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Activity and substrate use of *Bothrops atrox* (Serpentes: Viperidae) in a floodplain forest in the western Brazilian Amazon

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ABSTRACT
Basic information on the natural history of species is essential for studies of evolutionary biology and ecology, in addition to being fundamental for developing conservation strategies. This study aimed to provide information on the activity and substrate use of *Bothrops atrox* in a floodplain forest in the western Brazilian Amazon. With a sampling effort of 816 person-hours of time constrained, nocturnal visual search, 28 observations of 27 individuals were made, of which 16 were adults and 11 were juveniles. The encounter rate of *B. atrox* was one snake every 30 person-hours of searching, and most individuals were recorded during the rainy season. Considering the snake assemblage, *Bothrops atrox* represented 20.8% of the sampled snakes, out of a total of 130 individuals of 21 species, being the second most frequent species. The ecological and morphological differences between the congeneric species *B. atrox* and *B. bilineatus* in this floodplain forest, as well as resource availability, likely influence their local abundance. These factors would also help minimize the probability of interspecific competition between these syntopic species.

Key words: Upper Juruá; Reptilia; Squamata; Pitviper; Common lancehead.

RESUMO
Informações básicas sobre a história natural das espécies são essenciais para estudos de biologia evolutiva e ecologia, além de serem fundamentais para desenvolver estratégias de conservação. Este estudo teve como objetivo fornecer informações sobre a atividade e uso do substrato da serpente *Bothrops atrox* em uma floresta de várzea no oeste da Amazônia brasileira. Com um esforço amostral de 816 horas-pessoa de procura visual limitada por tempo noturna, foram realizadas 28 observações de 27 indivíduos, dos quais 16 eram adultos e 11 juvenis. A taxa de encontro de *B. atrox* foi de uma serpente a cada 30 horas-pessoa de procura, e a maioria dos indivíduos amostrados foi registrada durante a estação chuvosa. *Bothrops atrox* representou 20.8% das serpentes amostradas, de um total de 130 espécimes de 21 espécies, sendo a segunda espécie mais frequente. As diferenças ecológicas e morfológicas entre as espécies congenéricas *B. atrox* e *B. bilineatus* nesta floresta de várzea, bem como a disponibilidade de recursos, provavelmente influenciam a abundância local das espécies. Esses fatores também podem ajudar a minimizar a probabilidade de competição interespecífica entre as duas espécies.

Palavras-chaves: Alto Juruá; Reptilia; Squamata; Víbora; Jararaca.

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Introduction

Snakes are a diverse group of terrestrial vertebrates of the order Squamata, currently with 4145 described species (Uetz *et al.*, 2024). Basic information on the natural history of species is fundamental for studies on evolutionary biology and ecology (Greene, 1997; Martins and Oliveira, 1998) and with the speed at which forest areas in the Amazon are being destroyed, increasing knowledge about the ecology of species is fundamental for future management and conservation actions of species (Martins and Oliveira, 1998).

The family Viperidae is represented by venomous snakes distributed throughout almost all parts of the world, except Australia, the Arctic region of north-central Canada and Antarctica, and extreme southern Argentina (Campbell and Lamar, 2004). The genus *Bothrops* Wagler, 1824, includes 48 species occurring from Mexico to Argentina (Uetz *et al.*, 2024), including Brazil, where 30 species are recorded (Guedes *et al.*, 2023). These snakes are capable of occupying different types of habitats, from forests to anthropized environments (Martins *et al.*, 2001) and are the main species causing snakebites in Brazil (Souza *et al.*, 2022).

Some studies carried out with snakes of this genus *Bothrops* have focused on the activity and habitat use of species (e.g., Sazima, 1988; Oliveira and Martins, 2001; Nogueira *et al.*, 2003; Wasko and Sasa, 2012; Leão *et al.*, 2014; Fonseca *et al.*, 2021). Information on the natural history of species, for example, diet, habitat use, reproduction and period of activity, is fundamental for the implementation and development of conservation strategies for species that occur in a given area (Sawaya *et al.*, 2008). Furthermore, in the case of vipers, this information can help in understanding the circumstances in which snakebites occur (Sazima, 1988; Oliveira and Martins, 2001).

The pit viper *Bothrops atrox* (Linnaeus, 1758) is widely distributed in the Amazon Basin (Nogueira *et al.*, 2019) and the main cause of snakebites in this region (Monteiro *et al.*, 2020). This predominantly nocturnal snake can be found active also during the day and occurs mainly in forested areas, but can also be found in open areas and anthropized environments (Oliveira and Martins, 2001). It has a moderate size, reaching up to 2.1 m in length (Palmeirim *et al.*, 2021). Adults are usually found on the forest floor, while juveniles can be found hunting or moving over vegetation (Martins and Oliveira, 1998; Oliveira and Martins, 2001; Turci *et al.*, 2009).

Due to its wide distribution and relative ease of recording in the wild compared to other vipers in the Amazon, *B. atrox is* a good model for studies on habitat use and activity (Fraga *et al.*, 2013). This study aimed to provide information on the activity and substrate use of the snake *Bothrops atrox* in a floodplain forest in the western Brazilian Amazon, comparing it with the sympatric congeneric species *B. bilineatus* in this location.

Material y methods

Study area

The study was carried out in a floodplain forest in the Japiim Pentecoste Area of Relevant Ecological Interest (ARIE; 07° 37' 29.5 S; 72° 47' 22.6 W), in the municipality of Cruzeiro do Sul, state of Acre, western Brazilian Amazon (Fig. 1). The climate of the region is considered tropical, hot and humid, with an average annual temperature of 24°C. The months of May to October correspond to the driest period of the year and the rainy season occurs between the months of November to April, with annual precipitation varying between 1,140 and 2,700 millimeters and the relative humidity of the air always above 60% (Miranda *et al.*, 2015).

The Japiim Pentecoste ARIE is seasonally flooded by the influence of the Moa River, and the vegetation is characterized as Open Alluvial Forest with Palm Trees (Acre, 2010). The forest canopy has trees with an average height of approximately 20 m, with some emergent species reaching a maximum height of approximately 35 m. The canopy is closed, composed mainly of individuals of the genera *Brosimum* (Moraceae), *Enterolobium* (Fabaceae), and *Virola* (Myristicaceae). Most of the large trees have tabular roots (sapopembas), common in species that occur in unstable soils and are influenced by floods during a period of the year (Turci *et al.*, 2009). The understory has a great abundance of Poaceae, *Astrocaryum* (Arecaceae), small trees, and a low abundance of herbs (Heliconiaceae, Marantaceae, and Costaceae). The vegetation is not very abundant for representatives of the family Arecaceae (Palm trees), with some individuals of the species *Euterpe precatoria*, *Iriartella stenocarpa* and *Bactris* sp. being observed (Turci *et al.*, 2009; Miranda *et al.*, 2015).

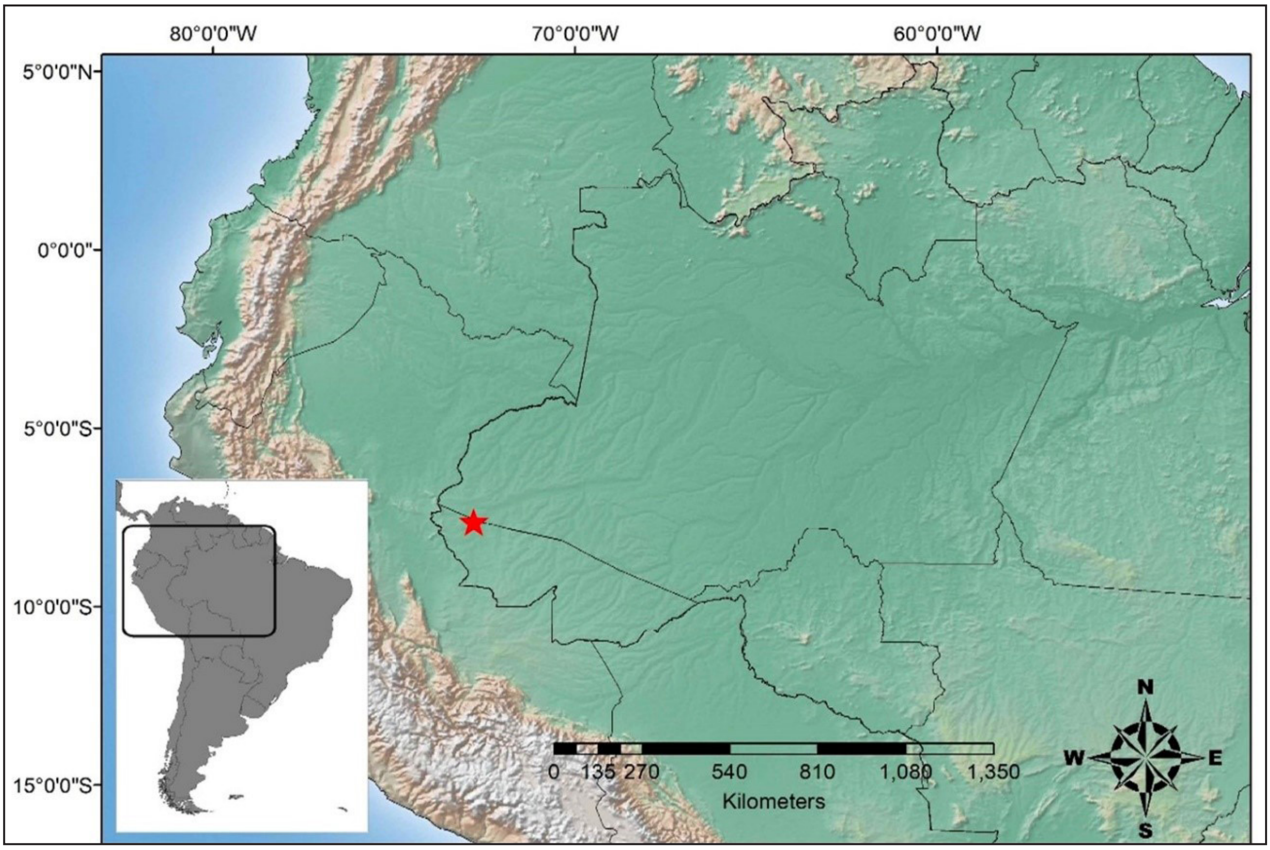

Figure 1. Location of ARIE Japiim Pentecoste in Cruzeiro do Sul, Acre, Brasil.

Data collection

The study was carried out by four researchers on three trails (one 800-m long and two 600-m long) between April 2018 and March 2019. Sampling was carried out at night, from 6:00 p.m. to 10:00 p.m., using the Night-Time Constrained Visual Search (NTCVS) method. This method consists of moving slowly on foot along a transect in search of visibly exposed snakes, and allows the collection of information on the activity and location of the animals in the habitat (Campbell and Christman, 1982).

During the study period, 68 person-hours of NTCVS were carried out per month, totaling 816 person-hours of sampling. On trail I (800 m), sampling was carried out over a three-hour period, with each pair traveling 400 m. Trails II and III were sampled simultaneously by one pair over a four-hour period. On trail I, snakes were not captured, but were only observed for possible records of natural history events, while on trails 2 and 3, all specimens found were collected. Collected specimens (SISBIO collection license 12,178) were deposited in the Herpetological Collection of UFAC Campus Floresta (MC06, MC07, MC28, MC29, MC31, MC32, MC38). In order to obtain more information about the size of *Bothrops atrox* individuals, some recently dead specimens that were occasionally found and also some that caused snakebites that were received at the Juruá Hospital during the research period were used in this study. The total length of each snake was assessed visually by comparison with a scale (Sazima, 1988), and some individuals were retained and measured with a tape measure (Fitch, 1987). The sex of snakes was verified by inserting a blunt probe into the tail and the collected snakes had their sex identified during the fixation process, with or without the eversion of the hemipenis (Fitch, 1987).

When snakes were found, they were observed for five minutes to record their activity. The following information was recorded: time of encounter, substrate used and activity (hunting, moving or resting), inferred from the posture of each observed snake (see Oliveira and Martins, 2001; Turci *et al*., 2009).

Data analysis

The data were organized and subjected to descriptive analysis, which included the calculation of simple and absolute frequencies, percentages, and descriptive measures for the variables studied. The total length (SVL) and tail length (TL) of each snake were measured using a tape measure and they were weighed with portable dynamometers. The snakes were measured and the average total length of the specimens (all individuals, adult males, adult females and juveniles) were calculated using simple arithmetic means. The ages of the specimens were classified following Silva *et al.* (2017) as follows: juvenile males (SVL under 460 mm), juvenile females (SVL under 800 mm), adult males (SVL above 470 mm) and adult females (SVL above 850 mm).

Results

Twenty-eight observations of 27 individuals were made in the floodplain forest, corresponding to 20.8% of the total number of snake specimens recorded (21 species) (See Appendix 1), of which 16 were adults and 11 were juveniles (Fig. 2 and 3). One rediscovered individual was recognized due to natural markings (heterochromia with one eye having dark spots). The sex could be identified in 20 individuals, of which 11 (55%) were males and nine (45%) were females. Seven individuals were collected from trails 2 and 3 (Table 1). The encounter rate was one individual every 30 person-hours or 0.03 snakes per person-hour, with the majority recorded during the rainy season (20 specimens; 74%) and on trail 1, close to two lakes (Fig. 2).

A total of 21 preserved specimens were obtained in this study: seven during visual surveys (36 cm – 131 cm; $\overline{x}$ = 80.2 cm), 11 that caused snakebites (25.5 cm – 165 cm; $\overline{x}$ = 48.13 cm) and three as occasional encounters (66 cm – 161 cm; $\overline{x}$ = 98.5 cm) (Table 1). Smaller specimens (25.5 cm to 50 cm) were responsible for half of the snakebites (54.5%), while during visual surveys they accounted for 37% of the specimens collected and observed.

The size of the specimens recorded in this study (including all methods!) ranged from 25.5 to 165 cm ($\overline{x}$ = 81.2 cm) (n = 41), with juveniles measuring

Figure 2. Distribution of records of *Bothrops atrox* on the three trails during the study period at ARIE Japiim Pentecoste in Cruzeiro do Sul, Acre, Brazil.

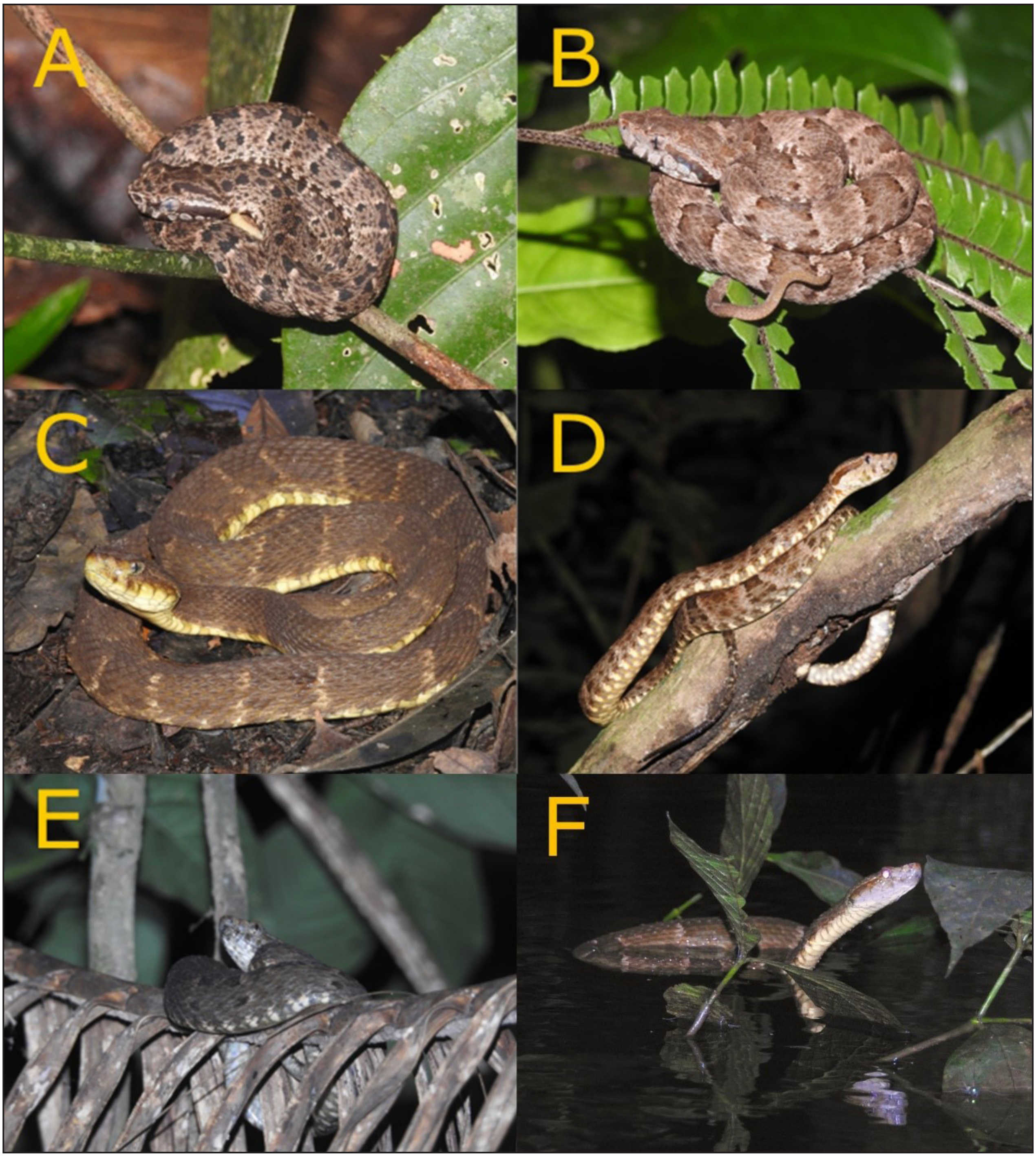

Figure 3. Photographs of some specimens of *Bothrops atrox* in the floodplain forest: A) Juvenile with light-colored tail tip in ambush over vegetation; B) Juvenile with brown tail in ambush over vegetation; C) Adult in ambush on the ground; D) Adult moving over vegetation at a height of 1.5 m; E) Adult in ambush over vegetation at a height of 4.1 m; F) Juvenile moving over water on a flooded trail. Photos A and B: Paulo Bernarde. Photos C – F: Wirven Lima da Fonseca.

from 25.5 to 68.5 cm ($\overline{X}$ = 41.9 cm) (n = 19) and adults measuring from 76 to 165 cm ($\overline{X}$ = 109.1 cm) (n = 22). Adult females ranged from 86 to 165 cm ($\overline{X}$ = 118.7 cm) (n = 9) and adult males from 76 to 130 cm ($\overline{X}$ = 101.9 cm) (n = 13). Analyzing all the specimens collected in this study together with those obtained in occasional encounters and those causing snakebites (Table 1), we observed that females are larger (up to 165 cm) than males (up to 130 cm).

Of the 11 juveniles recorded, seven (63.6%) had a brown tail tip and four (36.4%) had a white tail tip (Fig. 3A, B). The specimens were observed moving

Table 1. Data on sex, size, weight and source of preserved specimens obtained in this study.

Specimen	Total Length (cm)	Tail Length (cm)	Weight (gr)	Source
Juvenile	25.5	3.9	6	Snakebite
Juvenile	28	4.5	7.5	Snakebite
Juvenile	29	4.8	10	Snakebite
Juvenile	32.5	4.9	9.8	Snakebite
Juvenile	35	4.2	8	Snakebite
Juvenile female	36	4.4	13	Visual survey
Juvenile female	38	5.4	20	Snakebite
Juvenile female	47.6	5.9	18	Visual survey
Juvenile female	57.9	7.9	34	Visual survey
Juvenile female	59	9	40	Snakebite
Juvenile female	66	10.6	66	Occasional encounter
Juvenile female	68.5	9.4	100	Occasional encounter
Adult female	86	10.3	88	Visual survey
Adult male	86.2	13.2	120	Visual survey
Adult male	87.5	13	150	Snakebite
Adult female	89	13.3	155	Snakebite
Adult male	100	14.2	155	Snakebite
Adult female	127	18.5	350	Visual survey
Adult female	131	18.8	450	Visual survey
Adult female	161	22	1,100	Occasional encounter
Adult female	165	21.5	1,100	Snakebite

on 16 occasions and in ambush on 12 occasions. Two male individuals were observed in combat behavior (recorded previously by Fonseca *et al.*, 2022).

Moving snakes (n = 12 individuals) were observed on the ground and two, a juvenile (40 cm) and an adult male (100 cm), were recorded moving over vegetation at heights of 0.3 m and 1.5 m, respectively.

Of the juvenile individuals observed in ambush hunting (n = 5), three were recorded on vegetation at heights of 30 to 60 cm and two on the ground. Most (n = 5) of the adult specimens observed in ambush were on the ground. Two adult individuals (76 cm and 100 cm) were observed in ambush on vegetation at heights of 2.5 m and 4.1 m, respectively (Fig. 3).

Discussion

The snake *Bothrops atrox* is usually the most abundant species in studies on snake communities conducted in the Amazon (e.g., Martins and Oliveira, 1998; Frota *et al.*, 2005; Bernarde and Abe, 2006; Rodrigues *et al.*, 2016; Masseli *et al.*, 2019; Turci and Bernarde, 2022), and may correspond to up to 17.5% (Santos-Costa *et al.*, 2015) and 35.9% of the recorded species (Fraga *et al.*, 2011). In this study, *B. atrox* represented 20.8% of the snakes sampled in this assemblage out of a total of 130 specimens of 21 species, ranking second in terms of frequency of encounters, behind *B. bilineatus* with 27% of records (Fonseca *et al.*, 2021). However, only nocturnal searches were carried out, which may have influenced fewer records of other species, especially diurnal ones, that is, the frequency of *B. atrox* may be lower when the entire snake assemblage is considered.

The encounter rate of *Bothrops atrox* was 0.03 snakes per person-hour (one snake every 30 hours of searching), which is higher than that obtained by Martins and Oliveira (1998) in the Ducke Reserve (Manaus, AM), a dryland forest, which was 0.02 snakes per person-hour (one snake every 50 hours of searching) during the time-constrained visual search. One of the advantages of this sampling method is that it allows the encounter rate of a species in a location to be compared with another location or with other sympatric species. The encounter rate of the congeneric *B. bilineatus* in this location was 0.04 snakes per person-hour (one snake every 23 hours of searching), higher than that of *B. atrox* (Fonseca *et al*., 2021). In the study by Turci *et al.* (2009) carried out in this location previously (2008 to 2009), *B. atrox* was also less recorded (0.016 snakes per hour or one every 60 hours of searching) than *B. bilineatus* (0.03 snakes per hour or one every 30 hours of searching). In a study on the snake community also carried out in the Alto Juruá region in a terra firme forest in the Riozinho da Liberdade Extractive Reserve by Turci *et al.* (2021), the encounter rate was 0.005 specimens of *B. atrox* per hour (one snake every 180 hours of searching) and no individuals of *B. bilineatus* were found, indicating a possible difference in the faunal composition of snakes between these ecosystems (terra firme and várzea).

The majority (74%) of *Bothrops atrox* individuals were recorded during the rainy season, as in the previous study by Turci *et al.* (2009), a period in which snakes are most frequently found in studies on snake assemblages in the Amazon (e.g., Martins and Oliveira, 1998; Bernarde and Abe, 2006; Turci and Bernarde, 2022). However, the other viper that occurs in sympatry in this floodplain forest, *B. bilineatus*, is more frequently found during the dry season (75.9% of encounters) (Fonseca *et al*., 2021). The higher encounter rate of *B. atrox* in the rainy season also coincides with the greatest abundance of small mammals during this period (68.8%; Silva *et al*., 2020) and also with the greatest reproductive activity of anuran amphibians in this location (Miranda *et al*., 2015). However, the abundance of amphibians in the rainy season recorded on the trails is only slightly higher (52.8%) than during the dry season (47.2%) (Silva *et al*., 2020), which could explain the greater occurrence of *B. bilineatus* during the less rainy months in this location (Fonseca *et al*., 2021).

The greater abundance and activity of *B. atrox* during the rainy season also contributes to the increase in the number of snakebites with this species during this period in this region (Mota-da-Silva *et al*., 2019). Newborns of *B. atrox* also occur in the rainy season (Oliveira and Martins, 2001), which also contributes to the greater encounter of individuals of this species during this period and perhaps explains the occurrence of half of the cases of snakebites with juveniles (smaller than 50 cm in length) (Mota-da-Silva *et al*., 2019). Despite the greater abundance of newborns, as reported by Fraga *et al.* (2013) and Silva *et al.* (2020), smaller specimens of *B. atrox* are more difficult for researchers to detect during searches in the forests due to their small size. This would be another reason that could explain the greater number of snakebites involving juveniles (Mota-da-Silva *et al*., 2019).

Bothrops atrox has a maximum recorded length of 2.1 m (Palmeirim *et al*., 2021), presenting notable sexual dimorphism due to the larger size of females (e.g., Silva *et al*., 2017; Silva *et al*., 2019), which was also found in this study with the largest specimens recorded corresponding to females measuring 1.61 m and 1.65 m. Specimens of *B. bilineatus* are relatively smaller (up to 75.8 cm), also presenting sexual dimorphism with males smaller ($\overline{X}$ = 58.7 cm) than females ($\overline{X}$ = 59.2 cm) (Fonseca *et al*., 2019).

Most juveniles of *B. atrox* had a light-colored tail tip, which is used as a tail luring strategy during ambush (Martins and Oliveira, 1998). As observed for *B. jararaca* in southeastern Brazil (Sazima, 1991), some juveniles did not have a tail tip with a coloration distinct from the rest of the body. No juveniles were observed performing tail luring, a hunting tactic that is frequently observed in juveniles and adults of *B. bilineatus* in this location (Fonseca *et al*., 2019). In some species of *Bothrops* (e.g., *B. atrox*, *B. jararaca*) juveniles lose the light tail tip and caudal luring behavior when they become adults and begin to prey on rodents rather than amphibians (e.g., Sazima, 1992; Oliveira and Martins, 2001) Adult individuals of *B. bilineatus* continue to have the tip of the tail with a coloration distinct from the rest of the body and to perform caudal luring, and continue to prey on amphibians besides small mammals (Fonseca *et al*., 2019; 2021).

Three of the five juveniles of *B. atrox* were observed in ambush on vegetation, as reported in other studies (e.g., Oliveira and Martins, 2001; Turci *et al*., 2009). The greater use of vegetation during hunting by juveniles than adults is probably associated with the availability of small anurans in this microhabitat (e.g., *Pristimantis fenestratus*) (Oliveira and Martins, 2001) and also as a way to avoid predators that move across the forest floor (Martins, 1993), such as tarantulas that can prey on them (Almeida *et al*., 2019). Adult individuals are observed less frequently than juveniles on vegetation (Oliveira and Martins, 2001). Oliveira and Martins (2001) observed two inactive individuals at heights of 1.2 and 1.3 m and Melo-Sampaio and Maciel (2018) observed an individual in hunting activity at a height of 4 m on a palm leaf. The two adult individuals observed in hunting activity in this study on vegetation (2.5 and 4.1 m tall) were during the rainy season when the forest was flooded, and this situation may influence this snake to occur in the arboreal substrate during this period when a large part of the forest is flooded.

In this study, we observed that time constrained visual searches allow the comparison of the relative abundance of sympatric snake species and also allows comparison with other studies that used this method in other locations. Two species of vipers were the most abundant snakes in this floodplain forest, with *B. atrox* being the second most frequent, unlike other studies in the Amazon where it was the most abundant. The two species of *Bothrops* in this study differ in seasonal frequency – with *B. atrox* being more frequent during the rainy season and *B. bilineatus* in the dry season –, in size (individuals of *B. atrox* are larger) and in substrate use (adult individuals of *B. atrox* occur mainly on the ground and offspring also in low vegetation, while *B. bilineatus* is arboreal). These differences between these two congeneric sympatric species, among other factors (e.g., availability of resources), should influence their abundance in this location, potentially minimizing the probability of interspecific competition.

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Appendix I

Snakes registered in the Japiim Pentecoste Area of Relevant Ecological Interest (ARIE; 07° 37' 29.5 S; 72° 47' 22.6 W), in the municipality of Cruzeiro do Sul, state of Acre, western Brazilian Amazon between April 2018 and March 2019.

TÁXON	AMOUNT
BOIDAE	
Corallus hortulana (Linnaeus, 1758)	1
Epicrates cenchria (Linnaeus, 1758)	2
COLUBRIDAE	
Chironius carinatus (Wied, 1820)	11
Leptophis nigromarginatus (Günther, 1866)	1
Phrynonax polylepis (Peters, 1867)	1

DIPSADIDAE	
Atractus sp.	2
Dipsas catesbyi (Sentzen, 1796)	1
Dipsas indica indica Laurenti, 1768	1
Erythrolamprus reginae (Linnaeus, 1758)	1
Erythrolamprus typhlus typhlus (Linnaeus, 1758)	1
Imantodes cenchoa (Linnaeus, 1758)	14
Leptodeira annulata annulata (Linnaeus, 1758)	1
Helicops angulatus (Linnaeus, 1758)	6
Helicops hagmanni Roux, 1910	1
Oxyrhopus melanogenys melanogenys (Tschudi, 1845)	5
Oxyrhopus petolarius digitalis (Reuss, 1834)	1
Xenoxybelis argenteus (Daudin, 1803)	11
ELAPIDAE	
Micrurus lemniscatus (Linnaeus, 1758)	2
Micrurus surinamensis (Cuvier, 1817)	5
VIPERIDAE	
Bothrops atrox (Linnaeus, 1758)	27
Bothrops bilineatus smaragdinus Hoge, 1966	35
TOTAL	**130**

Trabajo

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Antecedentes ecológicos de la Lagartija de Schmidt *Liolaemus schmidti* (Marx, 1960) (Squamata, Liolaemidae) en el altiplano de la Región de Tarapacá, Chile

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ABSTRACT
The ecological background of abundance, environment use, microhabitat use, and escape behavior of *Liolaemus schmidti* in the altiplano of the Tarapacá Region, Chile, is described. This species shows greater frequency and abundance in terrestrial environments with grasslands, followed by shrublands. In addition, it is primarily terrestrial and frequently uses the escape behavior of hiding under bushes. These antecedents contribute to the scarce information documented for this species, whose range is in Chile and Bolivia.

Key words: Abundance; Chile; Grasslands; Lizards; Microhabitat.

RESUMEN
Se describen antecedentes ecológicos de abundancia, uso de ambiente, uso de microhábitat y conducta de escape de *Liolaemus schmidti* en el altiplano de la Región de Tarapacá, Chile. Esta especie muestra mayor frecuencia y abundancia en ambientes terrestres con coironales, seguido por matorrales. Además, es mayoritariamente terrícola y utiliza frecuentemente la conducta de escape de ocultarse bajo arbustos. Estos antecedentes aportan a la escasa información documentada para esta especie con distribución conocida en Chile y Bolivia.

Palabras claves: Abundancia; Chile; Coironales; Lagartijas; Microhábitat.

Introducción

La lagartija de Schmidt *Liolaemus schmidti* (Marx, 1960) es una especie de lagartija perteneciente al subgénero *Eulaemus*, a la sección de *L. montanus*, grupo de *L. montanus* en el clado de *L. multicolor* (Abdala *et al*., 2021c). Fue originalmente descrita dentro del género *Ctenoblepharys* (Marx, 1960), y posteriormente sinonimizada dentro de *Liolaemus* (Laurent, 1984), pero cuya confusión taxonómica la ha asociado históricamente a varias especies, como *L. andinus, L. pantherinus* y *L. islugensis* (Abdala *et al*., 2021d; Pincheira-Donoso y Núñez, 2005; Lobo *et al*., 2010; Ruiz de Gamboa y Ortiz, 2020). De ellas, *L. andinus* y *L. pantherinus* se reconocen actualmente como especies válidas (Ruiz de Gamboa y Ortiz, 2020; Abdala *et al.,* 2021b, c, d), mientras que *L. islugensis* fue considerada sinónimo junior de *L. schmidti*, por Langstroth (2021), propuesta aceptada por Abdala *et al*. (2021a) y Aguilar-Kirigin *et al*. (2021).

En relación con su estado de conservación, *Liolaemus schmidti* se cataloga como una especie de Preocupación Menor a nivel internacional (Núñez *et al*., 2017), en tanto que en Chile su estado de conservación a nivel nacional no se ha clarificado, ya que en el periodo de su evaluación, estaba asignado

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a *L. andinus* (MMA, 2013), mientras que como *L. islugensis* (antes de ser sinonimizada) se consideraba como en Preocupación Menor (Fauna Nativa-MMA, 2018; Ruiz de Gamboa, 2020), por lo que requiere de una nueva evaluación, considerando su estatus taxonómico formal.

Liolaemus schmidti habita en Bolivia y Chile, y en Chile se distribuye desde las Termas de Polloquere (Región de Arica y Parinacota) hasta el Volcán Tatio (Región de Antofagasta), con 32 localidades conocidas, entre 3685 (Salar de Carcote) y 4390 m snm (Ujina, ver revisión en Mella, 2025). En Bolivia, esta especie se ha registrado en el Departamento de Potosí, en la Provincia Antonio Quijarro, en los alrededores de Uyuni, en la provincia Nor Lípez, en las cercanías del Volcán Ollagüe, y en la Provincia Sur Lípez, en Pena Barrosa y en la Reserva Nacional de Fauna Andina Eduardo Avaroa (Aguilar-Kirigin, 2021; Aguilar-Kirigin *et al.*, 2021).

En Chile, esta especie habita en ambientes de matorral bajo altoandino dominado por *Parastrephia lepidophylla-P. quadrangularis* y *Fabiana ramulosa-Diplostephium meyenii* (Luebert y Pliscoff, 2107), con baja cobertura arbustiva (Mella, 2017), mientras que en Bolivia se ha asociado a varios ambientes como matorral de resinosas, tolares, lampayales, cactáceas, pajonales, praderas halofíticas, bofedales y arenales en la Puna desértica de la Cordillera Occidental (Aguilar-Kirigin, 2021).

De *Liolaemus schmidti* se conocen escasos antecedentes ecológicos, con estudios realizados en Chile, como aspectos termorregulatorios y período de actividad diaria (Marquet *et al.*, 1989, como *L. islugensis*) alimentación (Ortiz y Marquet, 1987, como *L. islugensis*) y abundancia en distintos ambientes (Mella y Venegas, 2019, como *L. pantherinus*). En Bolivia, no existen estudios ecológicos de la especie (Luis F. Pacheco y Alvaro Aguilar Kirigin, comunicación personal).

El objetivo de este estudio es proporcionar antecedentes ecológicos básicos de *Liolaemus schmidti*, con datos cuantitativos sobre su abundancia en distintos ambientes, uso de ambientes, uso de microhábitats y conductas de escape, en el altiplano de la Región de Tarapacá, Chile.

Materiales y métodos

En una prospección faunística realizada en el altiplano de la Región de Tarapacá, Chile, en febrero de 2023, se realizó un muestreo de *Liolaemus schmidti*. El estudio se realizó en tres días, entre las 1000 y las 1700 horas.

Específicamente, se recorrieron cerca de 15 km pedestres, en la planicie de altura entre el Salar de Lagunillas (19°56’ S, 68°50’ O, 4026 m snm), hasta las cercanías del poblado de Lirima (19°52’ S, 68°51’ O, 4060 m snm), en el altiplano de la Región de Tarapacá, Chile. La zona de estudio se ubica en la formación vegetal de Matorral Desértico, abarcando el piso vegetacional de Matorral bajo tropical andino (Luebert y Pliscoff, 2017), y el recorrido incluye ambientes de sustrato terroso-arenoso, con cobertura vegetacional baja (menos de 30%), dominada por parches de coironales (pajonales de altura, *Festuca orthophylla*), y/o arbustos como *Fabiana ramulosa* y *Parastrephia* spp. (Fig. 1).

En el área de estudio se realizaron 14 transectos pedestres de 1000 m de longitud y 20 m de ancho (2.0 ha de superficie), donde se registró: (a) el número observado de ejemplares de *Liolaemus schmidti* (para cuantificar frecuencia y abundancia relativas); (b) su sexo, ya que es una especie con evidente dimorfismo sexual (Mella, 2017); (c) su edad (en base al tamaño corporal, estimado visualmente), en categorías:

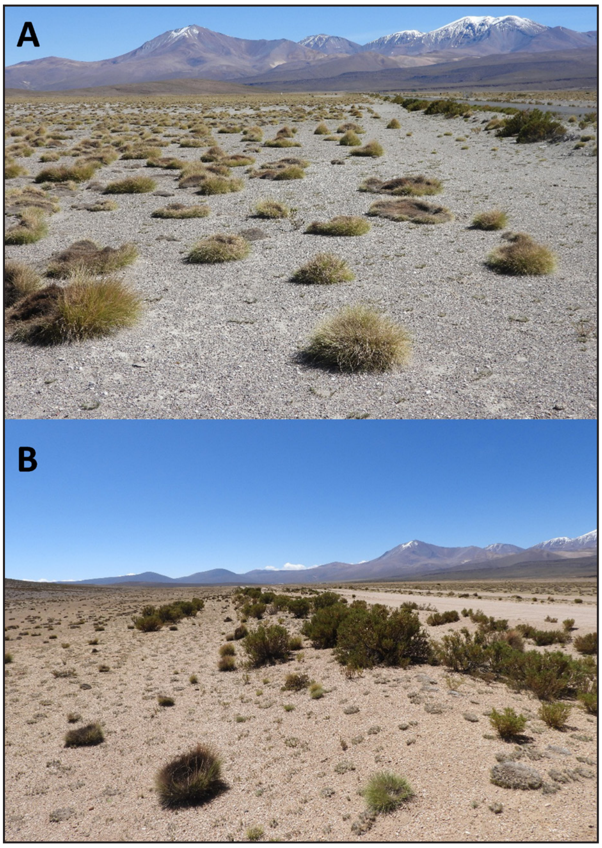

Figura 1. Vistas panorámicas de los ambientes muestreados en la Región de Tarapacá, Chile: (A) Coironal; (B) Matorral.

juveniles (menos de 8 cm de longitud total), subadultos (entre 8 a 12 cm) y adultos (más de 12 cm; Mella, 2017; Fig. 2); (d) su uso de microhábitat, en categorías de: tierra (incluyendo arena), roca, sobre coirón, bajo arbusto y bajo coirón; y (e) la conducta de escape, considerando las siguientes categorías de ocultarse: cuevas de Tuco tuco (*Ctenomys fulvus*), cuevas propias (en suelo desnudo), bajo piedra,

Figura 2. Ejemplar juvenil (A) y adulto, macho (B) de *Liolaemus schmidti*. La barra negra representa aproximadamente 5 cm.

bajo roca, bajo coirón y bajo arbusto (Fig. 3). Se debe entender que lo que se registra es la conducta primaria de escape, ya que algunas categorías no son necesariamente excluyentes (p. ej. un ejemplar puede ocultarse primero bajo piedra y luego esconderse en cueva, Fig 3B).

Los transectos fueron recorridos en un solo sentido (de sur a norte), de modo que cada observación corresponde a un individuo, sin réplicas ni reconteos. La frecuencia relativa se calculó como el cociente entre el número de transectos con registro de al menos un individuo en relación a los transectos totales (en %), y la abundancia relativa se estimó como el número medio de individuos por transecto (por cada tipo de ambiente).

Resultados

En el total de transectos se registraron 116 ejemplares de *L. schmidti*, con 14 machos, 29 hembras, 33 adultos sin sexar, siete subadultos y 33 juveniles. La proporción M:H fue de 0.48.

La frecuencia de *L. schmidti* fue alta, ya que se registraron ejemplares en 11 de los 14 transectos (78.6%). Por otra parte, la abundancia fue variable, dependiendo del tipo de ambiente muestreado. Así, la abundancia fue mayor en el ambiente de Coironal, con una media de 14.0 individuos/transecto, seguido por el ambiente de Matorral/Coironal, con 11.3 individuos/transecto, y por el Matorral, con 5.5 individuos/transecto, mientras que en los otros ambientes de Matorral la abundancia fue nula o muy baja, con un máximo de un individuo/transecto (Tabla 1).

El tipo de microhábitat más utilizado fue el suelo (arena o tierra), con 69.8% (81 de 116), seguido por la categoría bajo arbusto (21.6%), en tanto que el resto de los microhábitats son poco utilizados: sobre coirón, bajo coirón y sobre roca (10 registros en total; 8.6%, Fig. 4A).

En base al total de registros de escape, la conducta más frecuente fue el ocultarse bajo arbusto, con 73.3% (85 de 116), seguido por ocultarse bajo coirón (19.0%), mientras que las conductas de escape menos frecuentes fueron esconderse en cueva de Tuco tuco, en cueva propia, bajo piedra y bajo roca (con nueve registros en total; 7.7%; Fig. 4B).

La única otra especie de reptil registrado fue *L. jamesi* Boulenger, 1891, con un total de 12 ejemplares observados, por lo que su abundancia relativa fue de 9.4%, en tanto que la abundancia relativa de *L. schmidti* alcanzó el 90.6%.

Discusión y Conclusión

En el área de estudio, *L. schmidti* es claramente la especie de reptil dominante, con un 90.6% de abundancia relativa. Lo anterior puede relacionarse con varios factores, como la altitud (cercano a los 4000 m snm), los ambientes muestreados, con baja cobertura vegetacional y con poca cobertura rocosa, factores favorables para la presencia de *L. schmidti*. Así, en áreas cercanas, fuera de los transectos, y en ambientes con mayor dominancia de rocas y matorrales, se observó mayor abundancia de *L. jamesi* (especie saxícola; Mella, 2017; Abdala y Valladares, 2021), y se registró además la presencia de *L. puna* Lobo & Espinoza 2004, en tanto que en ambientes de menor altitud (también con roqueríos y matorrales), se observó la presencia de *Microlophus theresioides* Donoso Barros 1966.

Por otra parte, la frecuencia y abundancia de *L. schmidti* parece variar con el tipo y la cobertura vegetacional, además del tipo de sustrato, ya que fue mayor en los ambientes de Coironal y Matorral-Coironal de baja cobertura y con sustrato terroso, en tanto que fue menor en los matorrales densos, o matorrales con sustrato pedregoso y con roqueríos. Lo anterior concuerda con lo documentado por Mella y Venegas (2019) para esta especie (adscrita en dicho estudio como *L. pantherinus*), quienes detallan que utiliza tres ambientes: Herbazal-Pajonal (análoga a Coironal), Matorral y Quebrada (este último ambiente no presente en nuestro estudio), y no se encuentra en humedales ni en roqueríos. Aunque el número de transectos por ambiente se pudiera considerar bajo, como éstos son de gran extensión (1 km de longitud), sumado al alto número de ejemplares observados (n = 116), los resultados se consideran representativos de la frecuencia y abundancia de la especie. Así, comparada con otros reptiles presentes en la Región de Tarapacá (Bonacic *et al*., 2015), *L. schmidti* no es especialista en su uso de ambientes, a diferencia de *Microlophus quadrivitattus* (Tschudi, 1845), que sólo se encuentra en ambientes rocosos costeros, pero tampoco es generalista, al ocupar prácticamente todos los ambientes disponibles, como ocurre con *M. theresioides* Donoso-Barros, 1966 y *L. jamesi* (Mella y Venegas, 2019).

Los resultados de frecuencia de este estudio son mayores a lo registrado por Mella y Venegas (2019), quienes evaluaron en centenares de puntos muestreados de la Región de Tarapacá. *Liolaemus schmidti* es una especie poco frecuente (estacionalmente), variando entre 0% a un máximo de 4.07%,

Figura 3. Conducta de escape de *Liolaemus schmidti*: A) ejemplar macho a la entrada de cueva bajo coirón, donde se oculta posteriormente, y B) ejemplar oculto bajo piedra (recuadro superior derecho muestra la piedra en su posición natural, antes de removerla y encontrar al ejemplar oculto debajo).

valores mucho menores a lo registrado en nuestro estudio (78.6%). La diferencia se explica por el contexto espacial diferente: en Mella y Venegas (2019) se incluye una gran variedad de ambientes dentro de la Región de Tarapacá, con una amplia variación altitudinal (23 a 3534 m snm), abarcando altitudes y ambientes donde generalmente *L. schmidti* no se encuentra. En tanto, este estudio se acotó a un pequeño rango altitudinal, cercano a los 4000 m snm, que es donde justamente donde habita *L. schmidti*, ya que es una especie básicamente andina, registrada en Bolivia entre los 3687 a 4500 m snm

Tabla 1. Abundancia de *Liolaemus schmidti* por tipo de ambiente, Altiplano de Región de Tarapacá, Chile (n = tamaño muestral).

Ambientes	**Abundancia** (N° individuos/transecto)
Coironal (*n* = 3)	14.0 (12-17)
Matorral (*n* = 4)	5.5 (3-10)
Matorral/coironal (*n* = 3)	11.3 (3-18)
Matorral/coironal/pedregal (*n* = 1)	0
Matorral Denso (*n* = 2)	0.5 (0-1)
Matorral/Roqueríos (*n* = 1)	0

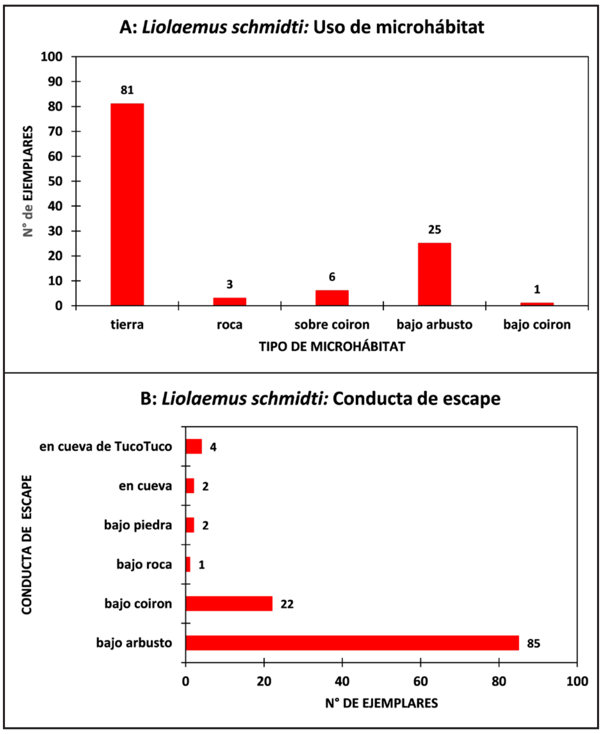

Figura 4. (A) Uso de microhábitat y (B) Conducta de escape de *Liolaemus schmidti*, Región de Tarapacá, Chile

(Aguilar-Kirigin, 2021), en tanto que en Chile se ha registrado entre los 3685 (Salar de Carcote) a 4390 m snm (Ujina, ver revisión en Mella, 2025).

En cuanto a la abundancia relativa, *L. schmidti* varió dependiendo del tipo de ambiente, con mayores abundancias en el Coironal (con una media de 14.0 individuos/transecto), seguido por el Matorral (11.3 individuos/transecto). Dichos valores son comparables (al menos en términos de orden), a los obtenidos por Mella y Venegas (2019), quienes documentan que esta especie también posee la mayor abundancia en ambientes de Herbazal/Pajonal (análogo a Coironal), con 0.15 individuos/transecto, seguido por el Matorral (con 0.05 individuos/transecto). Como la longitud de los transectos en ambos estudios fue diferente (200 m x 20 m = 0.4 ha, en Mella y Venegas (2019), y 2.0 ha en este estudio), nuestros datos fueron estandarizados, obteniendo una abundancia de 2.8 individuos/transecto en Coironal y 2.26 individuos/transecto en Matorral, valores igualmente superiores a los obtenidos por Mella y Venegas (2019). Las diferencias se pueden explicar porque nuestro estudio se llevó a cabo en la altitud en la que habita *L. schmidti*. En todo caso, para poder comparar fácilmente las abundancias relativas en muestreo de reptiles, se sugiere estandarizar las abundancias a los individuos contabilizados por unidad de superficie (p. ej. ha), y por tipo de ambiente. Así, las abundancias de *L. schmidti* son mayores en Coironal (7.0 individuos/ha), seguido por Matorral (5.65 individuos/ha). Estos resultados de abundancia diferencial en distintos ambientes pudieran servir de base para comparar con estudios de *L. schimdti* en Bolivia (sin antecedentes conocidos de abundancia por ambiente). Por otra parte, estos valores cuantitativos de abundancia son un aporte al escaso conocimiento de dicho parámetro ecológico básico de esta especie en particular y de los reptiles chilenos en general, lo que debe ser priorizado en los estudios futuros, como lo sugieren Moya *et al.* (2024).

En términos de abundancia estacional, como nuestro muestreo se efectuó en verano (febrero), dicha estación coincide con ser la más adecuada para el muestreo de reptiles en la zona, pues es donde se registran los mayores valores de abundancia, como lo documentan Mella y Venegas (2019). Así, la abundancia relativa de *L. schmidti* fue máxima en verano 2015 (4.07%, 10 de 246 transectos) y mínima en invierno, sin registro de ejemplares. Cabe mencionar que en invierno, gran parte de nuestra área de estudio se encuentra cubierta de nieve, y las bajas temperaturas no permiten la actividad de reptiles (observación personal).

Si bien no se pudo documentar rigurosamente el periodo de actividad (ya que el muestreo fue diferenciado a distintas horas), se registraron ejemplares en todo el periodo de muestreo (1000 a las 1700 h), y el máximo registro de ejemplares fue de 45 individuos (38.8% del total) entre las 1000 a las 1100 h (en cuatro transectos), en tanto que entre las 1100 a las 1500 h, se registraron entre 10 a 20 ejemplares/hora (con dos transectos/hora). Después de las 1500 h se registraron pocos ejemplares (menos de cuatro individuos/hora, aunque con sólo un transecto/hora). Los datos anteriores apoyan la idea que *L. schmidti* tiene un patrón de actividad unimodal, más concentrado en la mañana, como lo señalan Marquet *et al.* (1989, como *L. islugensis*), similar a lo registrado para otras especies andinas como *L. jamesi*, *L. ornatus* y *L. puna* (Marquet *et al.*, 1989). Antes de las 1000 h y después de las 1700 h (periodos fuera de nuestro muestreo) se registran ejemplares activos, sobre todo en verano, como lo documentan Marquet *et al.* (1989).

En cuanto al uso de microhábitat, *L. schmidti* muestra clara dominancia por el uso de la tierra (incluyendo sustratos arenosos, 69.8% de los registros), lo que avalaría su conducta como especie de hábitos predominantemente terrícolas y arenícolas (Mella, 2017 como *L. pantherinus*, Aguilar-Kirigin, 2021). Aparentemente, los sustratos blandos, como el terroso y/o arenoso, favorecerían a esta especie, la que puede excavar cuevas bajo los arbustos, bajo los coirones o incluso en suelo desnudo (como se observó en este estudio). A pesar de lo anterior, cabe considerar que no se pudo determinar preferencia por los distintos microhábitats, ya que no se cuantificó la disponibilidad de éstos. Comparada con otros reptiles presentes en la Región, los hábitos terrícolas y/o arenícolas dominantes de *L. schmidti* concuerdan con la conducta de *Phyllodactylus gerrhopygus* (Wiegmann, 1835) y *L. stolzmanni* (Steindachner, 1891), ambas especies psamófilas (Bonacic *et al.*, 2015; Donoso-Barros, 1966; Mella, 2017).

En cuanto a las conductas de escape, *L. schmidti* mostró también clara dominancia por ocultarse bajo arbustos (con 73.3%), seguido por esconderse bajo los coironales (19%), siendo las menos frecuentes el esconderse en cuevas (propias o de Tuco tuco), y ocultarse bajo piedras o rocas (aunque nuevamente, las conductas de escape menos frecuentes no indican necesariamente evasión, al no medirse disponibilidad de refugios). El ocultarse bajo arbustos concuerda con lo indicado por Aguilar-Kirigin (2021), quien señala que esta especie se refugia en cavidades bajo los arbustos excavadas por roedores. Es posible que dichas respuestas sean consecuencia de la disponibilidad de los diferentes micrositios y su cercanía: lo más probable es que los animales usen el primer escondite disponible. Asociado a lo anterior, es interesante mencionar que en este estudio, los pocos registros de ocultarse en cuevas de Tuco tuco (n = 4) coinciden con un pequeño parche de los transectos muestreados en que efectivamente se registró una colonia de *Ctenomys fulvus*. Es altamente probable que habiendo mayor disponibilidad de cuevas de Tuco tuco, *L. schimdti* muestre mayor uso por dichos refugios. Al parecer, *L. schmidti* posee un espectro más bien acotado de conductas de escape, a diferencia de otras especies de reptiles presentes en la zona, como *M. theresioides*, quien muestra una variada gama de estrategias escapatorias, como ocultarse bajo rocas, en cuevas, en grietas, incluso subiendo paredes verticales y árboles, como tamarugos (Mella, 2022).

Este estudio es un aporte cuantitativo al escaso conocimiento ecológico y de historia natural de esta especie presente en Bolivia y Chile, ya que la mayor parte de la historia natural conocida históricamente corresponde a notas cualitativas y anecdóticas.

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Nota

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Amphibians of caves in Serra do Ramalho karst area, a remarkable region of subterranean fauna in Brazil

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ABSTRACT
Serra do Ramalho karst area is part of the Bambuí group, the largest geomorphological unit of Brazil. It is in southwestern state of Bahia, and extends over the municipalities of Carinhanha, Feira da Mata, Coribe, and Serra do Ramalho. We inspected 34 caves of Serra do Ramalho karst area, actively looking for amphibians. We were able to find amphibians in 12 caves. We sequenced some of the specimens found for the barcode mitochondrial *16S* to confirm identifications. We found 13 species of amphibians, all anurans: *Rhinella granulosa*, *Rhinella mirandaribeiroi*, *Oreobates remotus*, *Boana crepitans*, *Scinax* sp. 26, *Scinax x-signatus*, *Leptodactylus macrosternum*, *L. troglodytes*, *L. vastus*, *Physalaemus cicada*, *P. cuvieri*, *P. albifrons*, and *Odontophrynus carvalhoi*. As far as it is possible to say, these amphibians are using the cave to daily and seasonal retreat, where they can possibly protect themselves from the drought and heat of Caatinga during the day.

Key Words: Anurans; Cerrado-Caatinga; Limestone caves; Refugia; Bahia state

The Bambuí group is the largest geomorphological unit of Brazil (Assis *et al.*, 2023; Auler and Piló, 2015; Campos-Filho *et al.*, 2016), sheltering one of the most rich subterranean biodiversity of the country (Gallão and Bichuette, 2018), occupying part of the states of Bahia, Goiás, Minas Gerais, and Tocantins (Auler, 2002; Gallão and Bichuette, 2018). It is formed by carbonate-siliciclastic rocks dated from Late Proterozoic, around 950–600 My (Dardenne *et al.*, 1986, apud Campos-Filho *et al.*, 2016).

Serra do Ramalho karst area is part of the Bambuí group and is located in the Middle Rio São Francisco basin, in southwestern state of Bahia (Mattox *et al.*, 2008). It is situated in an ecotone of Caatinga and Cerrado phytophysionogmies. The climate is tropical dry, with a dry winter (March to October) and average annual precipitation of 640 mm ("Aw" type of Köppen-Geiger classification, Beck *et al.*, 2018). The lithology of the Serra do Ramalho karst area is limestone, and includes the municipalities of Carinhanha, Cocos, Feira da Mata, Coribe, and Serra do Ramalho, all in state of Bahia (Rubbioli *et al.*, 2019).

The fauna of the caves of Serra do Ramalho is well characterized, with examples of studies with Actinopterygii (Bichuette and Rizzato, 2012; Bichuette and Trajano, 2005; Mattox *et al.*, 2008; Trajano *et al.*, 2009), Arachnida (Assis *et al.*, 2021; Assis *et al.*, 2023;

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Baptista and Giupponi, 2002; Bertani *et al.*, 2018; Brescovit *et al.*, 2023), Crustacea (Fernandes *et al.*, 2019), Malacostraca (Campos-Filho *et al.*, 2022a; Campos-Filho *et al.*, 2022b; Cardoso *et al.*, 2022, 2023), Insecta (Cordeiro *et al.*, 2023; Lamas *et al.*, 2023; Oliveira *et al.*, 2023; Pellegrini *et al.*, 2022), and Mollusca (Salvador and Bichuette, 2024; Salvador *et al.*, 2023; Simone, 2012, 2013).

Amphibians in Brazilian caves are barely known, but they are very common, especially in the semi-arid ecosystems, where caves constitute a refugee from hot and dry climate. Considering complete publications about amphibians in Brazilian caves, there are reports in faunal lists (Dessen *et al.*, 1980; Pinto-da-Rocha, 1995; Trajano, 1987; Trajano and Bichuette, 2006; Trajano and Gnaspini-Netto, 1991), species descriptions (Canedo *et al.*, 2012; Pansonato *et al.*, 2020; Vaz-Silva *et al.*, 2018), fossil descriptions (Barcelos *et al.*, 2020; Barcelos and Verdade, 2022), distribution extension (Lima *et al.*, 2012; Motta *et al.*, 2020), auto-ecology (Andrade *et al.*, 2021), anuran richness and community ecology studies (Matavelli *et al.*, 2015; Santos *et al.*, 2022), a commentary (Sperandei *et al.*, 2023), and a distribution review (Sperandei *et al.*, 2024).

Although Serra do Ramalho caves are well known (Trajano and Bichuette, 2010a), there are no amphibian surveys for their caves. In this study, we aimed to invent the amphibians present in Serra do Ramalho karst area. We also briefly comment on amphibian occurrences in caves.

We conducted fieldwork in 34 caves in Serra do Ramalho region (some caves in Figs. 1 and 2, Appendix A1). We searched all the accessible areas of the caves, such as unconsolidated substrates, leaf litter, trunk debris, crevices in the walls, and water bodies, during daytime, mostly in the dry season. We manually collected most of the amphibians, but some were only photographed. We euthanized the collected amphibians with 5 % lidocaine. We removed fingertips, toe tips, or whole feet as tissue samples, and stored them in 100 % ethanol. Then we fixed the specimens in 10 % formalin or 70 % ethanol. The specimens are stored in 70 % ethanol in the collection of the Laboratório de Estudos Subterrâneos (LES, Universidade Federal de São Carlos, São Carlos, SP, Brazil; curator: M.E. Bichuette) and the Coleção de Anfíbios Célio F. B. Haddad (CFBH, Universidade Estadual Paulista, Rio Claro, SP, Brazil; curator: C.F.B. Haddad). The collections were approved by MMA-SISBio collection permit number 28992.

Since there are no amphibian species lists for the Serra do Ramalho karst region, we used specimens from the CFBH for taxonomic comparisons. To help with identification, we also performed a barcode analysis, described below.

From the tissue samples, we extracted total DNA with a protocol of ammonium acetate (adapted by Lyra *et al.*, 2017). With the total DNA, we directly amplified the part 3' of ribosomal *16S* rRNA (herein called *16S*-ARBR), with primers 16Sar-L and 16Sbr-H (Palumbi *et al.*, 2002). To perform the PCR, we used 10.0 µL per sample of Taq DNA Polymerase Master Mix RED (©Ampliqon), 10.0 µL per sample of autoclaved distilled water, 0.4 µL of each primer, and 1.0 µL of the concentrated total DNA. The temperature program of the PCR consisted of an initial denaturation step of 95 °C for three minutes; 40 cycles of 95 °C for 20 seconds, 50 °C for 20 seconds, and 68 °C for one minute; and a final extension of 68 °C for three minutes. We checked the amplicons with agarose gel 1 % in electrophoresis, and we purified the positive amplicons with Exonuclease and Alkaline Phosphatase. We sequenced the positive amplicons in only one direction (the forward one) at Macrogen Inc. (Seoul, South Korea). We manually trimmed each individual's chromatogram in Geneious (Dotmatics, 2023). To associate each individual with the most likely species, we used the selected fragment *16S*-ARBR in a BLAST® search (NCBI *et al.*, 2019) in Geneious (Dotmatics, 2023) in October, 2023. The GenBank accession numbers will be provided upon acceptance of the manuscript.

Twelve out of the 34 studied caves presented amphibians (Fig. 3): Gruna Vila Nova, Gruna Google, Gruna do Cocho, Gruna do Domingão, Gruna da Altina and Gruna Bem Bom (Carinhanha); Gruna da Cacimbinha, Gruna Chico Pernambuco and Gruna Mamona (Coribe); Gruna Serra Solta II (Serra do Ramalho); Gruna do Engrunado and Gruna da Boca da Lapa (Feira da Mata). The amphibians found were all anurans, and correspond to 13 species distributed in five families: *Rhinella granulosa* (Spix, 1824), *R. mirandaribeiroi* (Gallardo, 1965) (Bufonidae); *Oreobates remotus* Teixeira, Amaro, Recoder, Sena, and Rodrigues, 2012 (Craugastoridae); *Boana crepitans* (Wied-Neuwied, 1824), *Scinax* sp. 26 (sensu Araujo-Vieira *et al.*, 2023), *Scinax x-signatus* (Spix, 1824) (Hylidae); *Leptodactylus macrosternum* Miranda-Ribeiro, 1926, *L. troglodytes* Lutz, 1926, *L. vastus* Lutz, 1930, *Physalaemus cicada* Bokermann, 1966, *P. cuvieri* Fitzinger, 1826, *P. albifrons* (Spix, 1824)

Figure 1. Some of the sampled caves in Serra do Ramalho karst area: (a) Gruna da Mamona, photo of Laboratório de Estudos Subterrâneos, UFSCar, São Carlos, Brazil; (b) Gruna Boca da Lapa, photo of A.O. Lobo.

(Leptodactylidae); and *Odontophrynus carvalhoi* Savage and Cei, 1925 (Odontophrynidae) (Table 1).

All the caves in which we found anurans possess permanent lentic water bodies, except for Gruna Google (Carinhanha), where we found the two *Odontophrynus* tadpoles (CFBH 32595), in which the lentic water body is temporary. All the species we found are nocturnal and reproduce during rainy season. This is a common pattern for anurans in arid and semi-arid environments (Hillman *et al.*, 2009). We found all the animals during the day, suggesting that the caves function as shelter in diurnal retreat. We also found all the animals in the dry season, probably hiding from the epigean drought while they are not in reproductive season. In Gruna da Cacimbinha, we found specimens that we could not collect, and we identified them as *Leptodactylus* cf. *macrosternum* (one individual) and *Leptodactylus* cf. *vastus* (a population of around 30 individuals, some of them were juveniles; Figs. 4C and 4D).

We found *Rhinella granulosa* in two caves (Gruna do Domingão and Gruna do Cocho, Carinhanha). This species is distributed in northeast Brazil and commonly found in epigean environments (Pereyra *et al.*, 2016). Matavelli *et al.* (2015) and Santos *et al.* (2022) also reported this species in caves in Caatinga. We confirmed with barcode the identity of the individual of *R. granulosa* from Gruna do Cocho (CFBH 32599, Table A2). We found *Rhinella mirandaribeiroi* in Gruna Serra Solta II (Serra do Ramalho municipality). *Rhinella mirandaribeiroi* is a species from Cerrado domain, and is known from Cerrado in Bahia (Narvaes and Rodrigues, 2009).

Oreobates remotus was described for Cavernas do Peruaçu National Park (Teixeira Jr. *et al.*, 2012), a federal conservation unit inserted in Bambuí geomorphological group, and is also registered in the vicinities of the National Park (Frost, 2025). *Oreobates antrum* Vaz-Silva, Maciel, Andrade, and Amaro, 2018, the sister species of *O. remotus*, is also registered in caves (Motta *et al.*, 2020; Vaz-Silva *et al.*, 2018). Another species of this genus, *Oreobates heterodactylus* (Miranda-Ribeiro, 1937), was described from a cave in the state of Mato Grosso (Gruta Fazendinha, Cáceres; Bokermann, 1966). These occurrences of *Oreobates* in caves suggest a

Figure 2. Some of the sampled caves in Serra do Ramalho karst area: (a) Salon of the Gruna da Serra Verde, showing a researcher collecting; (b) Entrance of the Gruna do Govi; (c) Gruna Bem Bom; (d) Gruna do Engrunado, with a researcher. Photos of Laboratório de Estudos Subterrâneos, UFSCar, São Carlos, Brazil.

pattern of the genus in the preference for shelter in subterranean environments. We found three individuals of *O. remotus* in caves of Serra do Ramalho karst area (Gruna do Engrunado, Fig. 4B, Feira da Mata; Gruna Bem Bom, Carinhanha), all confirmed by barcode (Table A2).

Boana crepitans is found in open areas in Caatinga, Cerrado, and in the Atlantic Forest (Orrico *et al.*, 2017). This is a species from the *Boana faber* group, firstly described for Bahia state, and well known in Brazilian Northeast (Frost, 2025). We found only one individual, in Gruna Bem Bom (Carinhanha), confirmed by barcode (LESV 754, Table A2). As far as we know, this is the first record of this species in caves.

The five individuals of *Scinax* found in Gruna Bem Bom (Carinhanha; two of them in Figs. 5B and 5C) are morphologically similar, of which two were barcoded (LESV 749 and 753). One of them (LESV 753) matched with *Scinax* sp. 26 (an unconfirmed candidate species—UCS—sensu Araujo-Vieira *et al.*, 2023) and the other matched with *Scinax x-signatus* (LESV 749). Since the taxonomic status of *Scinax* sp. 26 is a pending issue, we consider the other three individuals (not barcoded) as *Scinax x-signatus* (LESV 748, 750-751). These specimens must be further studied once the taxonomic limits between *Scinax* sp. 26 and *Scinax x-signatus* are better addressed. The species *Scinax x-signatus* and *S.* sp. 26 (sensu Araujo-Vieira *et al.*, 2023) are sister species and morphologically similar (Araujo-Vieira *et al.*, 2023; Araujo-Vieira *et al.*, 2020). Along with *Scinax fuscovarius* (Lutz, 1925), these two species form the *S. fuscovarius* group (Araujo-Vieira *et al.*, 2023). As these species lack morphological differences, it was only possible to recognize the occurrence of the two species in Gruna do Bem Bom through DNA barcode (Table A2). *Scinax x-signatus* is a

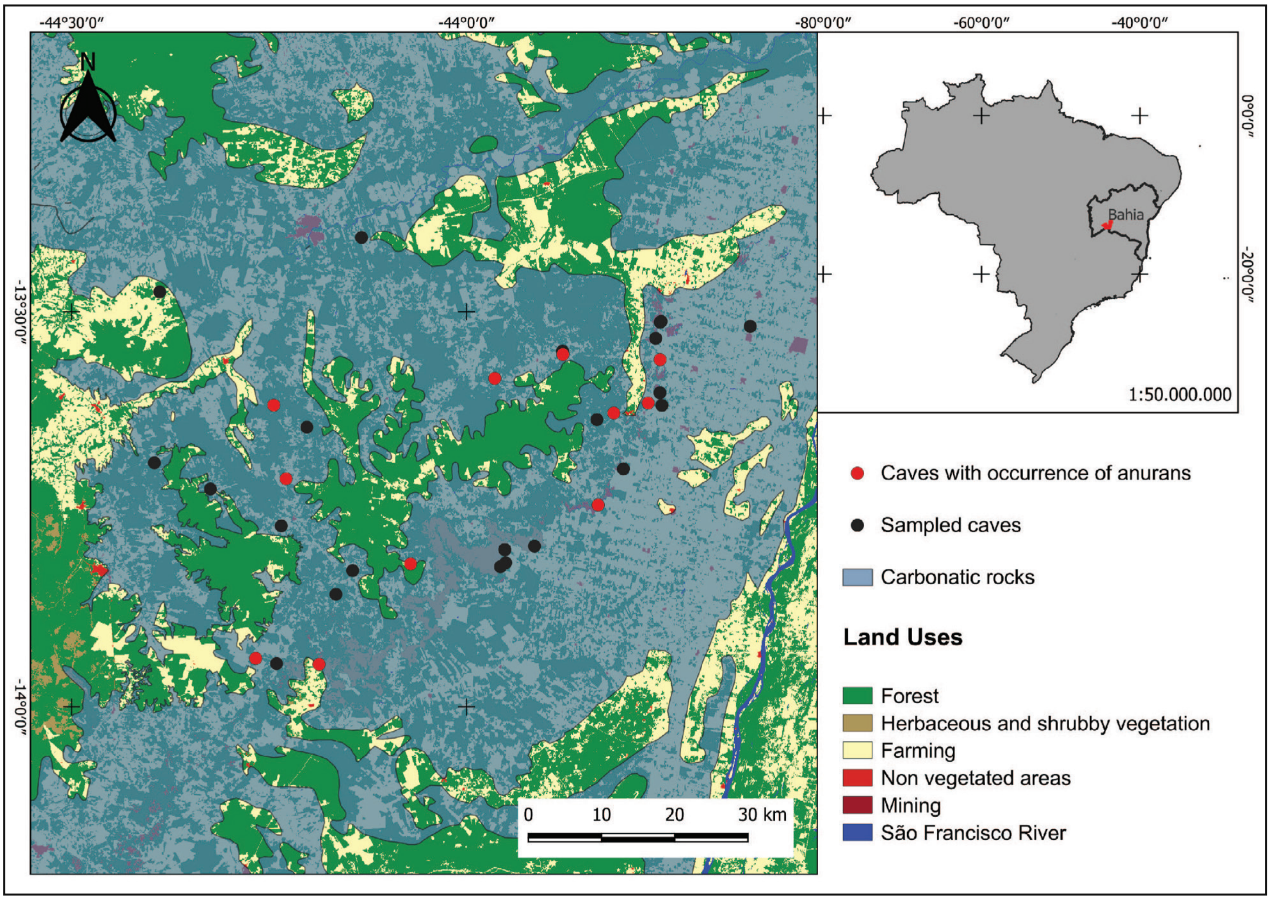

Figure 3. Distribution map of the studied caves, showing the caves in which we found amphibians (in red), regions with carbonatic rocks, and main land uses in the region.

species found in Caatinga, Atlantic Forest, Cerrado, and Amazon. It was reported as occurring in a cave (Sperandei *et al.*, 2023), but with no mention in which cave or biome. On the other hand, *Scinax* sp. 26 (sensu Araujo-Vieira *et al.*, 2023) was known only in epigean environments of Cavernas do Peruaçu National Park (Araujo-Vieira *et al.*, 2020) and from Caetité and Jacaraci municipalities, in the state of Bahia (Araujo-Vieira *et al.*, 2023).

Leptodactylus macrosternum is found in other parts of Carinhanha and Bom Jesus da Lapa municipalities (Magalhães *et al.*, 2020), localities close to Serra do Ramalho karst area. This species was also registered by Matavelli *et al.* (2015) and Santos *et al.* (2022) in caves in Caatinga and Cerrado. We registered this species in four caves: Gruna do Domingão (Carinhanha); Gruna do Engrunado and Gruna Boca da Lapa (Feira da Mata); Gruna da Mamona and Gruna da Cacimbinha (Coribe; the last one not collected, Fig. 4C), most of them confirmed by barcode (Tables 1 and A2). *Leptodactylus troglodytes* is distributed in Caatinga and Cerrado (Thomé *et al.*, 2021). We found this species in Gruna do Domingão (Carinhanha, Table 1). It has also been recorded in caves by Matavelli *et al.* (2015) and Santos *et al.* (2022). From the genus *Leptodactylus*, we also found *Leptodactylus vastus*, in Gruna Bem Bom (Carinhanha), and another population of around 30 individuals in Gruna da Cacimbinha (Coribe, not collected), including juveniles (Fig. 4D). This non-collected encounter is evidence that this species is using the cave as a shelter. *Leptodactylus vastus* was already recorded in the cave Toca da Raposa (Simão Dias municipality, state of Sergipe), where the authors state that the species was "a regular fauna" of the cave (A.S. Ferreira, M.A.T. Dantas & C.R. Donato, personal communication). This species was also recorded in the entrance of the cave Casa de Pedra (Itabaiana municipality, state of Sergipe) preying on bats (Gouveia *et al.*, 2009). Also, the species was found in a cave in Cerrado (Santos *et al.*, 2022).

Physalaemus cuvieri is a very common frog, known for Cerrado, Caatinga, and open areas in Atlantic Forest and Amazon (Frost, 2025). We

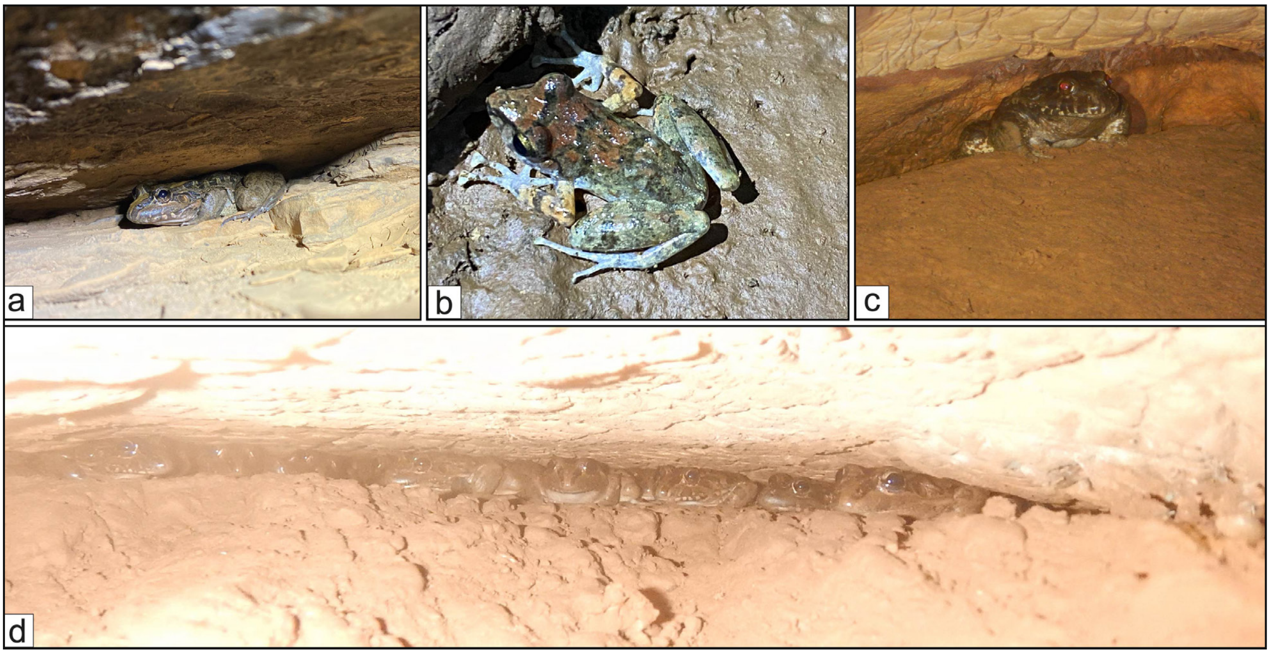

Figure 4. Anurans recorded in some caves in Coribe municipality, Bahia state, in Serra do Ramalho karst area: (a) *Leptodactylus macrosternum* in Gruna da Mamona; (b) *Orebates remotus* in Gruna do Engrunado; (c) *L. vastus* in Gruna da Cacimbinha, not collected; (d) Population of *L. macrosternum* in Gruna da Cacimbinha, not collected. Photos of Laboratório de Estudos Subterrâneos, UFSCar, São Carlos, Brazil.

found this species in Gruna Vila Nova and Gruna da Altina (Carinhanha). But it was already found in caves before, like the Pains karstic region (Ferreira *et al.*, 2022), and other unspecified caves (Matavelli *et al.*, 2015; Santos *et al.*, 2022; Sperandei *et al.*, 2023). Nevertheless, the other two species of the genus found in Serra do Ramalho karst area, *Physalaemus albifrons* (Gruna Serra Solta II, Serra do Ramalho) and *P. cicada* (Gruna Domingão, Carinhanha), have never been recorded in caves before. *Physalaemus albifrons* is a species from Caatinga, Atlantic Forest and ecotones (Palmeira *et al.*, 2011). And *Physalaemus cicada* is a species found in Caatinga, Cerrado and ecotones (Linares and Mello, 2011; Lisboa and Haddad, 2009).

Similarly, we found three individuals of *Odontophrynus* (CFBH 32944-32946; one of them in Fig. 6) in Gruna Chico Pernambuco (Coribe), that resembled *Odontophrynus carvalhoi*. One of them was barcoded and matched *Odontophrynus carvalhoi* (CFBH 32944, Table A2). The other two (CFBH 32945-32946) are morphologically similar to the barcoded one, so we considered them as *Odontophrynus carvalhoi*. In Gruna Google (Carinhanha), we found two tadpoles (CFBH 32595), identified as *Odontophrynus carvalhoi* following the description of Santos *et al.* (2017). *Odontophrynus carvalhoi* (Fig. 5) is a species from Caatinga and ecotones (Frost, 2025). It has never been registered for caves. We found adults in one cave (Gruta Chico Pernambuco, Coribe) and probably tadpoles in another cave (Gruna Google, Carinhanha). According to Haddad *et al.* (2013), *Odontophrynus carvalhoi* reproductive mode is defined by subaquatic eggs laid on bed of lotic water; offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and tadpoles developing in lotic water. This reproductive mode is currently the number 16 (sensu Nunes-de-Almeida *et al.*, 2021). Nevertheless, we found the tadpoles of *Odontophrynus carvalhoi* in Gruna Google (Carinhanha) in a lentic water. If we can confirm these tadpoles as *Odontophrynus carvalhoi*, this finding indicates some plasticity in the use of water bodies for reproduction in this species, allowing it to explore either lentic or lotic water for tadpole development. Another hypothesis is that these tadpoles entered in Gruna Google through the water flow or flood.

Anurans might enter in caves due to the more humid and cooler environment, and due to the presence of water bodies, especially in semi-arid biomes (Trajano and Bichuette, 2006). This is probably why recent reviews found more amphibians in caves of Caatinga and Cerrado than in caves of Amazonia and Atlantic Forest, that are more humid (Matavelli *et al.*, 2015; Santos *et al.*, 2022). Anyhow, there is a consensus that amphibians seek shelter in caves (e.g. Andrade *et al.*, 2021; Bichuette *et al.*, 2022; Matavelli *et al.*, 2015; Santos *et al.*, 2022; Sperandei *et al.*, 2023; Trajano and Bichuette, 2006).

Some studies considered that the search for the caves by amphibians might be somewhat motivated and not accidental, occurring all-year around (Santos *et al.*, 2022; Sperandei *et al.*, 2023). An accidental animal in a subterranean environment is an organism that has entered into the hypogean areas through falls or dragged by water, or maybe an organism that has entered the cave looking for a colder and more humid place (Trajano, 2005, apud Trajano, 2012).

Although incipient, the studies of amphibians in Brazilian caves have raised some questions and hypotheses suggesting that the caves are used "systematically" by these amphibians (Sperandei *et al.*, 2024). But as most of the studies are species –or genus– lists, the questions and hypotheses are currently being raised about the possible uses that amphibians make of the caves. It is not possible yet to classify most Brazilian amphibians found in caves in Schiner-Racovitza classification (Racovitza, 1907; Schiner, 1854). Some populations of *Bokermannohyla martinsi* Bokermann, 1964 from Serra do Gandarela National Park, state of Minas Gerais (Andrade *et al.*, 2021), and a population of *Pipa* cf. *pipa* from Refugio Maroaga in the municipality of Presidente Figueiredo, state of Manaus (M. E. Bichuette, unpublished data) might deserve Schiner-Racovitza classification after careful studies.

To adequately classify amphibians as cave organisms in Schiner-Racovitza classification (Racovitza, 1907; Schiner, 1854), it is necessary to study them monthly, for some annual cycles (Trajano

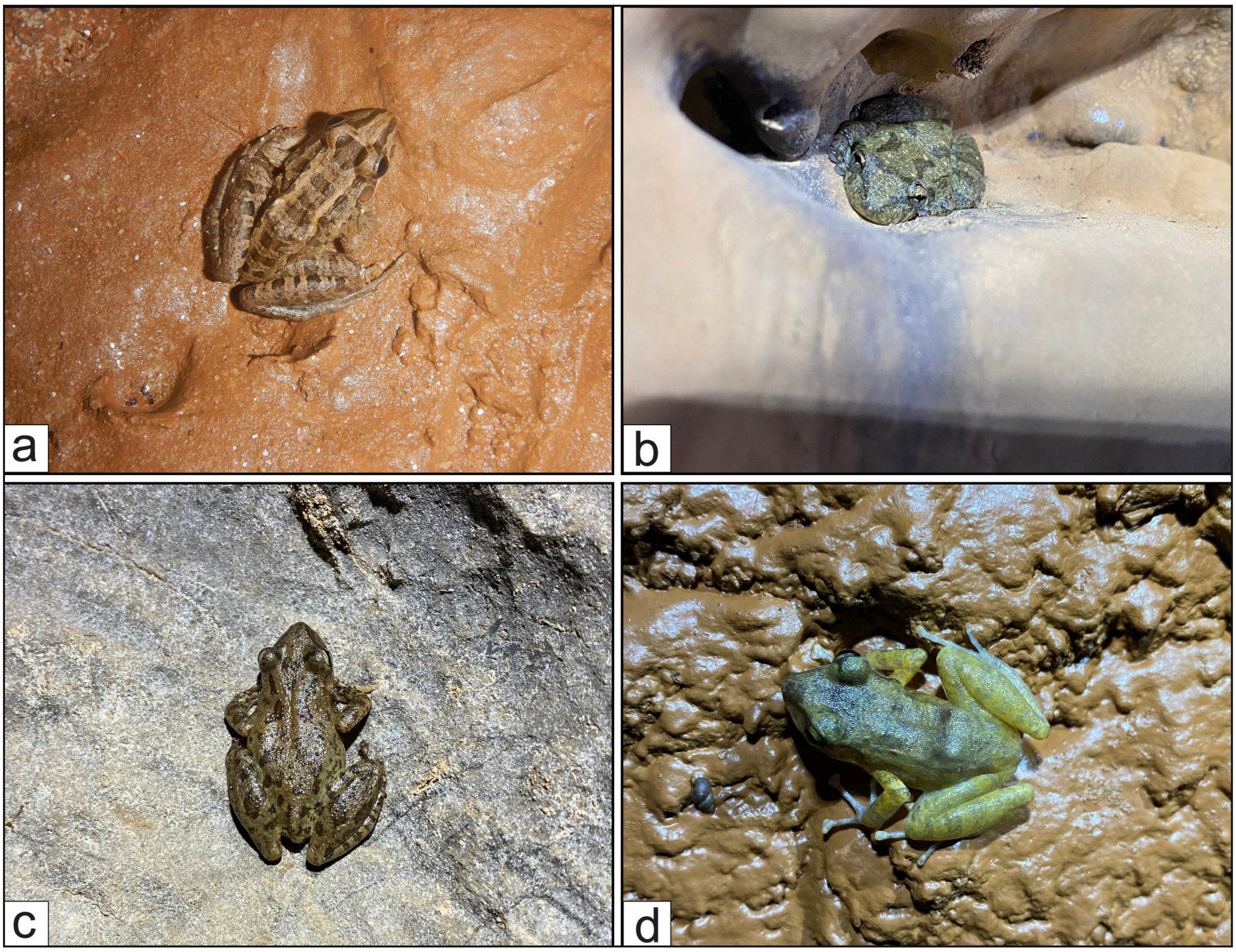

Figure 5. Anurans recorded in some caves in Serra do Ramalho karst area: (a) *Leptodactylus macrosternum* in twilight zone of Gruna Boca da Lapa (Feira da Mata, Bahia state); (b) *Scinax* cf. *x-signatus* in Gruna do Bem Bom (Carinhanha, Bahia state); (c) *Scinax* cf. *x-signatus* in Gruna do Bem Bom (Carinhanha, Bahia state); (d) *Oreobates remotus* in Gruna do Bem Bom (Carinhanha, Bahia state). Photos of Laboratório de Estudos Subterrâneos, UFSCar, São Carlos, Brazil.

and Bichuette, 2010b). We also consider that these studies must be done with samplings during the day (the period in which most amphibians are resting in shelters) and during the night (the period in which most amphibians are in activity). The difficulty here is that cave and subterranean specialists usually sample the caves during the day, and during dry season. During the day and during dry season, most of the amphibians are in fact sheltering, and not in activity.

Anyhow, regardless of the temporal aspects of the sampling, researchers should always remember that each cave has its own faunistic and diversity peculiarities (Trajano and Bichuette, 2006). This also means that each amphibian population found in a cave will be unique, and it could be difficult to define patterns of occupation beyond the amphibian search for shelter.

The physiological, morphological, and behavioral adaptations of anurans in the xeric environment of Caatinga are still mostly unknown (Jared *et al.*, 2019). The rain in Caatinga is markedly seasonal and finding a suitable site to retreat is necessary for these animals to survive (Navas *et al.*, 2004). The caves of Serra do Ramalho karst area have probably been used by anurans as a site for diurnal and winter retreat away from the adverse conditions of the Caatinga environment. To study the habitats and microhabitats used by Caatinga anurans during dry season and hot days is necessary to propose hypotheses regarding the physiology of these animals (Navas *et al.*, 2004). As several species of anurans use caves during part of their life cycles, the protection of this type of environment is necessary for the conservation of anurans.

Figure 6. *Odontophrynus carvalhoi* from Gruna Chico Pernambuco (Coribe, Bahia state), in Serra do Ramalho karst area. Photo of Pedro Pereira Rizatto.

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Appendix

Table A1. Caves sampled in the Serra do Ramalho, a limestone karst area, part of the Bambuí group. Each cave is with its respective "ID" number, elevation (in meters, a.s.l.), and coordinates (latitude and longitude, WGS84). Caves in bold are the caves in which we found amphibians.

ID	Cave	Elevation (m a.s.l.)	Latitude	Longitude
1	Gruna Baixão da Canoa	–	13°51'27.6000"S	44°09'55.3000"W
2	Gruna do Chico Pernambuco	697	13°49'09.0000"S	44°04'14.9000"W
3	Gruna do Domingão	799	13°44'40.7000"S	43°49'59.7000"W
4	Caverna Viração	702	13°32'58.8000"S	43°52'42.1000"W
5	Gruna Água Fina	803	13°41'55.6000"S	43°48'04.5000"W
6	Gruna Bem Bom	691	13°35'03.3000"S	43°57'51.2000"W
7	Gruna Boca da Lapa	544	13°56'46.3843"S	44°11'11.9794"W
8	Gruna da Água Clara	491	13°48'03.1478"S	43°57'05.5534"W
9	Gruna da Água Escura I	482	13°49'03.6997"S	43°57'01.3195"W
10	Gruna da Água Espalhada	–	13°41'28.4000"S	44°23'43.1000"W
11	Gruna da Altina	496	13°33'38.1000"S	43°45'17.2000"W
12	Gruna da Cacimbinha	676	13°42'41.1523"S	44°13'42.6306"W
13	Gruna da Mamona	573	13°37'05.1861"S	44°14'38.9007"W
14	Gruna da Pingueira II	715	13°49'39.4445"S	44°08'39.1169"W
15	Gruna da Serra Solta II	–	13°30'43.7000"S	43°45'12.3000"W
16	Gruna da Serra Solta III	506	13°30'47.6821"S	43°45'17.0714"W
17	Gruna da Serra Verde	–	13°43'27.9000"S	44°19'27.6000"W
18	Gruna das Três Cobras	804	13°37'06.3000"S	43°45'09.1000"W
19	Gruna do Cesário	457	13°31'06.1105"S	43°38'26.2070"W
20	Gruna do Cocho	514	13°36'55.6000"S	43°46'11.7000"W
21	Gruna do Enfurnado	638	13°38'45.8000"S	44°12'07.9000"W
22	Gruna do Engrunado	693	13°56'19.7664"S	44°16'01.1646"W
23	Gruna do Govi	684	13°56'43.3004"S	44°14'25.9451"W
24	Gruna do Ibelmon	–	13°24'21.5000"S	44°07'58.4000"W

25	Gruna do Mandiaçu	–	13°32'00.7000"S	43°45'37.2000"W
26	Gruna do Zeferini	708	13°46'15.6879"S	44°14'04.5732"W
27	Gruna dos Índios	494	13°48'04.7076"S	43°57'04.9468"W
28	Gruna Google	803	13°37'41.6000"S	43°48'48.3000"W
29	Gruna Grande	493	13°36'08.8977"S	43°45'18.1887"W
30	Gruna Pedro Cassiano	–	13°47'48.0000"S	43°54'50.0000"W
31	Gruna Vandercir I e II	725	13°38'11.4000"S	43°50'05.1000"W
32	Gruna Vila Nova	720	13°33'14.2673"S	43°52'40.7352"W
33	Lapa dos Peixes	487	13°49'22.0928"S	43°57'25.1839"W
34	Sistema Euzébio	–	13°28'29.2638"S	44°23'19.0320"W

Table A2. Specimens collected from Serra do Ramalho, part of the Bambuí group, with their respective specimen number in zoological collections, locality, municipality in Bahia, and collection date. The column "Barcode" marks the specimens that we confirmed through 16S sequencing. An asterisk (*) denote the species of *Scinax* that grouped with S. "sp. 26" from the study of Araujo-Vieira *et al.* (2023). The acronym LESV stands for Laboratório de Estudos Subterrâneos Vertebrate Collection (Universidade Federal de São Carlos, São Carlos, SP, Brazil; curator: M.E. Bichuette), and the acronym CFBH stands for the Coleção de Anfíbios Célio F. B. Haddad (CFBH, Universidade Estadual Paulista, Rio Claro, SP, Brazil; curator: C.F.B. Haddad).

Specimen number	Species	Locality	Municipality	Collection date	Barcoded
CFBH 32594	*Physalaemus cuvieri*	Gruna Vila Nova	Carinhanha	11.ix.2008	
CFBH 32595	*Odontophrynus carvalhoi*	Gruna Google	Carinhanha	13.ix.2008	
CFBH 32599	*Rhinella granulosa*	Gruna do Cocho	Carinhanha	02.vi.2012	X
CFBH 32942	*Leptodactylus macrosternum*	Gruna do Domingão	Carinhanha	27.vii.2012	X
CFBH 32943	*Leptodactylus macrosternum*	Gruna do Domingão	Carinhanha	27.vii.2012	X
CFBH 32944	*Odontophrynus* cf. *carvalhoi*	Gruna Chico Pernambuco	Coribe	28.vii.2012	X
CFBH 32945	*Odontophrynus* cf. *carvalhoi*	Gruna Chico Pernambuco	Coribe	28.vii.2012	
CFBH 32946	*Odontophrynus* cf. *carvalhoi*	Gruna Chico Pernambuco	Coribe	28.vii.2012	
CFBH 40905	*Physalaemus cuvieri*	Gruna da Altina	Carinhanha	27.xi.2015	
CFBH 48263	*Rhinella mirandaribeiroi*	Gruna Serra Solta II	Serra do Ramalho	24.x.2023	
CFBH 48264	*Physalaemus albifrons*	Gruna Serra Solta II	Serra do Ramalho	24.x.2023	
LESV 663	*Rhinella granulosa*	Gruna do Domingão	Carinhanha	01.viii.2019	
LESV 671	*Leptodactylus troglodytes*	Gruna do Domingão	Carinhanha	01.viii.2019	
LESV 671	*Physalaemus cicada*	Gruna do Domingão	Carinhanha	01.viii.2019	
LESV 710	*Leptodactylus macrosternum*	Gruna do Engrunado	Feira da Mata	13.x.2020	X
LESV 712	*Leptodactylus macrosternum*	Gruna da Boca da Lapa	Feira da Mata	15.x.2020	
LESV 713	*Oreobates remotus*	Gruna do Engrunado	Feira da Mata	13.x.2020	X
LESV 714	*Oreobates remotus*	Gruna do Engrunado	Feira da Mata	13.x.2020	X
LESV 748	*Scinax x-signatus*	Gruna Bem Bom	Carinhanha	07.vii.2021	
LESV 749	*Scinax x-signatus*	Gruna Bem Bom	Carinhanha	07.vii.2021	X
LESV 750	*Scinax x-signatus*	Gruna Bem Bom	Carinhanha	07.vii.2021	
LESV 751	*Scinax x-signatus*	Gruna Bem Bom	Carinhanha	07.vii.2021	
LESV 752	*Oreobates remotus*	Gruna Bem Bom	Carinhanha	07.vii.2021	X
LESV 753	*Scinax* sp. 26*	Gruna Bem Bom	Carinhanha	07.vii.2021	X
LESV 754	*Boana crepitans*	Gruna Bem Bom	Carinhanha	07.vii.2021	X
LESV 755	*Leptodactylus vastus*	Gruna da Mamona	Coribe	09.vii.2021	
LESV 756	*Leptodactylus macrosternum*	Gruna da Mamona	Coribe	09.vii.2021	X

Nota

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Natural history notes and micro-habitat use by *Bokermannohyla luctuosa* (Pombal & Haddad, 1993) (Anura: Hylidae)

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ABSTRACT

This study investigates the activity, habitat use, and ecological patterns of the arboreal treefrog *Bokermannohyla luctuosa*, based on long-term monitoring from April 2020 to August 2022 in São Francisco Xavier, São Paulo state, southeastern Brazil. Over 126 field trips, we recorded this frog 203 times across 17 sites, with significant seasonal variation in activity and habitat use. During the dry season (April to September), the animals frequently occupied waterfall spray zones, while wetter months saw decreased reliance on these habitats. Reproductive activity, including vocalizing males, gravid females, and tadpoles, was observed across multiple months, which indicates an extended reproductive period. Notable trophic interactions included predation by the larger treefrog *Boana faber* and the consumption of a harvestman by *B. luctuosa*. These findings highlight the importance of long-term monitoring to address knowledge gaps, particularly as climate change threatens amphibian habitats. Understanding seasonal microhabitat preferences can guide conservation strategies and improve fieldwork outcomes.

Key Words: Amphibian Ecology; Atlantic Forest; Climate Change Impacts; Predation; Seasonal Habitat Use.

Studies on diversity depend on the success of field trips to underexplored areas. Tropical forests are biodiversity hotspots, and the Atlantic Forest in Brazil is home to thousands of species, many of them endemic (Meyers *et al.*, 2000; Jenkins *et al.*, 2015). Expeditions focusing on Atlantic Forest amphibians are frequent, as this ecoregion hosts more than 600 species of anurans (Rossa-Feres *et al.*, 2017). As in most of the Neotropical ecoregions with seasonal climate regime, the reproductive season for most anurans occurs in the warmer and wetter months, from October to February (Duellman and Trueb, 1986; Donnelly and Crump, 1998; Haddad and Prado, 2005; Prado *et al.*, 2005; Gomez-Mestre *et al.* 2012; Verdade *et al.*, 2019), despite the consistently high humidity levels throughout the year and the diversity of reproductive modes observed among Atlantic Forest anurans (Nunes-de-Almeida *et al.*, 2021).

Focusing herpetological campaigns during the wetter months creates a major knowledge gap in relation to behaviours displayed during the dry season, such as microhabitat and shelters use, movement patterns, and activity levels. Global climate change

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is threatening delimitation and predictability of seasons, altering temperature and rainfall patterns, therefore impacting biodiversity, particularly of frogs (Luedtke *et al.*, 2023). There is an urgent need for natural history studies, as long-term monitoring plays a crucial role in providing insights into animal behaviour and strategies to overcome environment challenges (see Prado *et al.*, 2005; Verdade *et al.*, 2012; Muscat *et al.*, 2020; Moroti *et al.*, 2022; Botelho *et al.*, 2023).

Bokermannohyla luctuosa (Pombal and Haddad, 1993) is a large hylid treefrog (males SVL 55 mm, females 70 mm) from the *B. circumdata* group (Faivovich *et al.*, 2005; Carvalho *et al.*, 2012). This frog has arboreal and nocturnal habits and is commonly found in forested areas, forest edges, and wetlands. It is endemic to the mountainous regions of the Atlantic Forest (Haddad *et al.*, 2013). Some aspects of the defensive (Pombal and Haddad, 1993; Toledo and Haddad, 2009; Toledo *et al.*, 2011; Moroti *et al.*, 2018) and reproductive (Zornosa-Torres and Toledo, 2019) behaviours of *B. luctuosa* during the wet season are formally described: males release advertisement calls perched on arboreal vegetation; females lay eggs in temporary pools, streams, or on the edge of lentic streams; and tadpoles initially develop in mud depressions, rock crevices or under branches near streams, from where heavy rains carry them to larger bodies of water to complete their cycle. (Pombal Jr. and Haddad, 1993; Malagoli *et al.* 2021). Nothing is known about the species' habitat use during drier times of the year.

Herein we present year-round monitoring and natural history data of *B. luctuosa*. We highlight occasional trophic interactions and demonstrate how the occurrence sites of *B. luctuosa* are driven by temperature and humidity variations. This allows for the prediction of where these frogs can be found during different moisture conditions that vary seasonally in its occurrence area.

We monitored the activity of *B. luctuosa* from April 2020 to August 2022 in the Projeto Dacnis private reserve in São Francisco Xavier, São Paulo state (22°53'S 45°56'W, 842 m above sea level) (Fig. 1). Projeto Dacnis is a non-governmental organization dedicated to Atlantic Forest conservation through scientific research and environmental education. The climate is subtropical highland climate (Cwb)

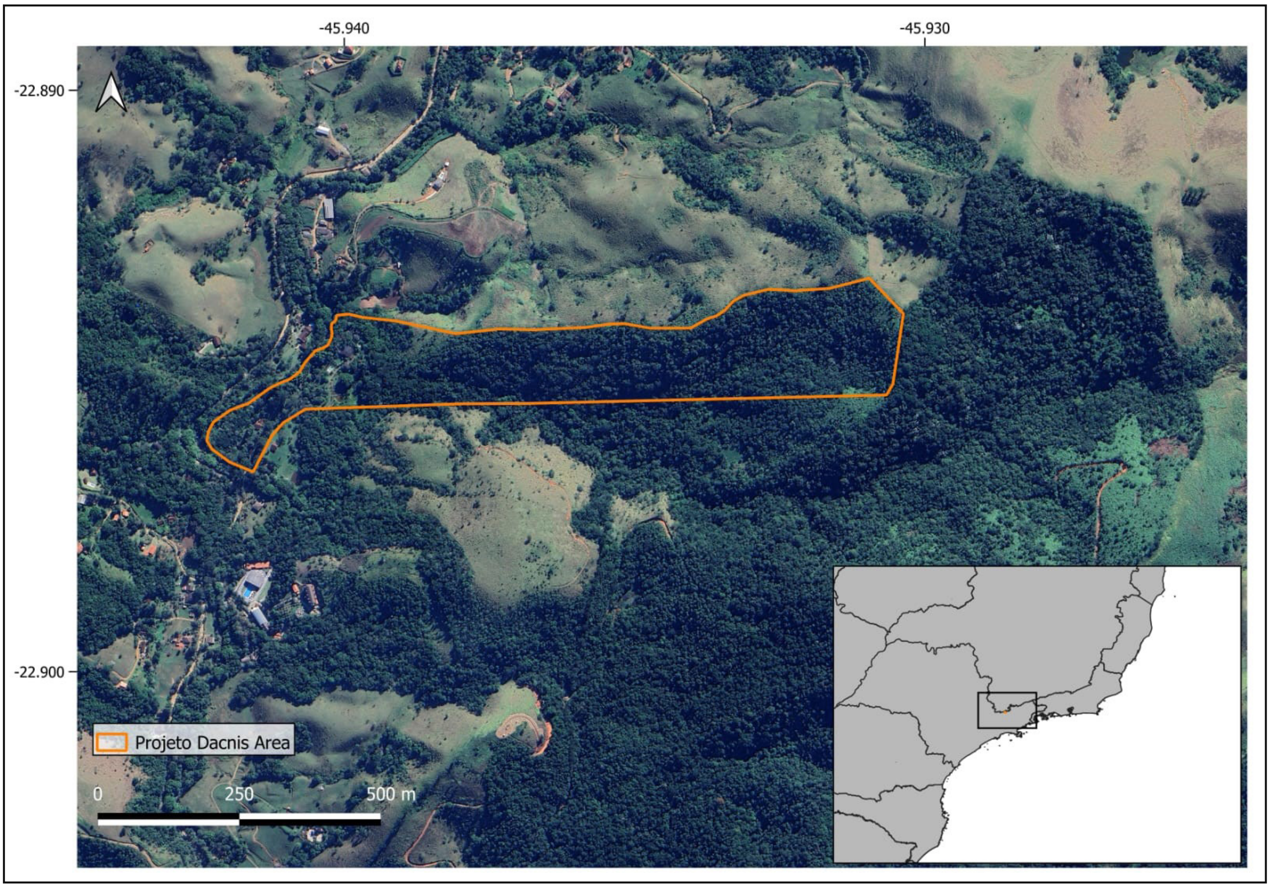

Figure 1. The Projeto Dacnis study area in which the survey took place. São Francisco Xavier, São José dos Campos, São Paulo, Brazil.

with substantial rainfall, according to the Köppen classification (Alvares *et al.* 2013). The annual mean rainfall exceeds 1,800 mm.

Sampling was carried out during routine trails once a week, covering 3 km alongside streams and waterfalls, and lasting 3 h per night. Two researchers conducted the field study, resulting in a total sampling effort of 756 person/hours across 126 field trips. For each individual of *B. luctuosa* found on the trail, we recorded the observation site and individual activity, and the site's air temperature (°C) and relative air humidity (%), measured with a digital thermo-hygrometer (Metrins INS-1383). Rainfall data during monitoring were obtained from a weather station at the Projeto Dacnis area. Average temperature and rainfall for the area during our monitoring is in a climogram (Fig. 2).

To gain a detailed understanding of the phenology of *B. luctuosa*, we employed circular statistics and the Rayleigh test (Agostinelli and Lund, 2024). We performed a bootstrap analysis (1000 replicates; Canty and Ripley, 2024) to estimate the average rainfall at which individuals were found associated to the waterfall in the area. Additionally, we used a logistic regression to test whether the occurrence of *B. luctuosa* in the waterfall was related to average rainfall during the monitoring period (Fig. 3). Monthly mean rainfall values were transformed using their natural logarithm. We conducted all analyses in the R environment (R Core Team 2020).

During the 126 field trips, we found *Bokermannohyla luctuosa* 203 times. In most encounters, there was more than one individual, usually perched on vegetation, not interacting, totalling 447 encounters in 29 months of monitoring. Throughout these observations, our records on activity, if any, life stage, calling, presence of females with eggs, and occurrence of tadpoles, provide detailed insights of the reproductive and ecological patterns of this treefrog in the area (see Table 1 and Figs. 2-5).

We found individuals of *B. luctuosa* in 17 different sites within the study area. Records for this frog were strongly seasonal (Rayleigh Test of Uniformity = 0.55, p-value < 0.01), predominantly concentrated during the drier months (n=398), from April to September (Figs. 2 and 3A), when it was the single frog species recorded in our monitoring. There were 181 sightings at waterfalls over the whole study period, of which 173 happened during the dry season. Waterfalls accounted for 43.5% of all

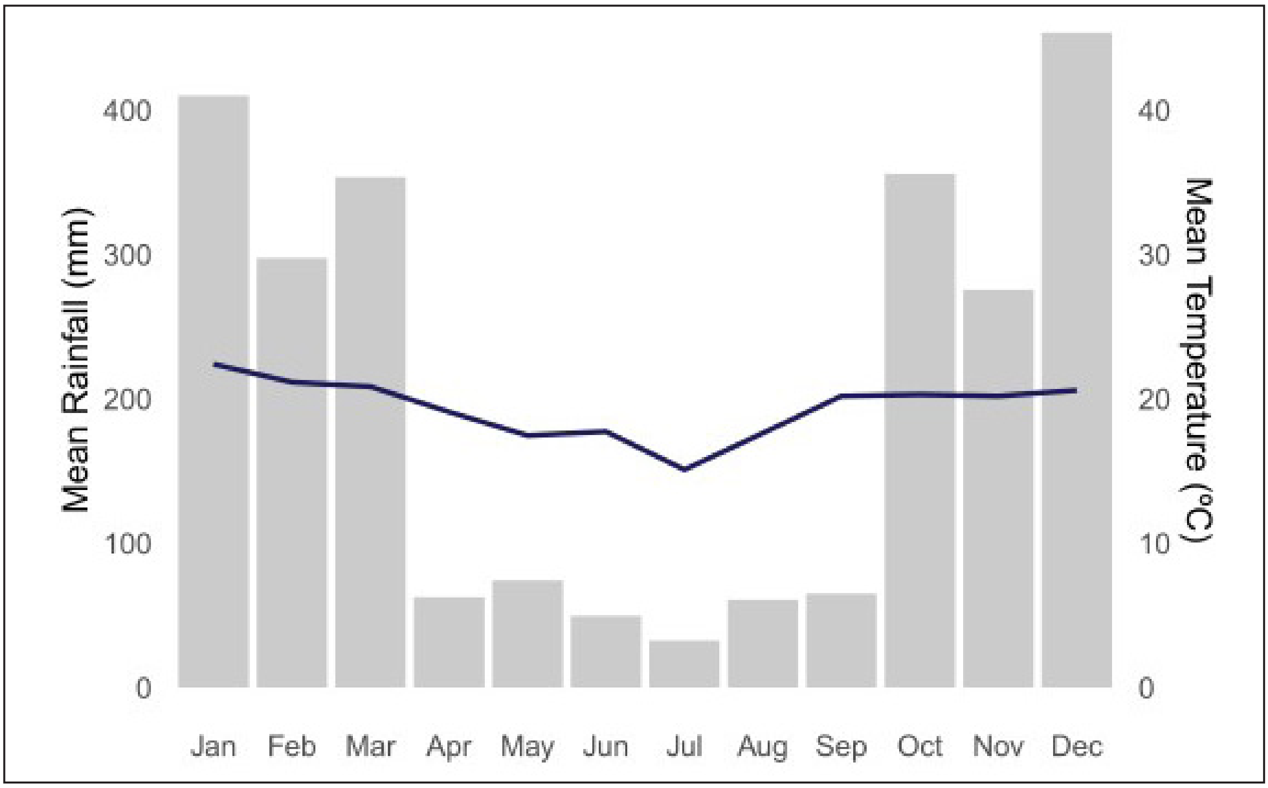

Figure 2. Monthly average temperature and rainfall from April 2020 to August 2022 in São Francisco Xavier, São José dos Campos, São Paulo, Brazil.

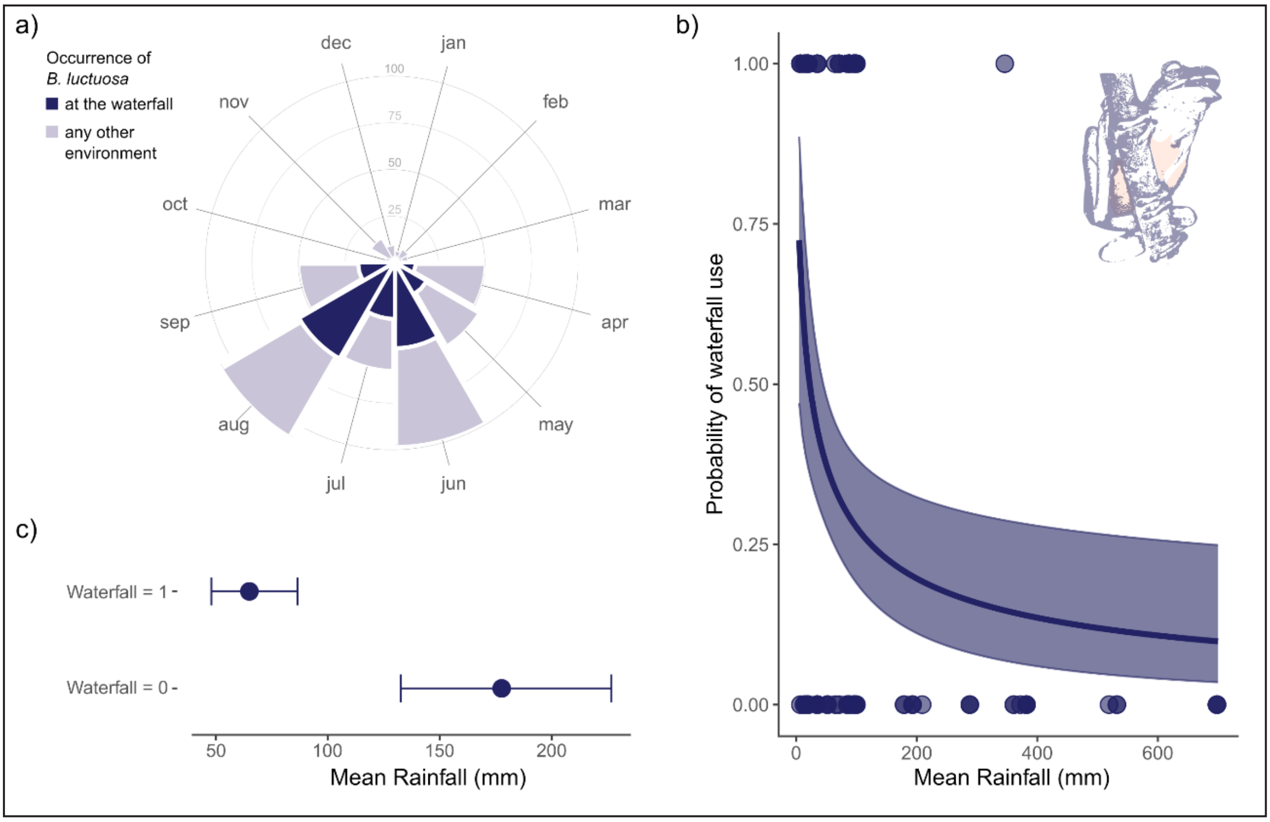

Figure 3. Probability of waterfall use by *Bokermannohyla luctuosa* in the Projeto Dacnis reserve, São Francisco Xavier, São José dos Campos, São Paulo, Brazil. (a) The occurrence of this frog was highly seasonal during the sampling period, with most individuals found during the dry season (April to September). (b) Individuals were commonly observed in the waterfall spray zone when mean rainfall was below 100 mm/month. (c) The frequency of waterfall use increased as rainfall decreased.

B. luctuosa found during this period, highlighting their importance as a water resource when there was reduced rainfall (Fig. 3A). We found that the occurrence of *B. luctuosa* in waterfall zones was associated with a mean rainfall of less than 100 mm/month (Fig. 3B), while the dependence of this moist habitat decreased with increasing rainfall in warmer months (Fig. 3C, Table 1).

We recorded *B. luctuosa* calling activity in April, June, and August, and once in November. We observed a female with eggs far from the waterfall in June. We found tadpoles in May, August, September and October, in different water bodies inside the forest, swimming at a depth of 30 to 50 cm, once observed in water as cold as 16°C. Tadpoles in early developmental stages were found in shallow, lentic-like streams with muddy or sandy bottoms, and their maximum numbers were around 30 individuals. Juvenile and adult frogs were commonly found perched between 30 and 200 cm high on vegetation within the forest. All observations above occurred during night time surveys, when temperatures ranged from 9.8°C to 25.9°C and humidity ranged from 51 to 100%. During the dry season, we recorded the frogs in retreats in the axils of banana plants (*Musa* sp.) and bromeliads (Fig. 4).

Additionally, we also documented predatory interactions involving *B. luctuosa*. On November 12, 2019, before formal monitoring began, we recorded a *B. luctuosa* adult on vegetation, preying on a gon-

Table 1. Influence of rainfall on the use of waterfall zones by *Bokermannohyla luctuosa*, as inferred from a logistic regression between the natural logarithm of monthly mean rainfall and the species' occurrence.

	Estimate	**Std. error**	**z-value**	p-value
Intercept	2.00	0.87	2.30	0.02
Ln (Mean rainfall)	-0.64	0.21	-3.09	<0.01

Figure 4. Habitat and microhabitats of *Bokermannohyla luctuosa* in the Projeto Dacnis reserve in São Francisco Xavier, São José dos Campos, São Paulo, Brazil. (a) Waterfall where the frog was usually found. (b-c) The frog in day shelters, the axil of a banana plant (Musa sp.) and bromeliads, recorded during the night after active search. Photos by Edelcio Muscat.

yleptid opilion, *Gonyleptes* sp. (Fig. 5A). On April 1, 2020, we recorded the larger hylid treefrog *Boana faber* (Wied-Neuwied, 1821) perched on vegetation and preying on *B. luctuosa* (Fig. 5B). At the time we found the two frogs, only the hind legs of *B. luctuosa* were protruding from the mouth of *B. faber*. To be sure of the identity of the preyed frog, we caught *B. faber* and carefully removed the prey from its mouth. Remarkably, the juvenile *B. luctuosa* was still alive. Both frogs were released at the same site and a video documenting this event was deposited in the digital collection of the Jacques Vielliard Neotropical Sound Archive (ZUEC-VID 0001321).

Our data indicate seasonal habitat variation by *B. luctuosa* related to humidity levels. Rainfall below 100mm/month is more common from April to September in the study area, during which the frogs were often found in humid habitats like waterfall splash zones. As rainfall declined, the frogs increasingly depended on these spray zones, where humidity remained high throughout the dry season. Conversely, the number of frogs recorded near waterfalls decreased during wetter months. These findings are in line with our expectations based on the life history traits of anurans in general, and of some Atlantic Forest species (Duellman and Trueb 1994; Moroti *et al.* 2022).

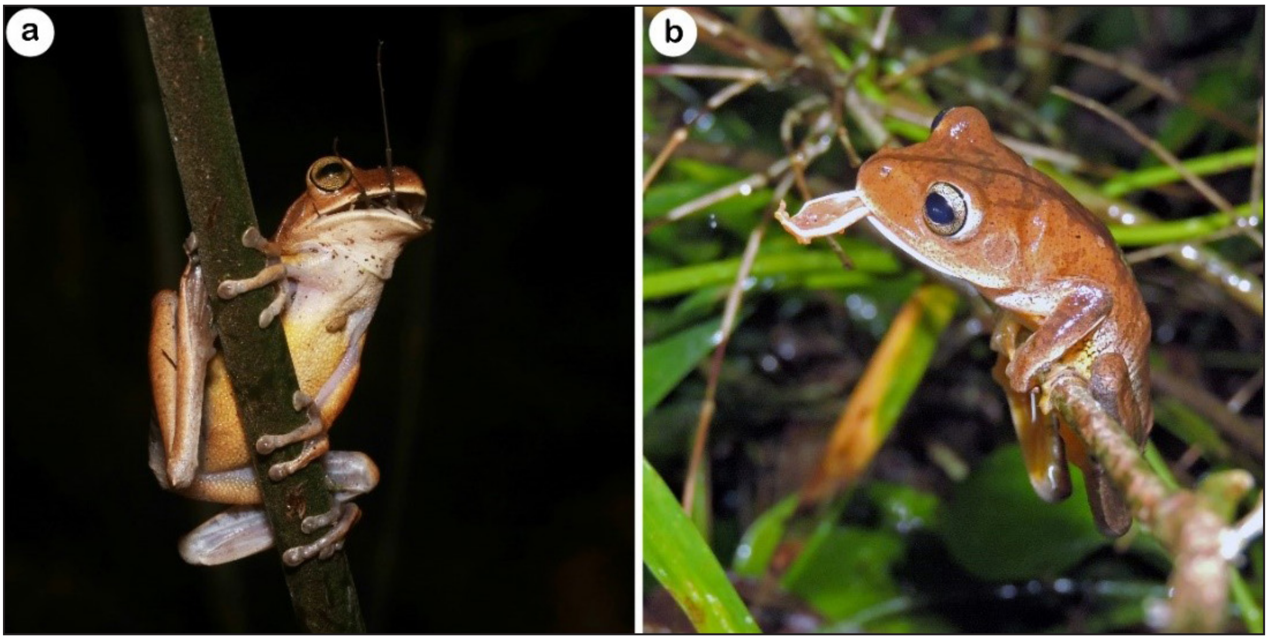

Figure 5. Predation records. (a) *Opilion Gonyleptes* sp. (Gonyleptidae) preyed on by *Bokermannohyla luctuosa* and (b) *B. luctuosa* preyed upon by the larger treefrog *Boana faber* (Hylidae). Photos by Edelcio Muscat.

The high permeability of amphibian skin leads to elevated rates of moisture loss, thereby increasing the risk of dehydration when these animals are in terrestrial environments during dry periods. Water plays a critical role in maintaining the integrity of amphibian skin functions (Feder and Burggren, 1992; McNab, 2002; Junior and Gomes, 2012; Botelho *et al.*, 2023). Evaluations of high-quality habitats for amphibians should consider the availability of water for rehydration during dry periods (Silva *et al.*, 2012), such as splash zones around fast-flowing streams, bromeliads, and water accumulated in axils of large-leaved plants such as *Heliconia* sp. (Botelho *et al.* 2023). Changes in rainfall patterns are potentially harmful if the number of consecutive dry days increases, even if mean precipitation is maintained. Longer dry periods may restrict or eliminate wet microhabitats (Pounds *et al.*, 1999). *Bokermanohyla luctuosa* is the only species of the genus in the study area, and we know climate changes are projected to shrink and cluster occurrence areas for many species, including in the high endemic and diverse areas of south eastern Atlantic forests, affecting differentially species richness, phylogenetic endemism, phylogenetic and functional diversity (e.g. Alves-Ferreira *et al.*, 2025; Bolochio *et al.*, 2025).

During the rainy season between November 2014 and March 2015, Zornosa-Torres and Toledo (2019) conducted their studies and observed that *B. luctuosa* exhibited reproductive activity throughout this interval. Our data indicates a broader period, as males were found vocalizing from April to November, a female with eggs was recorded in June, and tadpoles in May, September and October, supporting the hypothesis that this treefrog has an extended reproductive period. This distribution of tadpole sightings across several months indicates that reproduction may be sustained over time, rather than confined to a single season. Extended reproductive periods are documented for other species in the *B. circumdata* group (Malagoli *et al.*, 2021).

Predation events are poorly documented for *B. luctuosa*. While it is generally known that frog's prey on invertebrates, the records of harvestmen as prey are unusual (see Machado *et al.*, 2005), as these arachnids have chemical defences that may lead to regurgitation by the predator (Machado *et al.*, 2005).

Boana faber is a large treefrog that includes other frogs in its diet (e.g. Craugastoridae, Leite *et al.*, 2008, and Hylidae, Oliveira *et al.*, 2023). Ours is the first record of a treefrog from the genus *Bokermannohyla* as part of its diet. The co-occurrence of both species in swamps or flooded areas at the forest edge (Moura *et al.*, 2012; this paper) favours predation events, which may be more common than currently recognised.

Our study adds to the understanding of the natural history of Atlantic Forest frogs, their trophic interactions, and potential future threats resulting from climate changes. The observed seasonality in microhabitat use and its relationship with rainfall can enhance fieldwork success by identifying suitable microhabitats during drier periods. We emphasise the role of long-term monitoring and natural history studies as important tools for understanding fundamental requirements for countless animal species, as well as for management and conservation of frogs and other animals in our quickly-changing environment.

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Declaration of interest

No conflicts of interest.

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Nota

Cuad. herpetol. 39 (2): 123-126 (*2025*)

Predation of the rare casque-headed treefrog *Trachycephalus mambaiensis* (Hylidae: Lophiohylini) by the parrot-snake *Leptophis mystacinus* (Colubridae) in a Cerrado-Caatinga ecotone

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ABSTRACT
Anurans are key prey for snakes, and their decline can affect snake diversity. Defensive behaviors in frogs are diverse and include secretions, distress calls, and body inflation. Frogs of the genus *Trachycephalus*, known as “milk frogs,” produce sticky and potentially toxic secretions. Predation events involving these frogs are rarely documented. We observed an adult parrot-snake *Leptophis mystacinus* preying on an adult treefrog *Trachycephalus mambaiensis* in a Cerrado–Caatinga transitional area in Minas Gerais, Brazil. The frog briefly escaped but was recaptured and ingested within 10 minutes. This is the first documented case of *L. mystacinus* preying on *T. mambaiensis*. Although *Leptophis* species are known to prey primarily on hylid frogs, little is known about the diet of *L. mystacinus*. This observation supports its potential specialization on nocturnal treefrogs and suggests that it may use both visual and olfactory cues to detect inactive prey during day.

Key Words: Scansorial Snakes; Milky Secretion; Trophic Ecology.

Anurans are relevant prey for various snake species (e.g., Santos-Silva *et al.*, 2014; Parreira *et al.*, 2023) and declines in their availability can have pervasive effects on snake diversity (Zipkin *et al.*, 2020). Therefore, predator-prey interactions between snakes and anurans play a pivotal role in the dynamics and structure of amphibian communities and the evolution of anuran defensive behaviors (Toledo *et al.*, 2011). Anuran defense mechanisms are multimodal, encompassing different and escalated strategies, such as cloacal discharge, body inflation, distress calls, and skin secretions (Toledo *et al.*, 2011), likely providing defense in rich tropical predator communities.

The genus *Trachycephalus* (Anura: Hylidae) comprises 17 species of nocturnal large-sized arboreal frogs, commonly known as ‘milk frogs’, which secrete a milky, latex-like substance. These copious and eventually noxious secretions are notable defenses against predators and collectors, acting both mechanically (as glue) and chemically (Rigolo *et al.*, 2008; Brown, 2020; Frost, 2025). Considering this chemical defense mechanism, only a few *Trachycephalus* species have been documented as prey for other anurans (Mira-Mendes *et al.*, 2012; Cervantes-López *et al.*, 2024) and reptiles, including arboreal snakes of the genus *Chironius* (Dias-Silva

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et al., 2021; George, 2023) and *Leptophis* (Solé *et al.,* 2010; Clegg, 2015; Hayes, 2023). *Trachycephalus mambaiensis* Cintra, Silva, Silva, Garcia, and Zaher, 2009 is a rare species known only from the Brazilian biome Cerrado (Cintra *et al.,* 2009; Vaz-Silva *et al.*, 2020).

The Neotropical genus *Leptophis* comprises 20 species widely distributed from Mexico through Central and South America (Albuquerque *et al.*, 2025; Uetz *et al.,* 2025). These diurnal snakes inhabit arboreal and terrestrial environments (Albuquerque and Fernandes, 2022). Parrot snakes are opportunistic predators feeding on frogs, lizards, snakes, and small birds (López *et al.,* 2003; Mumaw *et al.,* 2015; Vieira and Gomez, 2016). *Leptophis mystacinus* Albuquerque, Martins, Carvalho, Shepard, and Santana, 2025 is a recently described, large, slender, and diurnal species found in open vegetation formations within the Cerrado biome, particularly in the states of Tocantins and Minas Gerais, as well as in regions influenced by the humid Amazon rainforest (Albuquerque *et al.*, 2025). However, little is known about their dietary habits. Herein, we report a predation of the casque-headed treefrog *Trachycephalus mambaiensis* by the parrot snake *Leptophis mystacinus* in a transitional Cerrado-Caatinga habitat.

On 24 January 2025, at 14:40, a predation event involving *Leptophis mystacinus* and the casque-headed tree frog *Trachycephalus mambaiensis* was observed at the Cavernas do Peruaçu National Park, Minas Gerais, Brazil. The event occurred during transit between the research station and visitor center (15°09'23"S 44°13'52"W; datum: SAD69; 530 m a.s.l.) in a transitional area between the Cerrado and Caatinga biomes, characterized by Dry Forest habitat (Dryflor *et al.*, 2016). The environment was humid at the time, as January is a rainy month. Despite clear weather, the road was shaded by a continuous canopy of tall trees (10–15 m in height).

The adult *Leptophis mystacinus* was sighted at the roadside holding an adult *Trachycephalus mambaiensis* in its mouth, which already showed signs of injury, including lacerations of the skin in the dorsal and ventral regions of the head and on the lateral side of the body with bleeding (Figs. 1A, 1B), suggesting that the snake had seized the frog before our observation. When sighted, both animals were motionless. The frog soon tried to escape but was quickly chased and recaptured by the snake (Fig. 1C). The parrot snake coiled around the frog and

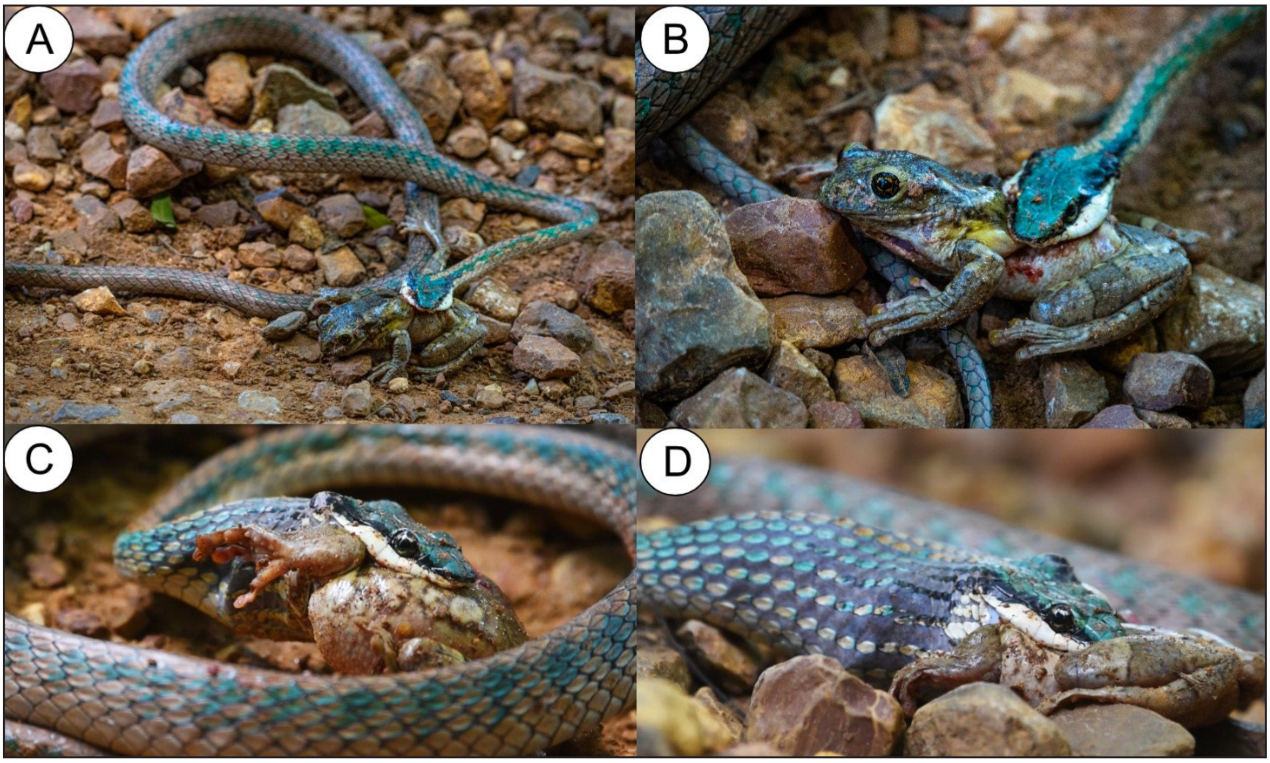

Figure 1. Predation event at Peruaçu National Park, Minas Gerais, Brazil, on 24 January 2025. A) An adult individual of *Leptophis mystacinus* seizing an adult individual of *Trachycephalus mambaiensis* as initially observed. B) Detail of the snake and the treefrog, before the frog's escape. C) *L. mystacinus* ingesting the *T. mambaiensis* after recapture. D) Detail of the greatly distended body of the parrot-snake during ingestion of the treefrog.

swallowed it headfirst in about 10 minutes (Fig. 1D). After consuming the prey, the snake swiftly moved into the adjacent forest, climbed a tree, and disappeared into the canopy.

We did not observe head rubbing behavior in *Leptophis mystacinus*, suggesting no apparent effect of the frog's milky secretions, although this behavior has been documented in some colubrid snakes when handling noxious amphibian prey (Feder & Arnold, 1971; Brodie *et al.*, 1980). However, it is possible that the secretion of *Trachycephalus mambaiensis* momentarily affected the snake, facilitating the frog's initial escape.

Since we did not collect the animals, species identification was based on external morphological traits and geographic location. The snake was identified as *Leptophis mystacinus* due to its general coloration, distinctive black pigmentation around the rostral scale (creating a mustache-like appearance) (Albuquerque *et al.,* 2025). The frog was identified as *Trachycephalus mambaiensis* based on the poorly ossified skull, particularly in the squamosal region (Fig. 1B) (Cintra *et al.,* 2009).

This observation represents the first documented case of *Leptophis mystacinus* preying on *Trachycephalus mambaiensis*, contributing to our understanding of the trophic interactions within these genera. To date, predation within the clade *T. nigromaculatus* has only been recorded for *Trachycephalus nigromaculatus* Tschudi, 1838, preyed upon by the ocellated treefrog *Itapotihyla langsdorffii* (Duméril and Bibron, 1841) (Cervantes-López *et al.*, 2024).

Species of the family Hylidae account for 90% of the diet of *Leptophis ahaetulla* (Linnaeus, 1758) in northern Brazil (Albuquerque *et al.*, 2007) and 63% of the diet of *Leptophis marginatus* (Cope, 1862) in northeastern Argentina (López *et al.*, 2003). Although no predation records are available for *L. mystacinus*, our observation suggests that this species also targets nocturnal treefrogs when they are inactive during the day. Such behavior likely relies on visual cues, as reported for other diurnal colubrids, including species of genus *Chironius* (Dias-Silva *et al.*, 2021; George, 2023; Parreira *et al.*, 2023).

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Nota

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New records of predation and feeding behavior of the vine snake *Chironius brazili* (Squamata: Colubridae) in the Espinhaço Mountain Range, Brazil

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ABSTRACT
The vine snake *Chironius brazili* inhabits rocky *campo rupestre* environments in the Espinhaço Mountain Range, Brazil. Although species of *Chironius* primarily feed on anurans, we report new prey records for *C. brazili*, including the Cycloramphidae and the first documented case of fish predation in the genus. These records expand the known diet of *C. brazili* and demonstrate its ability to exploit different environments while foraging.

Key Words: : Snake, Diet, Cycloramphidae, Fish.

The vine snake *Chironius brazili* Hamdan and Fernandes, 2015, is found in the ecoregions of the Cerrado, Atlantic Forest, and Pampa, primarily inhabiting gallery forests and open areas (Hamdan and Fernandes, 2015; Ugalde *et al*., 2024). Species of the genus *Chironius* Fitzinger, 1826, exhibit morphology primarily adapted for an arboreal lifestyle (*i.e.* slender body, long tail, and large number of vertebrae; Banci *et al*., 2022; Parreira *et al*., 2024) and have a predominantly batrachophagous diet, although they also feed on reptiles, mammals, and birds (Roberto and Souza, 2020). However, *C. brazili* can exploit different substrates while foraging, including rocky outcrops along waterfall margins in mountainous regions of the Brazilian Cerrado (Parreira *et al*., 2024).

The Espinhaço Mountain Range, in eastern Brazil, extends for approximately 1200 km across the states of Minas Gerais and Bahia, with altitudes ranging from 800 to 2000 m a.s.l. (Silveira *et al*., 2016). This mountain range forms a transition between the Atlantic Forest to the east and the open landscapes of the Cerrado and Caatinga to the north and west (Guedes *et al*., 2020; Santana *et al*., 2023). Above 1000 m a.s.l., *campo rupestre* (rupestrian fields) predominates, an environment characterised by shrub-grass vegetation interspersed with rocky outcrops and open areas with sandy soil and low water availability (Silveira *et al*., 2016; Santana *et al*., 2023).

Although the low tree cover density in the open areas of the Cerrado and *campo rupestre*, *Chironius* species occurring in these environments primarily feed on hylids (Kok, 2010; Fernandes and Hamdan, 2014; Hamdan and Fernandes, 2015; Roberto and Souza, 2020; Parreira *et al*., 2024). This association suggests that, even in predominantly open habitats, *Chironius* maintains its dietary preference for arboreal anurans (Roberto and Souza, 2020; Parreira *et al*., 2024). This study presents new observations

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on the feeding and hunting behavior of *C. brazili* in the *campo rupestre*, highlighting a new predation record on the Cycloramphidae big-eared river frog, *Thoropa megatympanum* Caramaschi and Sazima, 1984, and the first documented case of fish predation in *Chironius*.

On 16 October 2022, at approximately 03:40 pm, in the southern region of the Espinhaço Mountain Range, in the municipality of Presidente Kubitschek, Minas Gerais, Brazil (18°27'16.7"S 43°36'10.9"W) (Fig. 1), an adult *C. brazili* was observed foraging on a rocky outcrop, moving through crevices and cavities on the rock surface, close water bodies and waterfalls, as reported by Parreira *et al.* (2024). The snake inserted its head into a rocky foramen, struck, and captured an adult *T. megatympanum* (Fig. 2), extracting it from the rock crevices and swallowing it. After digestion, the snake resumed its foraging activity, climbed onto the rocks, and captured another *T. megatympanum*, repeating the same capture and consumption process. Both anurans were ingested in a postero-anterior direction within approximately 20 minutes.

The second record was made on 10 October 2024, at approximately 02:20 pm, also in the southern region of the Espinhaço Mountain Range, in the municipality of Diamantina, Minas Gerais, Brazil (18°11'01.08"S, 43°37'05.60"W) (Fig. 1). An adult *C. brazili* was observed foraging within a waterfall, near rocky outcrops. During the observation, the snake submerged in the water and, while still underwater, it grabbed an unidentified fish, which it carried to the surface and swam towards one of the banks surrounding the waterfall. This is the first known record of *Chironius* preying on a fish.

Information on the foraging and diet of *C. brazili* is scarce (Roberto and Souza, 2020; Parreira *et al.*, 2024). Until now, only two prey species have been recorded for this snake, both occurring in high-altitude rocky streams being *Bokermannohyla martinsi* (Bokermann, 1964) (n= 1) and *B. pseudopseudis* (Miranda-Ribeiro, 1937) (n= 3) (Lucas *et al.*, 2017;

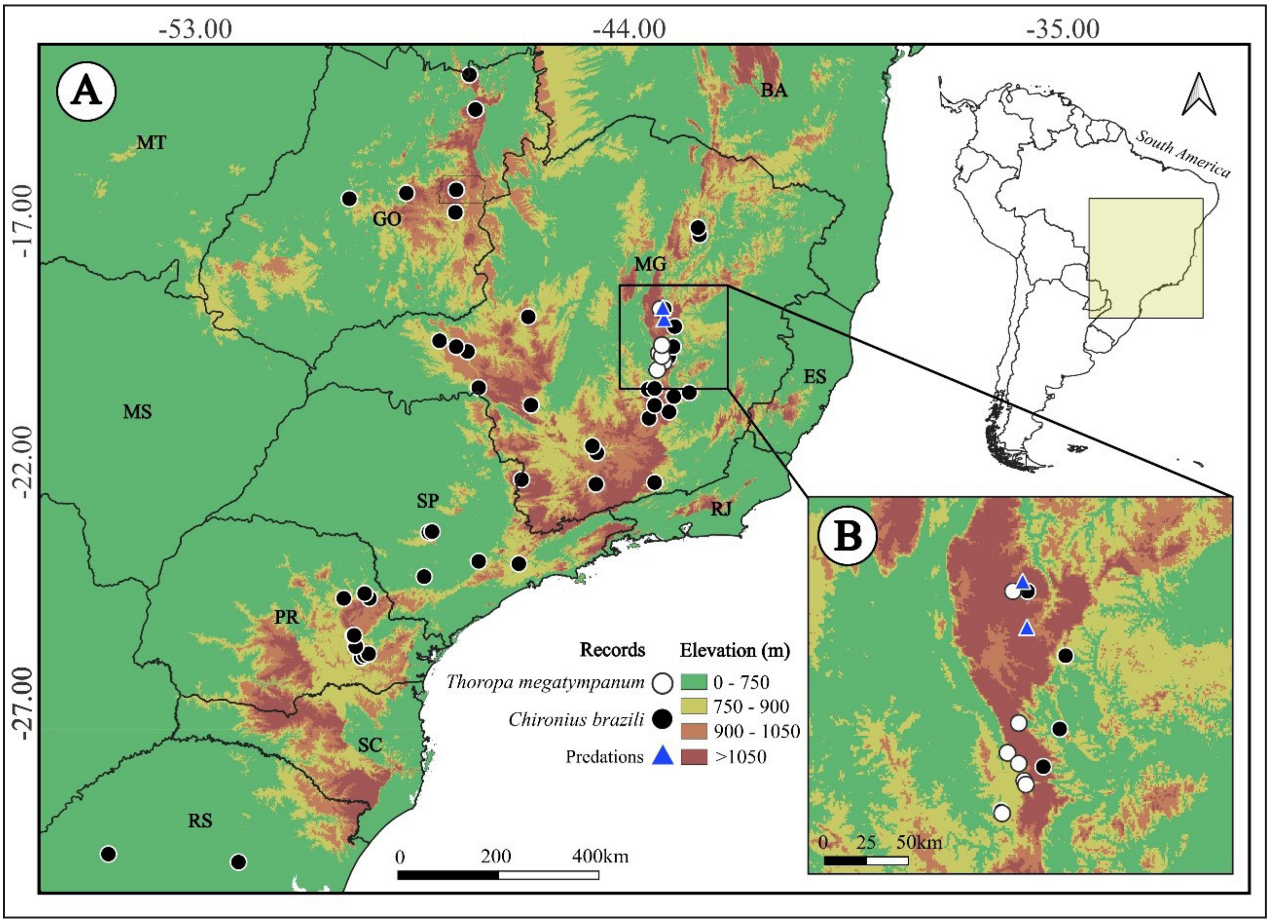

Figure 1. (A) Topographic map showing the known distribution of vine snake *Chironius brazili* (black circles), big-eared river frog *Thoropa megatympanum* (white circles) and our records (blue triangles). (B) Enlarged region showing the location of predation events in the southern portion of the Espinhaço Mountain Range (Minas Gerais, Brazil).

Figure 2. Adulte vine snake *Chironius brazili* with an adult big-eared river frog *Thoropa megatympanum* in its mouth in Espinhaço Mountain Range (Minas Gerais, Brazil).

Parreira *et al.*, 2024). Similarly, *T. megatympanum* also inhabits high-altitude *campo rupestre* environments (Fig. 1B), using these habitats for shelter and reproductive vocalization (Caramaschi and Sazima, 1983; Sabbag *et al.*, 2018). The association of these anurans with streams, rocky outcrops, and sparse vegetation makes them potential prey for snakes that forage in such environments (*e.g.*, Roberto and Souza, 2020; Parreira *et al.*, 2024). Although the diet of the genus *Chironius* is largely based on hylid frogs (Roberto and Souza, 2020), our records indicate that *C. brazili* exhibits an opportunistic feeding strategy, consuming the prey available in its habitat. This report expands the knowledge of the species diet and highlights its efficient foraging capability in rocky Cerrado environments. Moreover, the predation of a fish by this species suggests a greater dietary flexibility, as well as the ability to explore aquatic environments in search of prey.

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Novedad zoogeográfica

Cuad. herpetol. 39 (2): 131-134 (*2025*)

Nuevos registros altitudinales de *Bothrops ammodytoides* Leybold, 1873 (Serpentes: Viperidae: Crotalinae) en la Cordillera de los Andes, San Juan, Argentina

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Localidad.— República Argentina. Provincia de San Juan, Departamento Iglesia (30° 40' 07.77" S; 69° 33' 0.82" O, 3122 m s.n.m.) ejemplares 1 y 2; Departamento Calingasta (31° 21' 25" S; 69° 51' 04" O, 2631 m s.n.m.) ejemplar 3. Fecha de colección: 29 de diciembre de 2023, 26 de marzo de 2024 y 21 de abril de 2024, respectivamente. Colectores: Feldman M., Gómez Alés R., Méndez Osorio Y., Valdez Ovallez F., Villafañe J., Gómez F. Los ejemplares colectados fueron depositados en la Colección Herpetológica del Departamento de Biología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan (Ejemplar 1: UNSJ- 3705; ejemplar 2: UNSJ- 3706; ejemplar 3: UNSJ- 3702) (Figs. 1 y 2).

Comentarios.— *Bothrops* (Viperidae) es un género representado por 48 especies y con una amplia distribución geográfica en América del Sur y Centroamérica (Uetz *et al.*, 2024). En Argentina están presentes 12 especies incluyendo a *Bothrops ammodytoides*, especie endémica del país y la serpiente con la distribución más austral del mundo (Campbell *et al.*, 2004; Carrasco *et al.*, 2010; Williams y Vera, 2023). Es una especie terrestre y vivípara cuya dieta incluye presas ectotérmicas como saurios (Gómez Alés *et al.*, 2013; Zaldua *et al.*, 2020; Tettamanti *et al.*, 2024) y anuros, junto con roedores y aves (Acosta *et al.*, 2018; Williams y Vera, 2023). Su presencia está asociada a ambientes áridos, con suelos desnudos rocosos, arenosos y salinos; encontrándose citada para las provincias de Salta, Catamarca, La Rioja, Tucumán, San Juan, Mendoza, San Luis, La Pampa, Neuquén, Río Negro, Chubut, Santa Cruz, Córdoba y Buenos Aires (Giraudo y Scrocchi, 2002; Carrasco *et al.*, 2010; Williams *et al.*, 2021).

Respecto a la distribución altitudinal de *Bothrops ammodytoides*, sus registros conocidos se hallan generalmente entre los 500-2000 m s.n.m., pudiendo llegar su límite inferior hasta localidades cercanas al nivel del mar en el sudeste de Argentina (Campbell *et al.*, 2004; Carrasco *et al.*, 2010). La máxima altitud mencionada para la especie se reporta en Carrasco *et al.* (2010), en la localidad de Tres Cruces, provincia de Jujuy, a una altitud de 3700 m s.n.m.; sin embargo, el registro proviene de una comunicación personal, no habiendo material de referencia disponible. Posteriormente, Burgos *et al.* (2020) indicaron que dicha observación corresponde en realidad a una localidad de la provincia de Salta, no existiendo registros confirmados para Jujuy. De manera similar, en Barrionuevo *et al.* (2016) se reportan observaciones visuales acompañadas de material fotográfico de *B. ammodytoides* a altitudes entre los 3090 y 3430 m s.n.m. En Scrocchi *et al.* (2023) se menciona que la especie puede encontrarse a más de 3000 m s.n.m. en la región de la Puna, e indica registros a partir de puntos geográficos asociados a un mapa de las provincias de Catamarca y Salta. El registro de mayor altitud para *B. ammodytoides* avalado por un voucher, corresponde a un ejemplar (IBIGEO 5692) colectado en el Departamento Ro-

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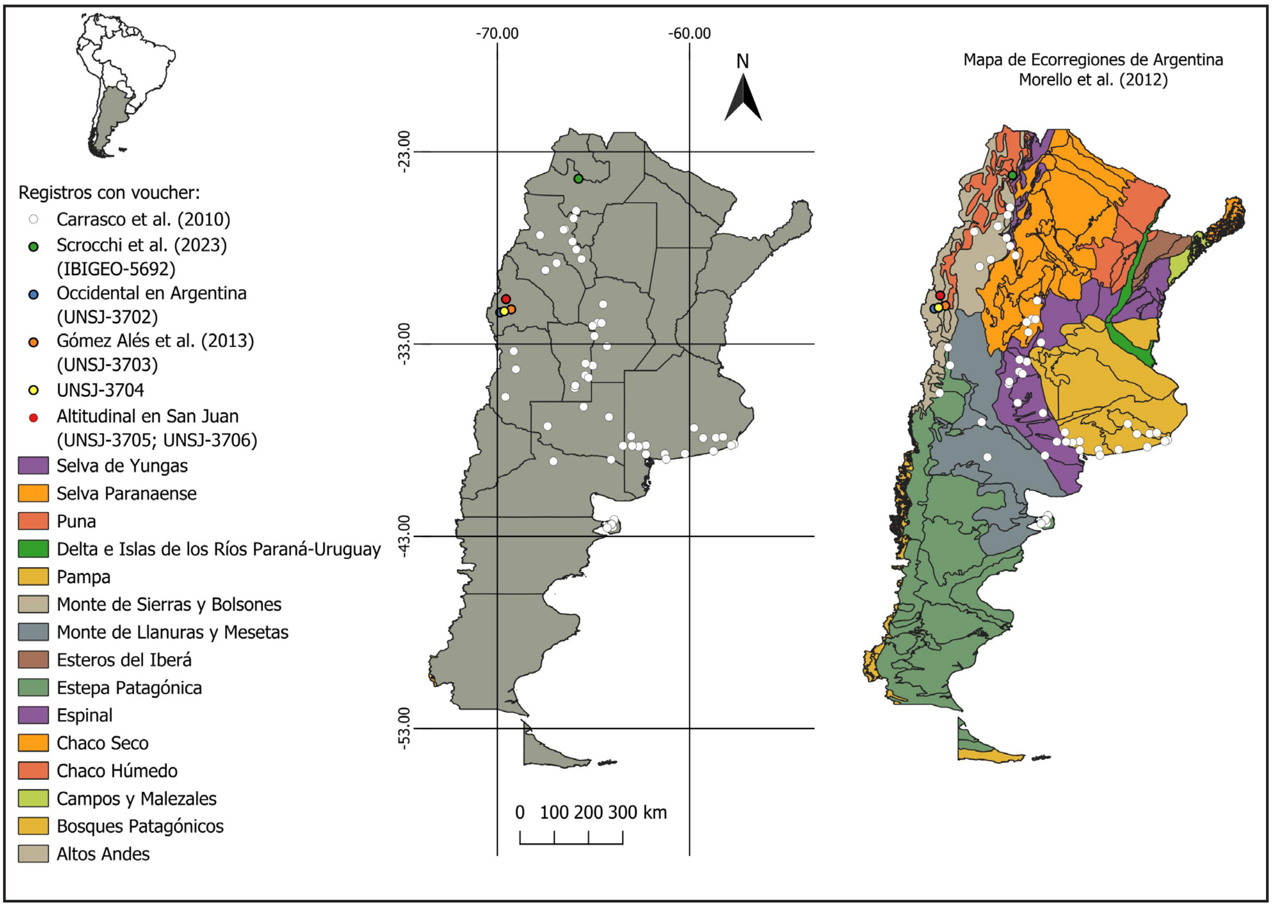

Figura 1. Registros de distribución geográfica de *Bothrops ammodytoides* en Argentina según Carrasco et al. (2010), adicionando ejemplares reportados en el presente trabajo (UNSJ- 3702; UNSJ- 3705; UNSJ- 3706), ejemplares depositados en la Colección Herpetológica del Departamento de Biología FCEFN, UNSJ (UNSJ- 3703; UNSJ- 3704) y ejemplar reportado en Scrocchi *et al.* (2023) (IBIGEO 5692).

sario de Lerma, Salta, a aproximadamente 3300 m s.n.m. (Scrocchi *et al.*, 2023; Carrasco com. pers.). Sin embargo, son escasos los registros confirmados de esta especie a elevadas altitudes y con material de referencia disponible. En el presente trabajo reportamos nuevos registros altitudinales para *Bothrops ammodytoides*, confirmando su presencia a altitudes elevadas, con ejemplares encontrados entre los 2600 y 3100 m s.n.m. en la provincia de San Juan. Además, ampliamos la distribución de esta especie hacia el oeste de la Argentina, proporcionando información sobre los especímenes y características ambientales de los sitios de colecta más elevados.

Los registros de mayor altitud aquí reportados, a los 3122 m s.n.m., corresponden a los ejemplares 1 y 2, los cuales fueron hallados durante una campaña herpetológica en el Departamento Iglesia, Provincia de San Juan, Argentina. El día 29 de diciembre de 2023 a las 13:20 h se halló un ejemplar macho juvenil de *Bothrops ammodytoides* (Ejemplar 1; UNSJ-3705; Fig. 2A,B) resguardado bajo una roca. El mismo presenta las siguientes características: largo hocico-cloaca (LHC) 164 mm y largo cola (LC) 29 mm; 11/11 supralabiales; 23-23-19 dorsales; 144 ventrales; 34 subcaudales. En el mismo sitio, el 26 de marzo de 2024 a las 19:55 h, se halló un macho adulto (Ejemplar 2; UNSJ-3706; Fig. 2C,D) enrollado en el suelo desnudo, presentando las siguientes características: LHC = 260 mm y LC = 14 mm, encontrándose esta última amputada; 11/11 supralabiales; 24-24-20 dorsales; 133 ventrales; 13 subcaudales. En ambos encuentros se registró información del microhábitat, para el ejemplar 1 se registró la temperatura de la superficie de la roca en contacto con el sustrato 22.5 °C y la temperatura del sustrato 27.5°C; para el ejemplar 2 se registró humedad relativa 76%, temperatura del aire 13.4°C, temperatura del sustrato 16°C y adicionalmente su temperatura corporal 14.5°C. El ejemplar 3, macho subadulto de *B. ammodytoides* (UNSJ-3702; Fig.

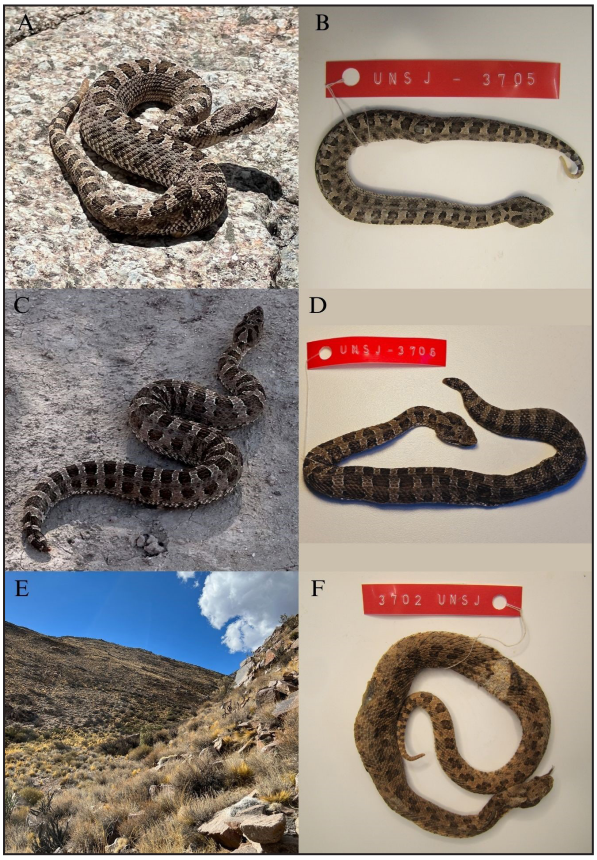

Figura 2. Ejemplares de *Bothrops ammodytoides* reportados en el presente trabajo UNSJ-3705 (A,B), UNSJ-3706 (C,D), UNSJ-3702 (F); y sitio de encuentro a mayor altitud, Cordillera de los Andes, Departamento Iglesia, Provincia de San Juan, Argentina (E).

2F), fue hallado el 21 de abril de 2024, a una altitud de 2631 m s.n.m. en el Campamento Candadito, Departamento Calingasta, Provincia de San Juan, Argentina. El mismo presentaba señales evidentes de haber sido atropellado, algunas características: LHC = 317 mm y LC = 42 mm; 10/11 supralabiales; 25-25-21 dorsales; 153 ventrales; 34 subcaudales. Este último registro amplía la distribución conocida de la especie hacia el oeste en Argentina con relación al registro publicado en Carrasco *et al.* (2010) correspondiente al ejemplar FML 7699 hallado en Malargüe, provincia de Mendoza.

En el presente trabajo también se incluye al ejemplar de *Bothrops ammodytoides* registrado en Gómez Alés *et al.* (2013), el cual fue encontrado en la Quebrada Vallecito, Departamento de Calingasta, Provincia de San Juan, a una altitud de 2860 m s.n.m. (31.20°S; 69.28°O) (UNSJ- 3703; Fig. 1), formando parte de la provincia fitogeográfica de la Puna. De esta manera, los nuevos registros correspondientes a los ejemplares 1 y 2 extienden el límite superior de distribución altitudinal en 262 metros con respecto al registro máximo reportado para la especie en la provincia. Adicionalmente, se agrega en el mapa (Fig. 1) el ejemplar UNSJ-3704 depositado en la Colección Herpetológica del Departamento de Biología, FCEFN, UNSJ. El mismo fue encontrado en la Quebrada Las Burras, Departamento de Calingasta, Provincia de San Juan, a una altitud de 1994 m s.n.m. (31° 17' 48" S; 69° 38' 11" O).

El sitio de mayor elevación donde fueron hallados los ejemplares (Fig. 2E) corresponde a la provincia fitogeográfica de la Puna (Marquez *et al.*, 2016), ambiente de altura que abarca desde los 3000 a los 3800 m de altitud, caracterizado por un clima frío y seco con gran amplitud térmica diaria y estacional, prolongados períodos de sequía, fuertes vientos y alta radiación solar. Se distingue por una vegetación xerófila representada por matorrales de *Lycium*, ajenjo (*Artemisia mendozana var. paramilloensis*), tolas (*Fabiana denudata*), leña amarilla (*Adesmia horrida*), y un estrato herbáceo con gramíneas pertenecientes a los géneros *Pappostipa* y *Jarava* (Marquez *et al.*, 2016; Gómez Alés *et al.*, 2021; Valdez Ovallez *et al.*, 2024).

Estos registros de *Bothrops ammodytoides* confirman la presencia de la especie en altitudes que superan los 3000 m s.n.m. y, junto con *B. jonathani* (Carrasco *et al.*, 2009, 2010), es una de las pocas especies del género presentes a dicha altitud en regiones andinas. Por otro lado, los registros reportados en este estudio corresponden al punto más occidental de su distribución actual conocida en Argentina. Por último, al tratarse de una serpiente venenosa y de importancia médico-sanitaria, la ampliación y el conocimiento de la distribución geográfica de *Bothrops ammodytoides* en la provincia constituye información relevante para la prevención y el tratamiento de accidentes ofídicos relacionados con esta especie.

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Range extension and natural history notes of *Siphlophis leucocephalus*

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Locality.— Brazil, state of Bahia, municipality of Paulo Afonso, Estação Ecológica Raso da Catarina (ESEC-RC) (9.65°S, 38.51°W; WGS84, 593 m above sea level); area of low Caatinga vegetation. We found the specimen on September 6, 2024, during a fieldwork carried out between 2–10 of September 2024 at the ESEC-RC. This is a 99,772 ha, fully protected conservation unit, in the São Francisco River valley (Garda *et al.*, 2013). We found the adult male *Siphlophis leucocephalus* while it was moving along a branch close to the ground, collected it manually and transported it to the improvised laboratory at ICMBIO (Instituto Chico Mendes de Conservação da Biodiversidade) headquarters. There, we anesthetized and euthanized it with a lethal dose of 2% lidocaine hydrochloride. Subsequently we fixed it in 10% formalin, preserved in 70% alcohol and deposited in the herpetological collection of the Universidade Federal de Pernambuco (CHUFPE-R 1943). The morphology and pholidosis of the specimen (Fig. 1) allowed us to identify it: Snout-vent length 728 mm; tail length 185 mm. Number of supralabial scales 8; supralabial touching ocular iv + v; preocular 1; postocular 2; temporal 2+3; infralabial 9. Nasal divided. Number of dorsal body scales 19–19–17; ventral 235; subcaudal 84. Cloacal scale single. Dark body bands 17; nine dark tail bands.

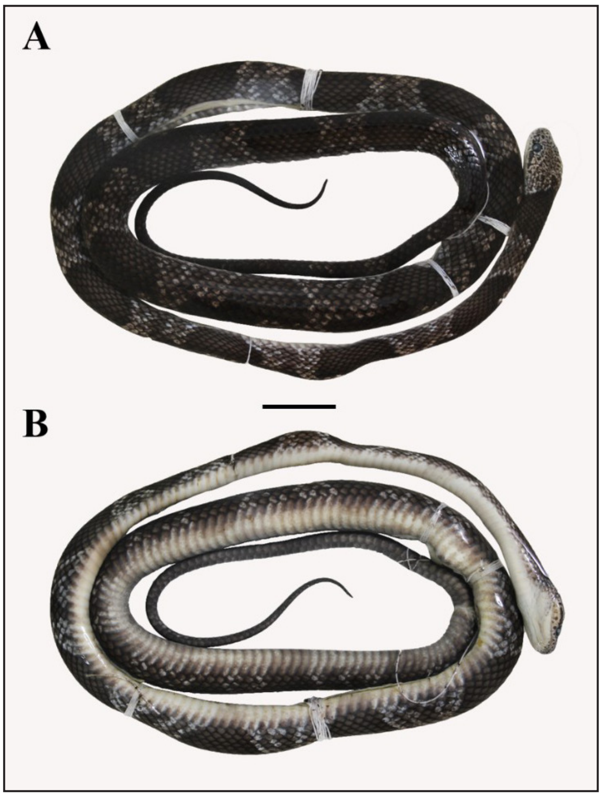

Figure 1. Specimen of *Siphlophis leucocephalus* (CHUFPE-R 1943), in dorsal (A) and ventral (B) views, collected at Estação Ecológica Raso da Catarina, Paulo Afonso, Bahia, Brazil. Scale bar = 20mm.

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Comment.— Caatinga, the predominant biome in the northeast region of Brazil, covers about 70% of the territory (da Silva *et al.*, 2017) and stands out as a unique habitat for reptiles and amphibians due to its climatic and geomorphological history (Rodrigues, 2003). Among the squamate reptiles of the Caatinga, snakes are particularly notable for their moderate to high endemism. They inhabit open and forested areas, ecotones, the Borborema Plateau highlands, and lowland semiarid zones such as the paleoclimatic dunes of the São Francisco River (Guedes *et al.*, 2014). The species *Siphlophis leucocephalus* (Günther, 1863), occurs from the Atlantic Forest in Bahia westward to the Caatinga and Cerrado biomes in Minas Gerais and Tocantins (Thomassen *et al.*, 2015; Nogueira *et al.*, 2019). It is identified by its dorsal pattern of approximately 18 large dark spots or saddles, four light-scaled head and collar spots, 13 solid maxillary teeth, two postoculars, and 17 scale rows anterior to the cloaca (Bailey, 1970; Thomassen *et al.*, 2015), and has limited natural history data available (see Maia-Carneiro *et al.*, 2016). This study expands *S. leucocephalus* range in the Caatinga, describes a new antipredator behavior, and reviews its known strategies.

Specifically, the species has been previously recorded in tropical and semideciduous forests in southeastern Bahia (Bahia Coastal Forests ecoregion), in the semideciduous forests of Chapada Diamantina, also in Bahia state (Caatinga ecoregion), in gallery forests in the Cerrado biome in the Arraias (Cana Brava) ecoregion in the state of Tocantins, and in Minas Gerais (Thomassen *et al.*, 2015) (Fig. 2, Table 1). In addition, the species occurs on both sides of the São Francisco River (see Prudente, 1998; Zaher & Prudente, 1999; Argôlo, 2004; Costa *et al.*, 2007; Freitas *et al.*, 2012; Thomassen *et al.*, 2015). Our new record at ESEC-RC extends the range of the species to lowland Caatinga forests, about 500 km north from the closest geographic record, in Mucugê, state of Bahia (Fig. 2). The map presented in Nogueira *et al.* (2019, Plate 340) mistakenly locates a record in northern Goiás state, which actually corresponds to the locality in Arraias, southern

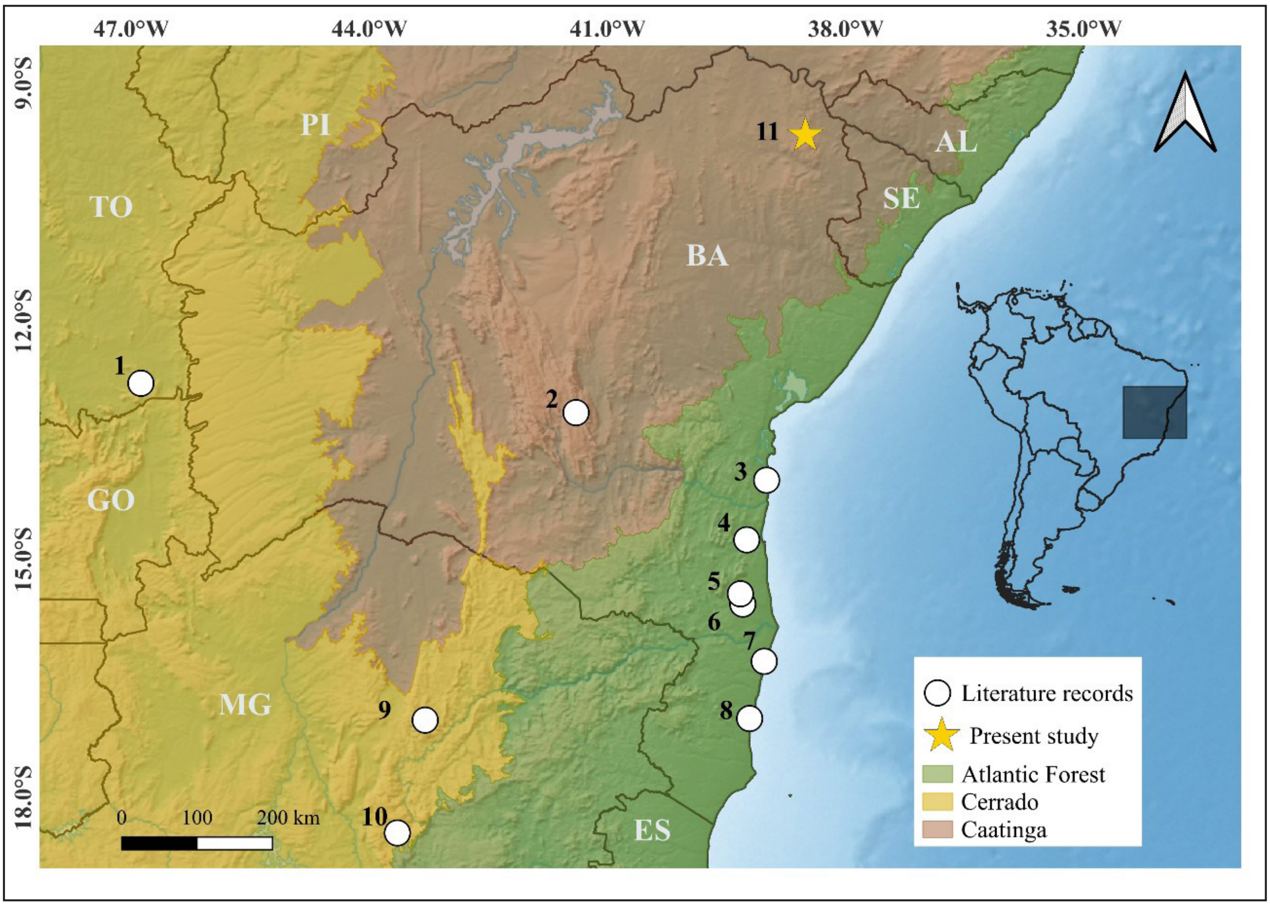

Figure 2. Geographic distribution records of *Siphlophis leucocephalus* across northeast Brazil's main phytogeographic regions. AL = Alagoas; BA = Bahia; ES = Espírito Santo; GO = Goiás; MG = Minas Gerais; PI = Piauí; SE = Sergipe; TO = Tocantins.

Table 1. Geographic records of *Siphlophis leucocephalus* (adapted from Thomassen *et al.*, 2015). For records lacking geographic coordinates, information was obtained from Paynter and Taylor (1991), IBGE (2011) or software Google Earth™. Latitude (Lat.) and longitude (Long.) in decimal degrees. * = present study. BA = Bahia; MG = Minas Gerais; TO = Tocantins.

State	Municipality/ Locality	Lat.	Long.	Elevation (m a.s.l.)	Source of Record	Source of coordinate
BA	Ilhéus (4 on the map)	14°45'00.0"S	39°15'00.0"W	90	Freitas 2003, Argôlo, 2004	County seat
BA	Mascote (6 on the map)	15°33'36.0"S	39°18'00.0"W	80	Argôlo, 2004	County seat
BA	Mucugê / distrito de Cascavel, Caraíbas (2 on the map)	13°09'00.0"S	41°24'00.0"W	1160	Freitas et al., 2012	Freitas et al. 2012
BA	Santa Cruz Cabrália (7 on the map)	16°16'48.0"S	39°01'48.0"W	80	Prudente, 1998	County seat
BA	Uruçuca / close to Serra Grande (4 on the map)	14°00'00.0"S	39°00'00.0"W	70	Rodrigo C. G. de Souza (Fig. 1 in Thomassen et al., 2015)	GPS
BA	Prado / Parque Nacional do Descobrimento (8 on the map)	17°00'00.0"S	39°00'00.0"W	75	Uetz, 2014 (photograph)	Approximate
BA	Santa Luzia (5 on the map)	15°25'48.0"S	39°19'48.0"W	290	Argôlo, 2004	County seat
BA *	Paulo Afonso / Estação Ecológica Raso da Catarina (11 on the map)	9°39'25.6"S	38°30'36.0"W	593	CHUFPE-R 1943	GPS
MG	Dantas (10 on the map)	18°26'24.0"S	43°39'00.0"W	1280	UFMG-R 197 (Thomassen et al., 2015)	County seat
MG	Itacambira / Serra de Itacambira, Tamanduá Village (9 on the map)	17°01'12.0"S	43°18'00.0"W	1230	UFMG-R 1020 (Thomassen et al., 2015)	GPS
TO	Arraias / Cana Brava (1 on the map)	12°46'48.0"S	46°52'48.0"W	600	Amaral, 1935 (as S. cervinus, S. geminatus), Prudente et al., 1998	Approximate

Tocantins state (Thomassen *et al*., 2015). So far, there are no published records of this species in the state of Goiás.

We also recorded some natural history observations (Fig. 3). The individual was found at night moving along a branch 40 cm above sandy soil. Upon capture, it displayed erratic movements as antipredator behavior. The next day, under daylight (Fig. 3A), we recorded additional strategies, such as coiling the body as a ball and hiding the head under or within coils. While being photographed, previously unreported displays were noted, including tail vibration, mouth strikes, head flattening and elevation, head triangulation (Figure 3B), and "S"-shaped neck curves (Fig. 3B and C). Cloacal discharge also occurred during handling.

Siphlophis leucocephalus is globally listed as Least Concern (LC) due to its large geographic distribution (Silveira *et al.*, 2020) in the Atlantic Forest of Brazil and in transition areas between Atlantic Forest, Cerrado and Caatinga biomes. Our record is the second within the Caatinga biome, expanding the geographic distribution of this snake northwards, close to the mid-course of the São Francisco River. Records in different biomes and ecoregions suggest that the species is a habitat generalist, occupying habitats with very distinct vegetation structure and subject to different climatic regimes —particularly

Figure 3. Male specimen of *Siphlophis leucocephalus* (CHUFPE-R 1943) photographed in life at rest (A) and while displaying anti-predator behaviors: flattening and elevation of anterior part of the body and head (B) and triangulation of the head (C). Photographs by Ubiratã Souza.

regarding annual rainfall. Additionally, *S. leucocephalus* was previously reported in two conservation areas (Reserva Particular do Patrimônio Natural Fazenda Araçari and Área de Proteção Ambiental Costa de Itacaré/Serra Grande) (Silveira *et al.*, 2020) and our record also occurred in a conservation area, underscoring the importance of protected areas for its conservation.

Behaviors such as adopting an S-shaped neck, triangulating the head, and tail shaking are associated with predator intimidation (Tozetti *et al.*, 2009), signaling potential danger—possibly mimicking the

Table 2. Antipredator behavioral data for species of the genus *Siphlophis*, based on new records and literature data. * = behaviors recorded in this study.

Species	***S. cervinus***	***S. compressus***	***S. leucocephalus***	***S. longicaudatus***	***S. pulcher***	***S. worontzowi***
Forming a ball	X	X	X	X	X	X
Cloacal discharge	X	X	X*	X		
Flattening			X*			
Hiding head between body	X	X	X	X	X	
Tail vibration		X	X*	X		
S-shaped neck		X	X*	X	X	
Erratic movements			X*	X		
Head triangulation		X	X*			
Elevation of the head and anterior portion of the body	X	X	X*	X	X	
Striking			X*	X		
Rotation of the body		X				
Mimetism		X		X	X	
Literature data	Martins *et al.*, 2008; Fraga *et al.*, 2013; Tozetti *et al.*, 2021	Martins *et al.*, 2008; Fraga *et al.*, 2013; Tozetti *et al.*, 2021	Carvalho *et al.*, 2017; present study	Martins *et al.*, 2008; Pereira *et al.*, 2018	Martins *et al.*, 2008; Tozetti *et al.*, 2021	Tozetti *et al.*, 2021

behavioral and morphological traits of pitvipers in the genus *Bothrops* (Martins *et al.*, 2008). A strategy that may be effective against visually guided predators (Dell'Aglio *et al.*, 2012). Literature reports information on the behavior of six representatives of the genus *Siphlophis* (Table 2), including antipredator repertoire (Laurenti, 1768; Daudin, 1803; Raddi, 1820; Prado, 1940; Martins *et al.*, 2008; Fraga *et al.*, 2013; De Carvalho *et al.*, 2017; Pereira *et al.*, 2018; Tozetti *et al.*, 2021). Our findings on defensive behavior of *S. leucocephalus* expand the knowledge on the defensive repertoire in *Siphlophis* snakes, revealing patterns in this genus and reporting new defensive strategies.

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