazonia (Silva and Sites, 1995; Rabosky *et al.*, 2016; Guedes *et al.*, 2018; Roll *et al.*, 2017). However, this condition is not observed when the snake assemblies located in the south (Frota, 2004; Frota *et al.*, 2005; Bernarde and Abe, 2006; Ávila-Pires *et al.*, 2009; Maschio *et al.*, 2009; Prudente *et al.*, 2010; Bernarde *et al.*, 2011; Silva *et al.*, 2011) are compared to those located north of the Amazon River (Avila-Pires, 2005; Lima, 2008; Avila-Pires *et al.*, 2010; Campos *et al.,* 2015; Moraes *et al.*, 2017; Prudente *et al.*, 2020) (see Table and Figure in Appendix). Specifically, comparing intensely sampled areas with similar sampling efforts and protocols, it is observed that sites north of the Amazon River (such as the Serra do Navio region, see Prudente *et al.*, 2020) have fewer snakes than the area southern area of the river (such as the National Forest de Caxiuanã, see Santos-Costa *et al.*, 2015) (see Table and Figure in the Appendix).

Comparing the richness and diversity of different snake communities has been a challenge for herpetologists working in the Amazon. According to Rabosky *et al.* (2019), the difficulty in understanding variations in species richness and turnover in the composition of the snake community can be attributed to three factors: variation of the geographical scale of sampling in published inventories; difficulty in sampling this group of animals; and absence of a standardized protocol for sampling squamate communities from tropical forests.

Using different snake sampling protocols, studies conducted south of the Amazon River revealed that the species use a wide variety of habitats, with variable patterns of seasonal activity, diet and reproduction (Santos-Costa *et al.*, 2006; Maschio *et al.*, 2007; Prudente *et al.*, 2007; Maschio *et al.*, 2009; Nascimento *et al.*, 2013; Santos-Costa *et al.*, 2015). Here, we present the inventory of the snake community at Parque Nacional da Amazônia (PARNA), located in a preserved forest in the central region south of the Amazon River, in Brazil. We provide information on composition, abundance, habitat use, daily activity, diet, and reproduction of the species, and compare our results with those of other snake communities located on both banks of the Amazon River.

Materials and methods

Study area

Parque Nacional da Amazônia (PARNA) (03º50'S, 56°32' W) is situated on the left bank of the Tapajós River, mostly within the municipality of Itaituba, along the middle Tapajós River in southwestern state of Pará, northern Brazil (Fig. 1) (IBDF, 1978; Silva-Forsberg, 2006).

Tapajós, a tributary of the right bank of the Amazon River, is a river of transparent waters approximately 760 km long, that flows into the Amazon River in the municipality of Santarém, Pará. The Tapajos's main tributaries are the Jamanxim, Crepori, Teles Pires and Juruena Rivers. The PARNA covers 1,100,679 hectares, and most of the area consists of dense submontane ombrophilous upland forest (Silva-Forsberg, 2006).

The main access route to the PARNA is the Trans-Amazon Highway (BR-230), an unpaved road that runs through the park for 116 km (from km-51 to km-167), linking the municipalities of Itaituba and Jacareacanga in the state of Pará, Brazil. Elevation in the region reaches up to 245 meters above sea level, with prevailing tropical rainy climate and an average annual temperature of 27°C. Annual rainfall (2009 to 2010) was approximately 2000 mm. Precipitation during the rainy season (December to June) is most intense from February to May, with average monthly rainfall of 245 mm. During the dry season (July and October) precipitation falls as low as 63 mm in the month of August.

We set up a total of 26 plots in dense ombrophilous forest (Fig. 1). We established the plots between km-51 and km-93 of the Trans-Amazon Highway, with the following geographic coordinates: **P 1** (4°28'0.02"S, 56°17'8.78"W); **P 2** (4°28'32.25"S, 56°16'45.03"W); **P 3** (4°29'10.83"S 56°17'0.47"W); **P 4** (4°29'17.83"S, 56°16'41.47"W); **P 5** (4°29'27.40"S, 56°16'10.80"W); **P 6** (4°29'52.70"S, 56°16'14.80"W); **P 7** (4°40'6.70"S, 56°27'22.80" W); **P 8** (4°32'38.65"S, 56°18'6.85"W); **P 9** (4°32'39.00"S, 56°18'34.80"W); **P 10** (4°32'18.40"S, 56°18'50.40"W);

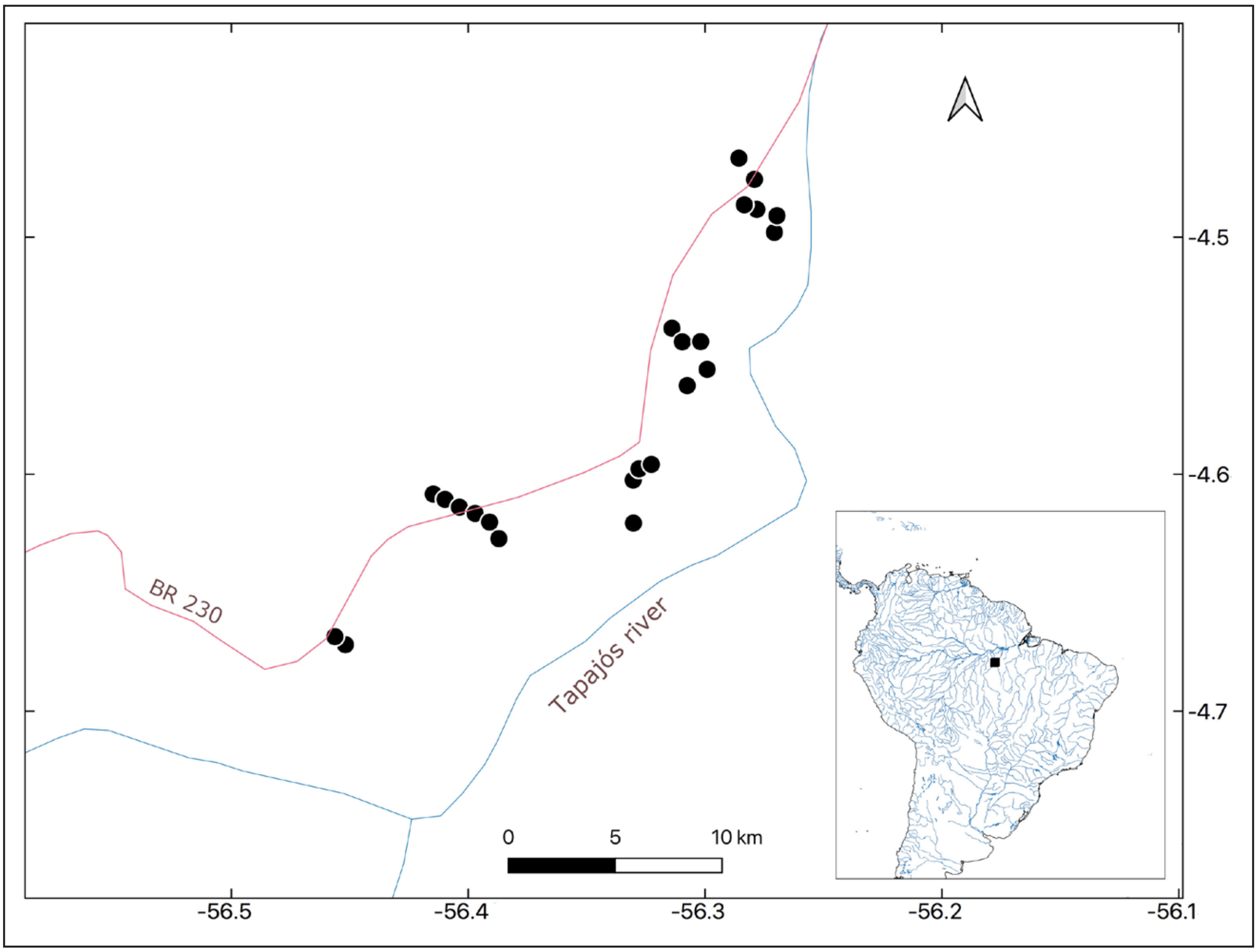

Figure 1. Location of the Parque Nacional da Amazônia, in the city of Itaituba, state of Pará, Brazil. Study area indicated by thered circle.

P 11 (4°33'20.82"S, 56°17'56.94"W); **P 12** (4°3P3'21.10" S, 56°18'13.30"W); **P 13** (4°33'45.50"S, 56°18'27.30"W); **P 14** (4°35'45.13" S, 56°19'21.74" W); **P 15** (4°35'52.00"S, 56°19'40.62"W); **P 16** (4°36'9.00"S, 56°19'49.40"W); **P 17** (4°37'14.35"S, 56°19'49.01"W); **P 18** (4°37'37.93"S, 56°23'13.54"W); **P 19**(4°37'12.79"S, 56°23'27.53"W); **P 20** (4°36'59.60"S, 56°23'49.60"W); **P 21** (4°36'50.20"S, 56°24'13.40"W); **P 22** (4°36'38.30" S, 56°24'35.40"W); **P 23** (4°36'30.20"S, 56°24'53.20"W); **P 24** (4°40'18.90" S, 56°27'6.80" W); **P 25** (4°28'57"S, 56°16'21"W); and **P 26** (4°34'30"S, 56°18'42"W).

Each plot had an area of 3,000 m² (150m x 20m) spread throughout an area of approximately 200 km². We inspected plots 1–24 over six expeditions in 2009 (August, September and November) and 2010 (January, March and July), each lasting 14 consecutive days. We set up the plots 25 and 26 and inspected then in August and November 2011, each for a period of eleven consecutive days.

Field methods

We captured the specimens manually using hooks or herpetological tongs, always by four observers, using three quantifiable capture methods: Time constrained search (TCS), Road Search by Car (RS) and Pitfall Traps with drift fence (PTF). TCS was performed in all plots and consisted of walking through each plot during the day and at night, inspecting all possible shelters and recording the elapsed time (adapted from Martins and Oliveira, 1999) for a total of 1,220 search hours.

We set up four sets of PTF, two in plot 25 and two in plot 26, arranged in rows 200 meters apart (modified from Cechin and Martins, 2000) (Fig. 1). In each row, we used ten 30-liter buckets, five meters apart and joined by a drift fence: a plastic sheet about 70 cm high by 50 m long. The buckets had holes drilled in the bottom to prevent the accumulation of water and we added pieces of styrofoam to avoid drowning in the event of a momentary flood. We buried the drift fence about 15 cm deep and supported it standing with wooden stakes. We installed a total of 40 buckets along 200 m of drift fence, remaining open for 22 days, totaling 880 bucket day. The inspection of PTFs occurred daily.

The RS consisted of displacement by car at a speed of up to 40 km/h along the Trans-Amazon Highway, between km-51 and km-167, to collect live or dead specimens found on the road. We conducted the search during the day, in 2010 (July, August, September, November and December) and 2011 (January, March, April, May and June), without calculating the sample effort. This qualitative method aimed to obtain complementary information about the animals found along the road, when we move between the collection sites.

We consider all snakes found by the team outside the allotted collection regimeas occasional enconters (OE) (Martins and Oliveira, 1999), while was considered third-party encounters (TE) those obtained by other people (Cunha and Nascimento, 1978). Live specimens were euthanized with an overdose of Lidocaine hydrochloride 5%. We deposited the specimens collected and tissue samples in the herpetological collection of Museu Paraense Emílio Goeldi (MPEG) (Appendix – Material analyzed). We used 28 specimens previously collected at PARNA from the MPEG collection to complement the data. We carried out identifications to the species level and, whenever possible, to the subspecies level, to increase the refinement of our results. The taxonomic nomenclature and species identification followed: Starace (1998); Fraga *et al.* (2013); Campbell and Lamar (2004); Graboski *et al.* (2015); Costa and Bérnils (2018); Ascenso *et al.* (2019); Nogueira *et al.* (2019); Uetz and Hosek (2020); and Melo-Sampaio *et al.* (2021).

Data acquisition and analysis

During fieldwork, we collected information about the period of activity (diurnal and nocturnal) and habitat (terrestrial, arboreal, and aquatic). Snakes were considered active when discovered in motion, immobile in thermoregulation activity or still, yet attentive and prepared to escape. Snakes were considered inactive when at rest and/or when they showed little or no immediate reaction when disturbed (Cadle and Green, 1993). For all the specimens analyzed, we measured snout-vent length (SVL) and tail length, with the aid of a graduated ruler (to the nearest 1.0 mm).

Snakes exhibit defensive behavior when they feel intimidated by a predator. At the time of capture, we observed whether the snake showed defensive behavior: preparing to strike, flattening, raising or hiding the head, opening the mouth, flattening the anterior dorsal region of the body, dorsoventral body compression, constricting, pressing with tail spine, shaped body S, cloacal discharge, hide your head, tongue exhibition, escape, stick with the tail, stays still, inflates the body, gular inflation, raise his head, erratic movement, protect the head in the shaped body ball, among others (Martins, 1996; Martins *et al.*, 2008).

To evaluate the diet, a dissection was performed (longitudinal incision on the venter for each specimen) only on specimens collected by TCS and RS. We analyzed and identified the stomach contents to major groups (lizard, bird, rodent, anuran, bird egg, centipede, earthworm,insect larva, mollusk, squamata egg, shrimp, tadpole, and fish).

To describe the reproductive aspects, all snakes collected or from scientific collection of specimens from the study area were dissected. Here, we assume that macroscopic analyzes of the gonads have methodological flaws and that histological studies are more appropriate (See Almeida-Santos *et al.*, 2014). However, the absence of studies using histological is rare for Amazonian snakes (Maschio *et al.*, in press). Therefore, we considered males mature when having a snout-vent length (SVL, mm) equal or superior to the length of the smallest male of its species that had coiled ductus deferens (Shine, 1988). Females were considered mature when eggs or embryos were found in the oviducts, and when they had a flaccidor pleated oviduct or, when information on the size of the follicles in secondary vitellogenesis was not available, when SVL was equal to or superior to that of the smallest female of its species that presented follicles in secondary vitellogenesis (largest diameter>10.0 mm; Shine, 1977, 1988). Specimens were considered newborns or young if they showed fissures or visible umbilical scars, or snout-vent length (SVL in mm) compatible to that presented by young specimens (Santos-Costa *et al.*, 2006). We inferred the oviposition period based on the seasonal distribution of pregnant females, and estimated fecundity (reproductive rate) based on the number of vitellogenic follicles (secondary yolk stage) or egg-bearing oviducts. The reproductive cycles of females were found by analyzing gonads and correlating the maturity stage (mature and immature) by seasons (rainy and dry).

Results

We recorded 61 species belonging to 38 genera and eight families (Aniliidae, Boidae, Colubridae, Dipsadidae, Elapidae, Thyphlopidae, Leptotyphlopidae and Viperidae) in the PARNA (N= 278 specimens; Table 1; Figs 2-5). Eleven other species were recorded in the vicinity of the PARNA (*Apostolepis nigrolineata, Erythrolamprus miliaris amazonicus, Helicops polylepis, Micrurus surinamensis* and *Typhlophis squamosus*) and the region of the middle Tapajós

Table 1. Species of snakes registered for the Parque Nacional da Amazonia, municipality of Itaituba, Pará State, Brazil. Legend: **N** = number of specimens collected in this study. **MPEG** = number of specimens deposited in the herpetological collection of Museu Paraense Emílio Goeldi, no methods, habitat, activity, diet, reproduction and defensive behavior information. **Methods**: TCS = Time constrained search; RS = Road search by car; PTF = Pitfall traps with drift fence; OE = Occasional enconters; and TE = Third-party encounters. **Habitat**: Te = Terrestrial; Arb = Arboreal; Aq = Aquatic. **Activity**: Di = Diurnal; No = Nocturnal; * inactive specimens. **Diet**: Li = Lizard; Bi = Bird; Ro = Rodent; An = Anura; Beg = Bird egg; Ce = Centipede; Ea = Earthworm; Il= Insect larva; Mo =Mollusk; Seg = Squamata egg; Sh = Shrimp; Ta = Tadpole; Fi = Fish. **Reproduction**: reproductive period prescribed in month; Fo2º = Secondary follicles vitellogenic; Eg = Eggs; Emb = Embryos; Ne = Newborns; Yo = Youth. **Defensive behavior**: 1 =flatten the head or triangular head; 2 =bite;3=constriction;4=shaped bodyS; 5 =cloacal discharges; 6= tail display; 7 = coiling; 8 =tail coiling; 9=hide the head; 10=tongue exhibition; 11=escape; 12=stick withthe tail; 13 =stays still; 14 = gape; 15 =inflates the body; 16=gular inflation; 17=raises his head; 18=erratic movement; 19=protect the head in the shaped body ball; 20 =body rotation; 21=hiss; 22 = strike; 23=vibrates its tail; 24 =motionless body in a zig-zag position; and 25 = evert hemipenis.

Family/Species	N	MPEG	Methods (specimens)	Habitat (specimens)	Activity (specimens)	Diet	Reproduction (month)	Defense behavior
ANILIIDAE								
Anilius scytale (Linnaeus, 1758)	1		RS(1)	Te(1)	Di(1)			5, 10, 19
BOIDAE								
Boa constrictor Linnaeus, 1758	5	1	RS(2), TE(3)	Arb(2), Te(3)	Di(5)	Li; Bi	Yo(Jan, Nov); Ne(Feb, May, Jul, Nov)	2, 4, 5
Corallus batesii (Gary, 1860)	5		TCS(4), OE(1)	Arb(5)	No(5)	Bi	Yo(Aug, Nov)	2, 3, 4, 5, 19
Corallus hortulana (Linnaeus, 1758)	4		TCS(3), TE(1)	Arb(4)	No(4)		Yo(Aug)	2, 3, 4, 5, 19
Epicrates cenchria (Linnaeus, 1758)	6		TCS(2), OE(3), TE(1)	Te(6)	No(6)		Ne(Jan, Feb)	3, 17, 19
Eunectes murinus Gray, 1849	3		TCS(2), RS(1)	Aq(2), Te(1)	Di(2), No(1)	Ro	Ne(Mar, Aug); Yo (Jul)	3, 5, 19, 21
COLUBRIDAE								
Chironius fuscus (Linnaeus, 1758)	9		TCS(3), RS(2), OE(3), TE(1)	Te(6), Arb(3)	Di(6), No(3*)	An	Fo2º(Jan)	4, 5, 16, 22, 23, 24
Chironius multiventris Schmidt and Walker, 1943	7		TCS(2), RS(1), TE(4)	Te(5), Arb(2)	Di(5), No(2*)	An		2,4,5,16,17, 22,23,24

Chironius scurrulus (Wagler, 1824)	2		OE(1), TE(1)	Te(2)	Di(2)		Fo2º(Jan)	2, 4, 17, 18, 20
Dendrophidion dendrophis (Schlegel, 1837)	2	1	TCS(1), TE(1)	Te (2)	Di(2)	An	Fo2º(Jan)	15, 17, 23
Drymarchon corais Boie, 1827	1	1	RS(1)	Te(1)	Di(1)	Li	Eg(Aug)	2, 5, 10, 15, 20
Drymoluber dichrous (Peters, 1863)	7	2	TCS(6), RS(1)	Te(3), Arb(4)	Di(3), No(4*)	Li; An	Fo2º(Mar, Jul); Eg(Jan); Yo(Nov)	2, 4, 15, 17, 18, 20
Leptophis ahaetulla (Linnaeus, 1758)	7		TCS(2), RS(2), OE(3)	Arb(7)	Di(7)	An		2, 4, 5, 14,17, 18, 20
Mastigodryas boddaerti (Sentzen, 1796)	8	2	RS(2), OE(1), TE(5)	Te(8)	Di(8)	Li	Eg(Dec, Jan); Yo(jun)	2, 11, 13
Oxybelis aeneus (Wagler, 1824)	8		RS(7), TE(1)	Te(8)	Di(8)	Li	Eg(Jul)	10, 13
Oxybelis fulgidus (Daudin, 1803)	9		TCS(1), RS(4), OE(3), TE(1)	Te(8), Arb(1)	Di(8), No(1*)	Li		2, 13
Phrynonax polylepis (Peters, 1867)	3		RS(2), OE(1)	Te(2), Arb(1)	Di(3)	Beg	Ne(Mar)	2, 16, 17, 18, 22, 24
Rhinobothryum lentiginosum (Scopoli, 1785)		1		Te(1)	No(1)			1, 23
Spilotes pullatus (Linnaeus, 1758)	6		RS(3), TE(3)	Te(6)	Di(6)		Ne(Jan, Nov, Dec)	17
Spilotes sulphureus (Wagler, 1824)	1	1	TCS(1)	Te(1)	Di(1)			3, 15, 16, 17
Tantilla melanocephala (Linnaeus, 1758)	2		TCS(2)	Te(2)	No(2)	Ce		5, 13, 18
DIPSADIDAE								
Atractus boimirim Passos, Prudente & Lynch, 2016	3		TCS(1), TE(1)	Te(3)	Di(3)	Ea	Ne(Jan, Mar); Fo2º(Feb)	18
Atractus snethlageae Cunha & Nascimento, 1983	2		PFT(1)	Te(2)	Di(2)	Ea; Il	Eg(Nov)	10
Dipsas catesbyi (Sentzen, 1796)	1		TCS(1)	Te(1)	No(1)	Mo		9, 20
Dipsas pavonina Schlegel, 1837	2		TCS(2)	Arb(2)	No(2)	Mo		13
Drepanoides anomalus (Jan, 1863)	4	1	TCS(4)	Te(4)	No(4)	Seg		10, 13, 20
Erythrolamprus aesculapii (Linnaeus, 1766)	1	4	RS(1)	Te(1)	Di(1)		Fo2º(Feb)	1, 8, 10, 17, 18, 25
Erythrolamprus oligolepis	3	1	TCS(1), RS(1), TE(1)	Te(3)	Di(3)		Fo2º(Aug, Sep)	10
Erythrolamprus poecilogyrus (Wied, 1824)	2		OE(1), TE(1)	Te(2)	Di(2)	An	Ne(Jul)	10, 18
Erythrolamprus reginae (Linnaeus, 1758)	4	2	OE(4)	Te(4)	Di(3), No(1)	An	Ne(Feb, Mar, Jul)	5, 10, 18

Erythrolamprus taeniogaster (Jan, 1863)	2		TE(2)	Te(2)	Di(2)			10, 18
Erythrolamprus typhlus (Linnaeus, 1758)	4		TCS(1), RS(1), OE(2)	Te(4)	Di(4)	An	Ne(Jul)	1, 5, 10, 13, 17
Helicops angulatus (Linnaeus, 1758)	20	2	TCS(19), OE(1)	Aq(20)	No(20)	An; Ta; Fi	Fo2(Jul); Ne(Jan, Jul, Nov); Yo(Aug)	1, 2, 3, 5, 20
Hydrodynastes bicinctus (Herrmann, 1804)	3		TCS(2), TE(1)	Aq(3)	Di(2),No(1)	Sh	Ne(Jan); Yo(Jun)	2, 10, 20
Hydrops martii (Wagler, 1824)	1		TCS(1)	Aq(1)	No(1)			10
Imantodes cenchoa (Linnaeus, 1758)	30	1	TCS(25), RS(1), OE(4)	Te(1), Arb(29)	No(30)	Li	Fo2º(Jan, Mar, Nov); Eg(Jan, Mar, Nov); Ne(Feb); Yo(Aug, Sep)	5, 10
Imantodes lentiferus (Cope, 1894)	2		TCS(2)	Arb(2)	No(2)			5, 10
Leptodeira annulata (Linnaeus, 1758)	5		TCS(3), RS(2)	Arb(5)	No(5)	An		5, 13
Oxyrhopus formosus (Wied, 1820)	3		OE(3)	Te(3)	No(3)	Li		10, 18
Oxyrhopus melanogenys (Tschudi, 1845)	5		RS(4), TE(1)	Te(4)	No(4)	Li	Ne(Aug)	18
Philodryas argentea (Daudin, 1803)	1		OE(1)	Arb(1)	Di(1)			24
Philodryas viridissima (Linnaeus, 1758)	2	1	OE(1), TE(1)	Te(2)	Di(2)		Yo(Feb)	
Pseudoboa coronata Schneider, 1801	3	1	TCS(2), RS(1)	Te(3)	No(3)	Li	Yo(Aug)	10, 13
Pseudoeryx plicatilis (Linnaeus, 1758)	1		RS(1)	Te(1)	Di(1)			
Siphlophis cervinus (Laurenti, 1768)	1		TCS(1)	Arb(1)	No(1)			1, 19
Siphlophis compressus (Daudin, 1803)	9		TCS(6), RS(1), OE(2)	Arb(9)	No(9)	Li	Fo2º(Aug); Eg(Sep)	4, 5, 10
Taeniophallus brevirostris (Peters, 1863)	2		OE(2)	Te(2)	Di(2)	Li	Eg(Jul); Ne(Aug)	5, 10
Taeniophallus quadriocellatus Santos, Di-Bernardo & Lema, 2008	5	2	TCS(2), RS(1), PTF(1), OE(1)	Te(5)	Di(3), No(1)	Li	Fo2º(Jul); Eg(Oct)	5, 10, 18
Xenodon rhabdocephalus (Wied, 1824)		1		Te(1)	Di(1)			
Xenopholis scalaris (Wucherer, 1861)	3	1	TCS(2), PFT(1), OE(1)	Te(3)	No(3)	An	Fo2º(Aug)	1, 5, 10, 13, 18, 19
ELAPIDAE								
Micrurus hemprichii (Jan, 1858)	1		OE(1)	Te(1)	No(1)			6, 17

Micrurus lemniscatus (Linnaeus, 1758)	2		TCS(1), RS(1)	Te(2)	No(2)		Ne(Jan)	
Micrurus paraensis Cunha & Nascimento, 1973	1		OE(1)	Te(1)	No(1)			2, 6, 9, 10, 18
Micrurus spixii Wagler, 1824	1		TCS(1)	Te(1)	No(1)			6, 9, 10, 18
LEPTOTYPHLOPIDAE								
Trilepida macrolepis (Peters, 1857)	3	1	TCS(3)	Arb(3)	No(3)		Ne(Oct)	10, 18
TYPHLOPIDAE								
Amerotyphlops reticulatus (Linnaeus, 1758)	2		PTF(2)	Te(2)	No(2)			10, 12, 18
VIPERIDAE								
Bothrops atrox (Linnaeus, 1758)	16	1	TCS(6), RS(5), OE(1), TE(4)	Te(14), Arb(2)	Di(4), No(12)	Li; Ro	Emb(Jul); Ne(Dec); Yo(Mar)	2, 5, 7, 22, 10, 13, 23
Bothrops bilineatus (Wied, 1821)	1		TCS(1)	Arb(1)	Di(1)			2, 4, 7, 17, 22
Bothrops brazili Hoge, 1954	1		TE(1)	Te(1)	Di(1)			
Bothrops taeniatus Wagler, 1824	1		RS(1)	Te(1)	No(1)			
Lachesis muta (Linnaeus 1766)	1		TE(1)	Te(1)	No(1)		Ne(Jan)	4, 10
TOTAL	250	28						

river (*Chironius exoletus, Clelia plumbea, Hydrops triangularis, Erythrolamprus breviceps, Sibon nebulatus* and *Xenodon severus*) (Frota, 2004).

Considering the five capture methods, both quantifiable and non-quantifiable, we registered a total of 250 individuals for 61 species. For each method, we record the following numbers and percentage of species: TCS (N= 35; 57.4%), PTF (N= 5; 8.2%), RS (N= 26; 42.6%), OE (N= 23; 37.7%), and TE (N= 22; 36%). Sampling effort using only quantifiable methods showed the following results: 1) TCS captured 117 specimens with a sampling effort of 1,220 hours/observer (616 hours during the dayand604 hours at night), with an average encounter rate of 0.09 snakes per person-hour (one snake very 11 person-hours of search).The encounter rate during the day was 0.04 (one snake every 27 hours), whereas, at night, it was 0.15 (one snake every 6hrs 50min); PTF had a sampling effort of 2,112 bucket-hours (22non-consecutive days)and an encounter rate of 0.0023 snakes per bucket-hour (one snake every 422 open bucket-hours); and RS recorded twenty-six species (N= 50) by traveling 1,624 km of road, with an encounter rate of 0.03 snakes/km (one snake every 32.5 km or every 50 min.

Imantodes cenchoa (N= 30; 12.0%), *Helicops angulatus* (N= 20; 8.0%), and *Bothrops atrox* (N= 16; 6.4%) were the most abundant species, considering all methods used (Table 1).The most common species recorded by TCS was *Imantodes cenchoa* (N= 25), while 10 species were recorded exclusively by this method (*Bothrops bilineatus, Dipsas catesbyi, D.pavonina, Drepanoides anomalus, Hydrops martii, Imantodes lentiferus, Micrurus spixii, Spilotes sulphureus, Siphlophis cervinus*, and *Tantilla melanocephala*). Four species (*Atractus snethlageae, Taeniophallus quadriocellatus, Amerotyphlops reticulatus*, and *Xenopholis scalaris*) were recorded using PTF, and *Amerotyphlops reticulatus* was recorded exclusively by this method. *Oxybelis fulgidus* was the most frequent species recorded by RS (N= 8), followed by *O. aeneus* (N= 7), *Bothrops atrox* (N= 6), and *Spilotes pullatus* (N= 5). Five species (*Anilius scytale, Bothrops taeniatus, Drymarchon corais, Erythrolamprus aesculapii* and *Pseudoeryx plicatilis*) were recorded only by RS.

Among the species recorded in this study at the PARNA, 34 were found exclusively in terrestrial habitat (55.7%), 12 in arboreal habitat (19.7%) and three in aquatic habitat (5.0%). Some species used more than one habitat, including *Boa constrictor, Bothrops atrox, Oxybelis fulgidus*, *Phrynonax polylepis*, and others found both on the ground and above. We highlight the record of *Trilepida macrolepis*, a

Figure 2. General view in life of snakes from Parque Nacional da Amazônia, Itaituba, Pará, Brazil. A – *Anilius scytale*; B - *Corallus batesii*; C - *Corallus hortulana*; D- *Epicrates cenchria*; E – *Chironius fuscus*; F – *Dendrophidion dendrophis*; G – *Drymarchon corais* (photo by Jerriane Gomes); H– *Drymoluber dichrous* (young).

Figure 3. General view in life of snakes from Parque Nacional da Amazônia, Itaituba, Pará, Brazil. **A** – *Leptophis ahaetulla*; **B** - *Mastigodryas boddaerti*; **C** – *Phrynonax polylepis*; **D**– *Spilotes sulphureus*; **E** – *Spilotes pullatus*; **F** – *Dipsas catesbyi*; **G**– *Dipsas pavonina*;**H** – *Drepanoides anomalus*.

Figure 4. General view in life of snakes from Parque Nacional da Amazônia, Itaituba, Pará, Brazil. **A** - *Erythrolamprus reginae*; **B** - *Erythrolamprus typhlus;* **C** – *Helicops angulatus*; **D**– *Hydrodynastes bicinctus;* **E** - *Hydrops martii;* **F**-*Imantodes cenchoa*; **G** – *Oxyrhopus formosus*; **H** - *Oxyrhopus melanogenys*.

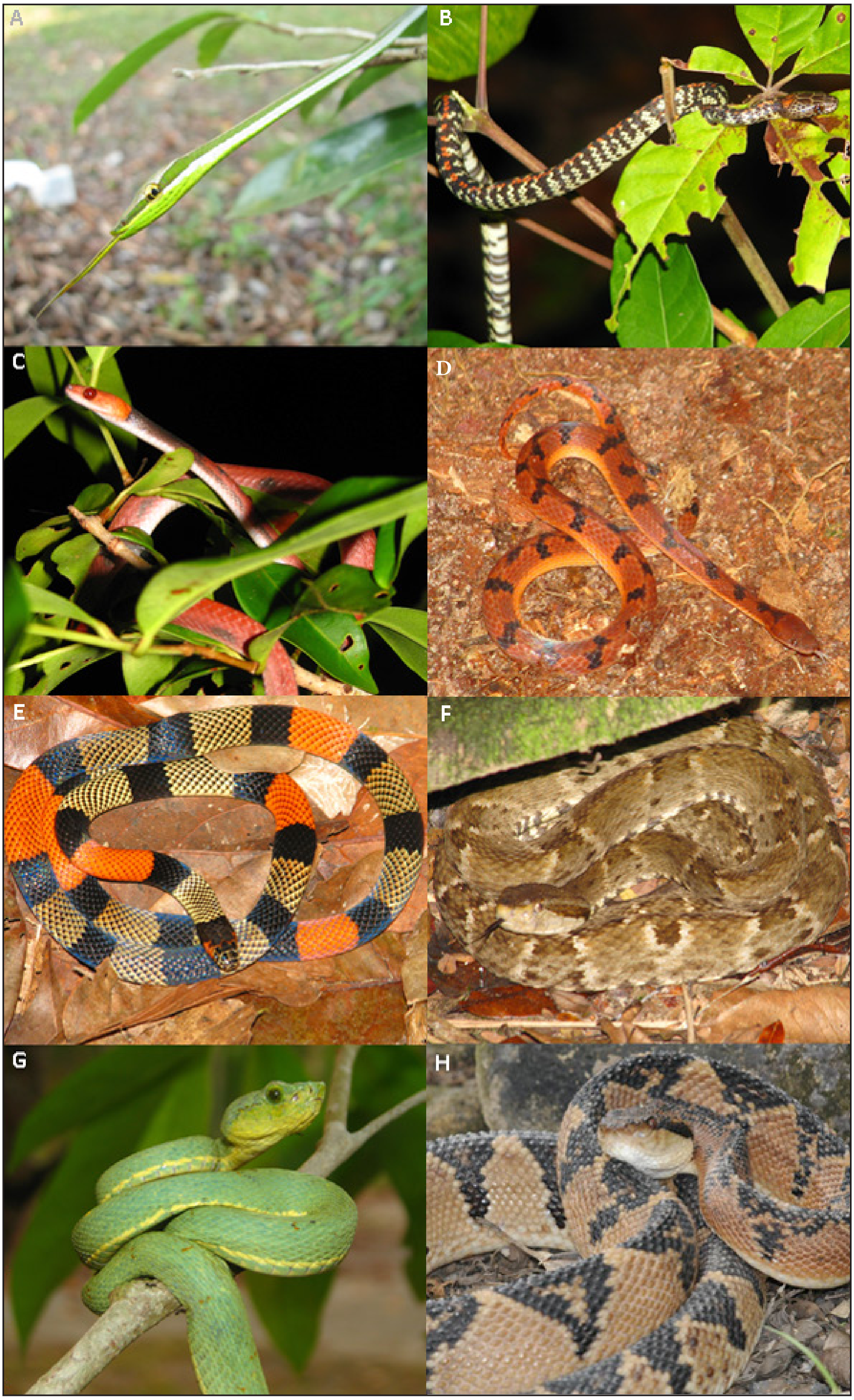

Figure 5. General view in life of snakes from Parque Nacional da Amazônia, Itaituba, Pará, Brazil. **A** – *Philodryas argentea;* **B** - *Siphlophis cervinus*; **C**– *Siphlophis compressus*; **D** - *Xenopholis scalaris;* **E** – *Micrurus spixii;* **F** - *Bothrops atrox*; **G**– *Bothrops bilineatus*; **H** – *Lachesis muta* (photo by Rafael Balestrin).

species considered fossorial, however, in this study we found three isolated specimens in arboreal settings (between 1 and 6 meters high). *Pseudoeryx plicatilis,* an aquatic species, was found dead on the road near a lake in the late afternoon. Two other specimens (not included in this study) were also found road killed during the day near flooded environments.

A total of 46 species were recorded in activity. Most species in this assemblage had nocturnal habits (28 species), followed by diurnal habits (25 species), and a few with both diurnal and nocturnal activities (*Bothrops atrox, Eunectes murinus*, *Erythrolamprus reginae,* and *Taeniophallus quadriocellatus*) (Table 1).

Of the total of 278 specimens analyzed, 87 (31.3%) had identifiable stomach contents (N= 121). The most frequent items consumed were lizards, adult anurans, tadpoles and fish (Table 1). Lizards were consumed exclusively by 11 species of snakes, and anurans by only nine species. Of the 121 items consumed it was possible to identify the direction of ingestion of 81% (N= 98). Prey ingested head-first (71.4%, N= 70) were more frequent than prey ingested tail-first (23.1%, N= 28). Lizards (88.9%, N= 32) and frogs (61.7%, N= 21) were ingested mostly by the anterior body region. Prey ingested from the anterior region of the body ranged from 8.0 to 187.0 mm TL (mean= 44.9 mm), representing 3-46% of the snake SVL. By contrast, prey ingested from the posterior region ranged from 17 to 56 mm TL (mean= 35.3 mm), accounting for 2–14% of the snake SVL.

Reproductive information was obtained for 35 species (n= 239, 148 males and 91 females). Observing the number of specimens distributed monthly (Fig. 6; Table 1), we note that some snakes with eggs and embryos were recorded in the dry season and the beginning of the rainy season, while births occurred throughout the year. We observed vitellogenic secondary follicles (>10 mm) from fifteen species, of which 10 were carrying eggs and one was carrying embryos (Table1).

The escape behavior (movement to get out of a dangerous situation) was the most recorded defensive act (N= 27), followed by cloacal discharge (N= 20) and erratic movements (N= 19). A few defensive behaviors involving intimidation or attack were observed (Table 1).

Discussion

We recorded 72 species in 42 genera and eight families of snakes in the Itaituba region on the middle Tapajós River, with 61 species found inside the PARNA and 11 species in surrounding areas. This represents a surprisingly high diversity, considering that this study area contains 47% (153 species) of species registered for the entire state of Pará (Costa and Bérnils, 2018) and 38% (189 species) of the species registered for the Brazilian Amazonia (Prudente, 2017). Historically, the state of Pará has been intensely sampled and several surveys of snake fauna point to a high diversity. Obviously, there are still regions that are difficult to access that were few samples, reflecting in knowledge gaps. The high diversity of snakes observed in the middle Tapajós region reflects a previously observed pattern for tropical forests, since localities with a predominance of forested vegetation types tend to have relatively higher diversity (Martins and Oliveira, 1999; Maschio *et al.*, 2009; Santos-Costa *et al.*, 2015; Guedes *et al.*, 2014; Rabosky *et al.*, 2019) when compared to open formations in Neotropics (Rocha and Prudente, 2010; Rodrigues and Prudente, 2011). On the other hand, other factors can influence the high diversity of species, for example, the type of matrix that is in contact with the forest, which depending on it can assist in the flow of animals or prevent their passage, such as the presence of urban areas and monocultures (Franklin and Lindenmayer, 2009). In the case of the study area, the great diversity can be explained in part by the structural complexity of the well-preserved continuous forest that forms a mosaic of protected areas, in addition to areas drained by several streams and rivers. However, the presence of a road (Trans-Amazon Highway) crossing PARNA, can negatively affect the local snake community, as shown by the high record of snakes run over on the road.

Choice of survey methods depends on the scope of the study (Doan, 2003). The combination of different collection methods in the same area can provide significant results in a short period of time; allow more robust comparisons between different areas (Cechin and Martins, 2000). The observed complementarity of quantifiable surveys (TCS, RS and PTF) with other methods (OE and TE) confirms the importance of optimizing these practices for surveying the herpetofauna, as noted by Cechin and Martins (2000). Subsequent studies have indicated that the combination of complementary methods is necessary for efficient sampling and that synchronized adoption of multiple techniques in field studies

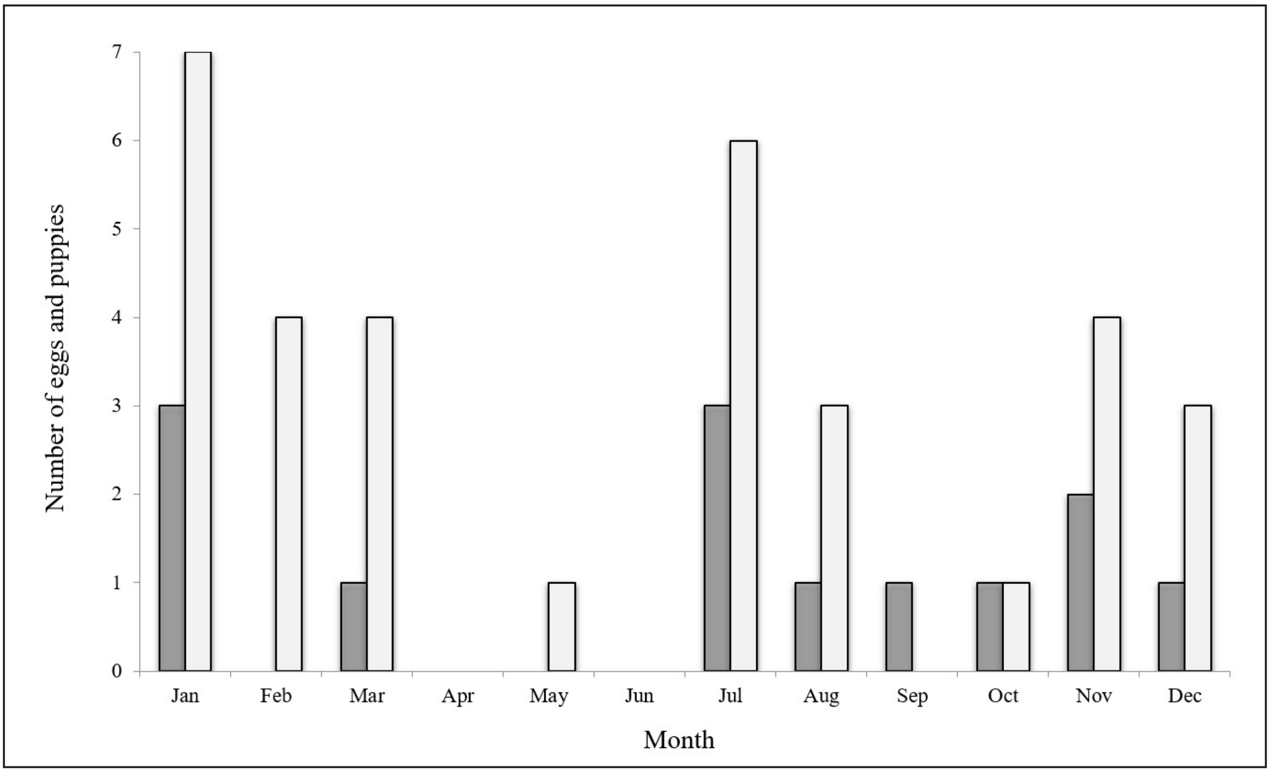

Figure 6. Proportion of eggs (gray bar) recorded in the oviduct of snakes and newborn (white bar) Parque Nacional da Amazônia, Itaituba, Pará, Brazil.

helps to improve sample representation and, thus, the understanding of species distribution and human impacts on herpetofauna in tropical florests (Ribeiro Jr. *et al.*, 2008).

The record of 35 species (11 exclusive) using the PLT is similar to the encounter rates in other snake communities in the Amazon (40 species, Frazão *et al.*, 2020), representing the method that most registers specimens and species. Despite the low efficiency of PTF in this study, this method is considered important in inventories of the herpetofauna because it accesses cryptozoic and fossorial species, which are usually difficult to observe or capture (Maschio *et al.*, 2009; Santos-Costa *et al.*, 2015). The choice of using traps should be evaluated considering the scope of the work, as mentioned by Ribeiro *et al.* (2011). As one of our goals was to obtain a complete list of PARNA snake species, we believe that the use of PTF was important, even if a single species was collected exclusively by this method. The results obtained for RS plus OE and TE indicate that 38 species (n= 88; 35.2% of the total specimens) were present, active or not, on the road. There are several factors that lead to the prevalence of snake road kill, such as foraging (Lima and Obara, 2004), mate seeking during reproductive periods (Marques *et al.*, 2000) and thermoregulation (Ashley and Robinson, 1996; Gokula, 1997). The availability of food along or near highways such as seeds, fruits, herbaceous plants, and so on attracts birds, mammals and other prey items (Lima and Obara, 2004).

Imantodes cenchoa is one of the most frequent species in PARNA, as in other Amazonian assemblages such as in Juruti (Menks, 2012) and Caxiuanã (Maschio *et al.*, 2009; Santos-Costa *et al.*, 2015). The high frequency of this species may be a reflection of the capture method (TCS) and consequently detectability. The ease in locating this species by TCS may be related to its nocturnal activity and foraging strategy in higher vegetation strata (Henderson and Nickerson, 1976; Bartlett and Bartlett, 2003; Sousa *et al.*, 2014). Many snakes are easily detected at night because the color and texture of their scales show up when spotlighting with headlamps (Martins and Oliveira, 1999). This easy detectability of snakes at night may also be related to their slower behavior, which would facilitate capture (Martins and Oliveira, 1999). These results were similar to those obtained by Maschio *et al.* (2009), who found a better efficiency in nocturnal collections. Despite the more efficient sampling of Amazonian snakes at night, we believe that focusing collections only in this period can lead to error or underestimation of the number of species in a given area. Diurnal collecting is also important to identify snakes with different habits, so were commended dividing surveys between both periods.

The snake community from PARNA is characterized by the predominance of terrestrial and nocturnal species, with prevalent richness of Dipsadidae and low richness of Boidae, Elapidae and Viperidae. The differences between the number of terrestrial species recorded in PARNA when compared with assemblages in western (Duellman, 1978) and Central (Martins and Oliveira, 1999) Amazonia may be related to species composition as well as to difficulties in categorizing habitat use for tropical snakes, since a single species may use the habitat in different ways (Cadle and Greene, 1993). In PARNA, it was common to find primarily terrestrial snakes (*Boa constrictor, Bothrops atrox, Chironius fuscus, Chironius multiventris, Drymoluber dichrous* and *Phrynonax polylepis*) resting on the vegetation as well as arboreal species (*Dipsas catesbyi*, *Oxybelis fulgidus* and *O. aeneus*) foraging on the ground. A similar structure was observed in relation to the patterns of spatial distribution of snakes in the regions close to PARNA, with some species exclusively terrestrial and others terrestrial, but using vegetation to sleep and forage (Silva *et al.*, 2011; Santos-Costa *et al.*, 2015). This variation in habitat may be associated with a decreased predation pressure that is less in tropical seasonal environments (Martins, 1993; Bernarde and Abe, 2006; Martins and Oliveira, 1999).

The low number of aquatic species recorded in PARNA when compared to that of other areas in the Amazon clearly reflects the lack of suitable capture methods, in addition to hydrographic and phytophysiognomic characteristics, where Terra Firme forests predominate.

The record of *Trilepida macrolepis*, a fossorial snake, in arboreal environments (between 1 and 6 meters in height), suggests that this species seeks food in termite mounds built on tree trunks in the Amazon, or that this species also seeks vegetation to shelter in rainy periods. Foraging behavior in vegetation was recorded for *Epictia diaplocia*, which was on the trunk of a palm tree ca. 2 m above the ground, trying to enter a termite nest during a light rain (Martins and Oliveira, 1999).

As confirmed in this study, snake diets in Amazonian community are composed mainly oflizards (Duellman, 1978; Martins and Oliveira, 1999; Bernarde and Abe, 2006; Bernarde and Abe, 2010; Santos-Costa *et al.*, 2015). By contrast, anurans are the most consumed food item in the Atlantic Forest (Marques and Sazima, 2004; Hartmann *et al.*, 2009), southern grasslands (Di-Bernardo *et al.*, 2007), Pantanal (Strüssmann and Sazima,1993), Cerrado (França *et al.*, 2008) and the Caatinga (Guedes *et al.*, 2014). These differences probably reflect differences in species composition, since the extra-Amazonian regions harbor a larger proportion of xenodontines that feed on anurans (Cadle and Greene, 1993; Colston *et al.*, 2010).

Regarding reproduction, the results show that some snakes with eggs and embryos were recorded in the dry season and the beginning of the rainy season, while births occurred throughout the year. We observed vitellogenic secondary follicles (>10 mm) in fifteen species, and 10 were carrying eggs and one was carrying embryos. We observed that several species in PARNA have distinct reproductive cycles than those recorded by other authors. For example, previous studies recorded *Dipsas catesbyi, D. neivai* (Alves *et al.,* 2005), *Tantilla melanocephala* (Santos-Costa *et al.*, 2006), *Dendrophidion dendrophis* (Prudente *et al.,* 2007), *Chironius fuscus* (Nascimento *et al.*, 2013) and *Mastigodryas boddaerti* (Siqueira *et al.*, 2013) as having a continuous reproductive cycle. However, some species, such as *Anilius scytale* (Maschio *et al.,* 2007), *Dipsas pavonina* and *Bothrops atrox* (Martins and Oliveira, 1999) have a seasonal reproductive cycle. These differences in the reproductive cycle can also occur between populations of the same species, as in the case of *Imantodes cenchoa*, where some populations exhibit two seasonal peaks of reproductive activity (Sousa *et al.,* 2014), while others reproduce throughout the year (Pizzatto *et al.*, 2008). These studies indicate that in order to study the reproductive cycle of snakes, it is necessary to consider that factors such as geographic distribution, phytophysiognomy, resource availability and season, among others, may interfere in the results.

Snakes have developed many strategies (behavioral and chemical) to prevent attack by predators, and the greater this defense capacity, the higher the chance of surviving an attack (Fraga *et al.*, 2013). The large number of escape behaviors observed in the snakes of PARNA, followed by cloacal discharges, was expected. Most snakes, when exposed to a predator, either escape or discharge their feces or other fetid substances to disrupt the predator and escape (Marques and Sazima, 2003). According to Martins *et al.* (2008), arboreal snakes, as they are more exposed to predators that approach from different directions, displayed more visual defensive tactics than terrestrial ones.

The great diversity of lineages found in the tropical region hinders our understanding of patterns involving the structuring of Amazonian snake communities. Ecological, biogeographical and natural history inventories require large sampling efforts and complementary methodologies in order to identify the largest possible number of species at the local level. In general, the study community is composed of species that mainly prey on frogs and lizards, use the terrestrial and arboreal layers both for foraging and resting, and have a continuous reproductive cycle. Some groups have specific morphological adaptations both in their diet (e.g. *Tantilla*/centipedes, *Dipsas*/mollusks, *Imantodes*/ lizards) and habitat use (e.g. *Corallus, Eunectes, Trilepida*).

Several authors have hypothesized that areas north of the Amazon River have greater diversity than areas to the south (Silva and Sites, 1995; Rabosky *et al.*, 2016; Guedes *et al.*, 2018; Roll *et al.*, 2017). To test this hypothesis, it is necessary to consider different factors such as environmental and physical variables. The gradient of snake species richness from north to south in the western Amazon basin, also observed in other organisms, has been related to environmental factors such as climate and vegetation (Rabosky *et al.*, 2019). This hypothesis has not yet been tested for snake communities in eastern Amazonia, however. We observed a high diversity of snakes recorded in communities with a sampling effort greater than 500 hours (using the active sampling method), regardless of their position in relation to the Amazon River (see in Appendix – Table and Figure). This fact indicates that any effort to test the gradient hypothesis must use comparable methods and sampling effort.

When comparing the number of species among communities in eastern Amazonia, we found that PARNA is among the areas with the highest richness, probably as a result of the presence of different evolutionary lineages, as well as different functional groups in the region. However, the fact that the Park is in the region of the middle Tapajós River, in the endemic area of Tapajós (Ribas *et al.*, 2012) and an area of environmental preservation, does not protect it from deforestation.

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APPENDIX - Material analyzed

Aniliidae: *Anilius scytale*: MPEG 25043. **Boidae**: *Boa constrictor:* MPEG 25049, MPEG 25050, MPEG 25051, MPEG 25052, MPEG 21221, MPEG 25053; *Corallus batesii:* MPEG 25054, MPEG 25055, MPEG 25056, MPEG 25293, MPEG 25294; *Corallus hortulana:* MPEG 25057, MPEG 25058, MPEG 25296, MPEG 25297; *Epicrates cenchria*: MPEG 25061, MPEG 25062, MPEG 25289, MPEG 25290, MPEG 25291, MPEG 25292; *Eunectes murinus:* MPEG 25059, MPEG 25060, MPEG 25295. **Colubridae**: *Apostolepis nigrolineata*: MPEG 27228;*Chironius fuscus:* MPEG 25227, MPEG 25265, MPEG 25266, MPEG 25267, MPEG 25268, MPEG 25279, MPEG 25280, MPEG 25281, MPEG 25306; *Chironius multiventris:* MPEG 25273, MPEG 25274, MPEG 25277, MPEG 25278, MPEG 25303, MPEG 25304, MPEG 25305; *Chironius scurrulus:* MPEG 25275, MPEG 25276; *Dendrophidion dendrophis*: MPEG 21243, MPEG 25093, MPEG 25094; *Drymarchon corais:* MPEG 25160, MPEG 25312; *Drymoluber dichrous:* MPEG 24620, MPEG 25100, MPEG 25101, MPEG 25102, MPEG 25103, MPEG 25104, MPEG 25110, MPEG 25111, MPEG 25112;*Leptophis ahaetulla*: MPEG 25194, MPEG 25195, MPEG 25196, MPEG 25197, MPEG 25198, MPEG 25199, MPEG 25200; *Mastigodryas boddaerti:* MPEG 21237, MPEG 21238, MPEG 25221, MPEG 25222, MPEG 25223, MPEG 25224, MPEG 25225, MPEG 25226, MPEG 25228, MPEG 25229; *Oxybelis aeneus*: MPEG 25113, MPEG 25114, MPEG 25115, MPEG 25116, MPEG 25117, MPEG 25118, MPEG 25119, MPEG 25120; *Oxybelis fulgidus:* MPEG 25121, MPEG 25122, MPEG 25123, MPEG 25124, MPEG 25125, MPEG 25269, MPEG 25270, MPEG 25271, MPEG 25272; *Phrynonax polylepis*: MPEG 25090, MPEG 25091, MPEG 25092; *Rhinobothryum lentiginosum*: MPEG 25232; *Spilotes pullatus*: MPEG 25233, MPEG 25234, MPEG 25235, MPEG 25236, MPEG 25299, MPEG 25300; *Spilotes sulphureus*: MPEG 21139, MPEG 25301; *Tantilla melanocephala*: MPEG 25147, MPEG 25148. **Dipsadidae**: *Atractus boimirim*: MPEG 25259, MPEG 25260, MPEG 21233; *Atractus snethlageae:* MPEG 25149, MPEG 25150; *Dipsas catesbyi*: MPEG 25097; *Dipsas pavonina*: MPEG 25095, MPEG 25096; *Drepanoides anomalus:* MPEG 25130, MPEG 25131, MPEG 25132, MPEG 25133, MPEG 25134; *Erythrolamprus aesculapii:* MPEG 25129, MPEG 21230, MPEG 25231, MPEG 24550, MPEG 26778; *Erythrolamprus oligolepis:* MPEG 25158, MPEG 25315, MPEG 25316, MPEG 25317; *Erythrolamprus poecilogyrus:* MPEG 25098, MPEG 25099; *Erythrolamprus reginae:* MPEG 21245, MPEG 24615, MPEG 25285, MPEG 25286, MPEG 25287, MPEG 25288; *Erythrolamprus taeniogaster:* MPEG 25248, MPEG 25313; *Erythrolamprus typhlus:* MPEG 21242, MPEG 25282, MPEG 25283, MPEG 25284; *Helicops angulatus*: MPEG 24617, MPEG 25201, MPEG 25202, MPEG 25203, MPEG 25204, MPEG 25205, MPEG 25206, MPEG 25206, MPEG 25207, MPEG 25208, MPEG 25209, MPEG 25210, MPEG 25211, MPEG 25212, MPEG 25213, MPEG 25214, MPEG 25215, MPEG 25216, MPEG 25217, MPEG 25218, MPEG 25219, MPEG 25220; *Helicops polylepis*: MPEG 27229;*Hydrodynastes bicinctus bicinctus:* MPEG 25230, MPEG 25231, MPEG 25232; *Hydrops martii*: MPEG 25249; *Imantodes cenchoa:* MPEG 21234, MPEG 21235, MPEG 25165, MPEG 25166, MPEG 25167, MPEG 25168, MPEG 25169, MPEG 25170, MPEG 25171, MPEG 25172, MPEG 25173, MPEG 25174, MPEG 25175, MPEG 25176, MPEG 25177, MPEG 25178, MPEG 25179, MPEG 25180, MPEG 25181, MPEG 25182, MPEG 25183, MPEG 25184, MPEG 25185,

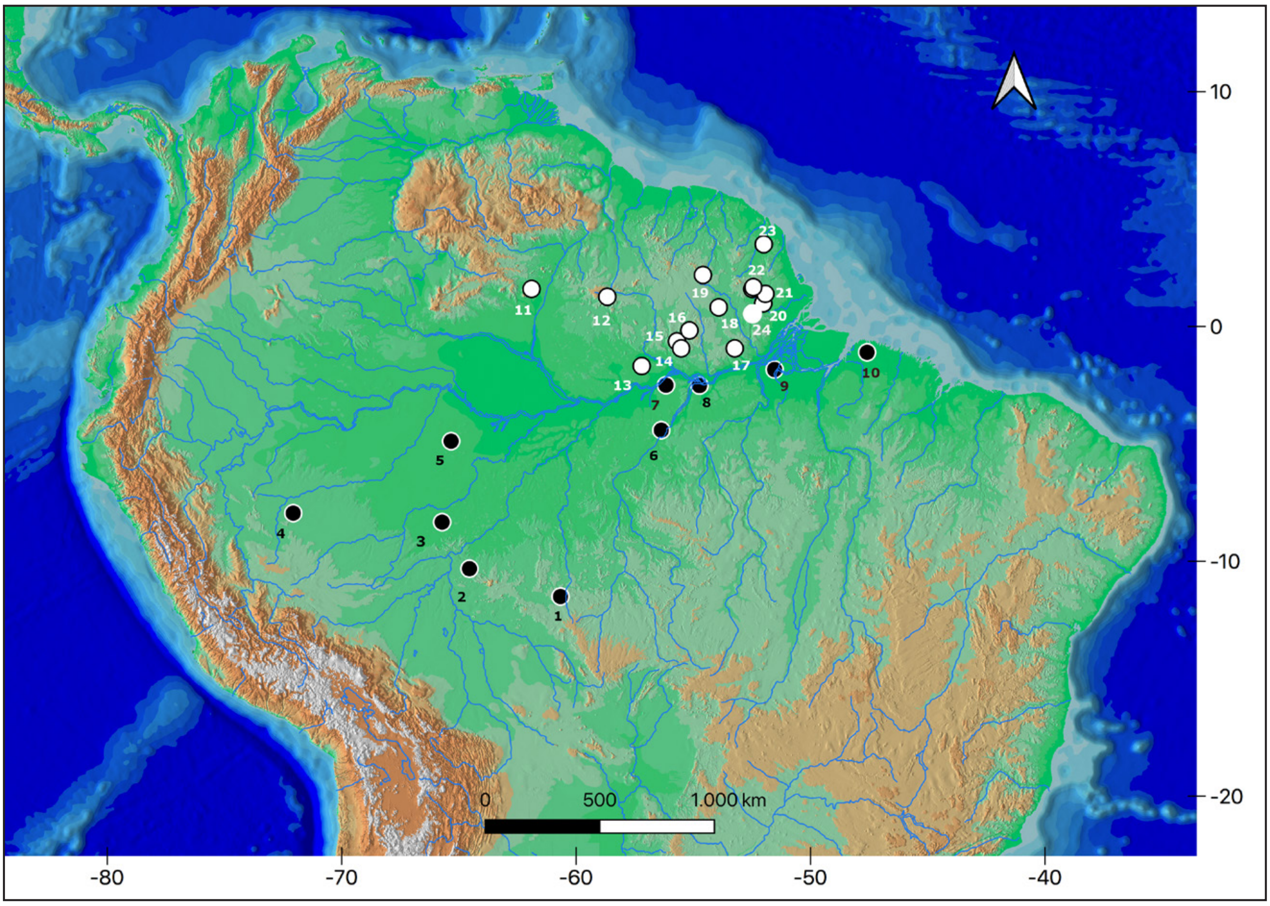
MPEG 25186, MPEG 25187, MPEG 25188, MPEG 25189, MPEG 25190, MPEG 25191, MPEG 25192, MPEG 25193; *Imantodes lentiferus:* MPEG 25238, MPEG 25239; *Leptodeira annulata:* MPEG 25105, MPEG 25106, MPEG 25107, MPEG 25108, MPEG 25109; *Oxyrhopus formosus:* MPEG 25126, MPEG 25127, MPEG 25128; *Oxyrhopus melanogenys:* MPEG 25240, MPEG 25241, MPEG 25242, MPEG 25243, MPEG 25244; *Philodryas argentea:* MPEG 25250; *Philodryas viridissima:* MPEG 21239, MPEG 25246,MPEG 25247; *Pseudoboa coronata:* MPEG 21244, MPEG 25135, MPEG 25136, MPEG 25137; *Pseudoeryx plicatilis:* MPEG 25245; *Siphlophis cervinus:* MPEG 25314; *Siphlophis compressus:* MPEG 25138, MPEG 25139, MPEG 25140, MPEG 25141, MPEG 25142, MPEG 25143, MPEG 25144, MPEG 25145, MPEG 25146; *Taeniophallus brevirostris*: MPEG 25253, MPEG 25255; *Taeniophallus quadriocellatus:* MPEG 25252, MPEG 25254, MPEG 25256, MPEG 25257, MPEG 25258, MPEG 24613, MPEG 24616; *Xenodon rhabdocephalus:*MPEG 21225; *Xenopholis scalaris:* MPEG 25261, MPEG 25262, MPEG 25263, MPEG 25264.**Elapidae**: *Micrurus hemprichii*: MPEG 25063; *Micrurus lemniscatus*: MPEG 25066, MPEG 25068; *Micrurus paraensis*: MPEG 25065; *Micrurus spixii*: MPEG 25064. **Leptotyphlopidae**: *Trilepida macrolepis:* MPEG 24618, MPEG 25046, MPEG 25047, MPEG 25048. **Typhlopidae**: *Amerotyphlops reticulatus*: MPEG 25044, MPEG 25045. **Viperidae**: *Bothrops atrox*: MPEG 25087, MPEG 25071, MPEG 25072, MPEG 25074, MPEG 25076, MPEG 25077, MPEG 25078, MPEG 25298, MPEG 25081, MPEG 25082, MPEG 25083, MPEG 25073, MPEG 25084, MPEG 25085, MPEG 25087, MPEG 25079, MPEG 25080; *Bothrops bilineatus*: MPEG 25070; *Bothrops brazili:* MPEG 25075; *Bothrops taeniatus*: MPEG 25069; *Lachesis muta*: MPEG 25088.

APPENDIX - Table. List of snake communities located south (1-10) and north (11-24) of the Amazon River, used for comparisons. Legends: TCS= Time constrained search; RS= road search by car; PTF= Pitfall traps with drift fences; CTP= Captures by third parties; OE = Occasional enconters; AS= active sampling; and TE = third-party encounters

Site number	Site name	Sampling methods	Number of species	Characteristic of vegetation	References
1	Município de Espigão do Oeste, Rondônia State (11030'S; 60o40'W)	TCS (960 hours), PTF, TE, OE	55	Deforested and transformed into pasture and farming areas	Bernarde and Abe (2006)
2	Parque Estadual de Guajará-Mirim, Rondônia State (10019'S; 64o33'W)	AS	39	Reduced hunting pressure due to its protected status as a state park	Ávila-Pires *et al.* (2009)
3	Rio Ituxi, Amazonas State (8° 20'S; 65°43'W)	AS	32	Consisted of a mix of varzea and terra firme forest.	Ávila-Pires *et al.* (2009)
4	Reserva Extrativista Riozinho da Liberdade, Acre State (7° 57'S; 72°04'W)	TCS (720 hours), PTF (90 days), OE	42	Open Ombrophilous Forest, characterized by the open dossel and the abundance of palm trees, liana or bamboo	Bernarde *et al.* (2011)
5	Província Petrolífera de Urucu, Amazonas State (4°53'S; 65°20'W)	TCS (51 days), RS, PTF, OE	45	Ombrophilous Forest, Terra Firme.	Prudente *et al.* (2010)
6	Município de Itaituba, Pará State (03°50'S, 56°32'W)	TCS (1,220 hours), RS, PTF (22 days), TE, OE	68	Dense submontane ombrophilous forest of low plateau and dense submontane forest of flattened relief and lowmountain ranges	This study
7	Município de Juruti, Pará State (02°09'S; 56°05'W)	TCS (1,160 hours), PTF (94 days), TE, OE	74	Dense ombrophilous forest, with lattosoil type Dystrophic Oxisol	Menks (2012)
8	Município de Belterra (2.5166 S; 54.733 W)	TCS, RS, PTF, TE, OE	53		Frota *et al.* (2005)
9	FLONA de Caxiuanã, Pará State (1o47'S;	TCS (2,639 hours), PTF (132 days), TE, OE	70	Dense ombrophilous forest	Maschio *et al.* (2009)

10	Município de Barcarena, Pará State (1°30'S; 48°37'W)	TCS (336 hours), PTF (37 days), OE	38	Primary Forest (vegetation without significant human disturbance) and degraded areas or areas in early stages of plant regeneration after suffering great human action	Silva *et al.* (2011)
11	Parque Nacional da Serra da Mocidade, Roraima State (01°36'N; 61°54'W)	AS (22 days), PTF (22 days), trammel nets, hook with meat bait, glue traps, shotgun.	12	Dense forests, shrubby vegetation or moss forests, surrounded by a lowland matrix of either tropical forests or savanna ecosystems	Moraes *et al.* (2017)
12	Estação Ecológica do Grão Pará (ESEC Grão Pará – North), Pará State (1°17'N; 58°41'W)	AS (200 hours), PTF (240 days)	16	Terra-firm forest, with steep slopes and creeks	Avila-Pires *et al.* (2010)
13	Floresta Estadual de Faro, Pará State (1°42' S; 57°12' W)	AS (144 hours), PTF (192 days)	12	Terra-firme forest (3 trails); flooded forest (1 trail); disturbed areas	Avila-Pires *et al.* (2010)
14	Floresta Estadual Trombetas, Pará State(0°57' S; 55°31' W)	AS (118 hours), PTF (237 days)	13	Terra-firme forest with creeks (some areas with many Cecropia); an open area with rock outcrop	Avila-Pires *et al.* (2010)
15	Estação Ecológica do Grão Pará (ESEC Grão Pará – Centre), Pará State (0°37'N; 55°43'W)	AS (260 hours), PTF (240 days)	12	Transition zone at the W margin of a large island of terra-firme forest within a large savanna enclave.	Avila-Pires *et al.* (2010)
16	Estação Ecológica do Grão Pará (ESEC Grão Pará – South), Pará State (0°9'S; 55° 11'W)	AS (170 hours), PTF (208 days)	10	Terra-firme forest with creeks bordered by flooded areas; an extensive lake bordered by palms	Avila-Pires *et al.* (2010)
17	Floresta Estadual Paru, Pará State (0°56'S; 53° 14'W)	AS (96 hours), PTF (208 days)	10	Terra-firme forest with creeks and different degrees of perturbation; (dry) flooded forest along margin of river	Avila-Pires *et al.* (2010)
18	Reserva Biológica de Maicuru, Pará State (0°49'N; 53°55' W)	AS (220 hours), PTF (240 days)	10	Terra-firme forest and (dry) flooded forest; small beach along margin of river	Avila-Pires *et al.* (2010)
19	Parque Nacional Montanhas do Tumucumaque 2, Amapá State (2º11'36"N; 54º35'15"W)	AS (400 hours), PTF	13	Terra-firme forest	Lima (2008)
20	Parque Nacional Montanhas do Tumucumaque 4, Amapá State (1º23'13"N; 51º55'39"W)	AS (400 hours), PTF	14	Terra-firme forest	Lima (2008)
21	Parque Nacional Montanhas do Tumucumaque 1, Amapá State (1°36'N; 52°29'W)	AS (400 hours), PTF	13	Terra-firme forest	Lima (2008)

22	Parque Nacional Montanhas do Tumucumaque 5, Amapá State (1°50’41”N; 52°44’28”W)	AS (300 hours), PTF	20	Terra-firme forest	Lima (2008)
23	Parque Nacional Montanhas do Tumucumaque 3, Amapá State (3°29’51”N; 52°18’0”W)	AS (400 hours), PTF	11	Terra-firme forest	Lima (2008)
24	Serra do Navio Region, Amapá State (01°00’N; 52°03’W)	AS(784 hours), PTF (98 days), TE, OE	57	Terra-firme forest	Prudente *et al.* (2020)



APPENDIX - Figure. List of snake communities located south (1-10) and north (11-24) of the Amazon River, Brazil (see Table). Legends: 1 - Município de Espigão do Oeste; 2 -Parque Estadual de Guajará-Mirim; 3- Rio Ituxi; 4- Reserva Extrativista Riozinho da Liberdade; 5 - Província Petrolífera de Urucu; 6 - Município de Itaituba; 7 - Município de Juruti; 8 - Município de Belterra; 9 - FLONA de Caxiuanã; 10 - Município de Barcarena; 11 - Parque Nacional da Serra da Mocidade; 12 - Estação Ecológica do Grão Pará (ESEC Grão Pará – North); 13 - Floresta Estadual de Faro; 14 - Floresta Estadual Trombetas; 15 - Estação Ecológica do Grão Pará (ESEC Grão Pará – Centre); 16 - Estação Ecológica do Grão Pará (ESEC Grão Pará – South); 17 - Floresta Estadual Paru; 18 - Reserva Biológica de Maicuru; 19 - Parque Nacional Montanhas do Tumucumaque 2; 20- Parque Nacional Montanhas do Tumucumaque 4; 21 - Parque Nacional Montanhas do Tumucumaque 1; 22- Parque Nacional Montanhas do Tumucumaque 5; 23- Parque Nacional Montanhas do Tumucumaque 3; 24 - Serra do Navio Region.