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Activity, foraging mode, and abundance of the aquatic coral snake *Micrurus surinamensis* (Cuvier, 1816) (Serpentes: Elapidae) in the western Brazilian Amazonia

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ABSTRACT

Elapids of the genus *Micrurus* actively search for their prey. Here we present new information on the foraging ecology of the aquatic coral snake *Micrurus surinamensis* based on observations in the western Amazon of Brazil. Eleven individuals of *M. surinamensis* were observed at night, four of them moving, four hunting in ambush posture, and three actively hunting. Here, we show that *M. surinamensis* is active mainly at night in aquatic environments and may also be active on the terrestrial environments. Land activity may be related with the search for fish which may eventually be found in this substrate, as well as with the search for water bodies, following the hydrological cycles of flooding and drought. When hunting, the snake uses both foraging modes, being able to actively search for its prey, or ambush it, by keeping the body partially in the water, with the head on the surface. Due to the greater availability of aquatic environments and available prey (fish), *M. surinamensis* should be more abundant in floodplain forest ecosystems. Additional field observations may help in elucidating the biology on this ecologically differentiated species within the genus *Micrurus*.

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Introduction

Snakes are predatory animals that exhibit several feeding behaviors. Some species are active foragers that move around the environment looking for their prey, whereas others are ambush hunters, and waiting for prey to approach within range of their predatory strike (Arnold 1993; Beaupre & Montgomery 2007). The predominant type of foraging mode is highly conserved amongst snake families (Beaupre & Montgomery 2007). Boids, pythonids, and viperids commonly hunt prey by ambush, whereas colubrids and elapids are mainly active foragers (Shine 1977, 1979; Glaudas et al. 2019).

Relative to colubrids and vipers, less is known about the foraging ecology of elapid snakes (Mushinsky 1987). With a few exceptions (e.g. the Australian *Acanthophis antarcticus* and *Hoplocephalus bungaroides*), elapids tend to actively hunt their prey in their habitats (Shine 1980; Webb & Shine 1997). In the New World, elapids belonging to the genus *Micrurus* (true coral snakes) are known to actively forage for their prey (Greene 1984; Martins & Oliveira 1998; Almeida

et al. 2016) by inspecting the substrate and galleries in the soil (e.g. Marques & Sazima 1997; Banci et al. 2017).

The 83 species of true Coral snakes of the genus *Micrurus* (Uetz et al. 2024) occur from sea level to altitudes above 1,500 m and in many different ecoregions (Campbell & Lamar 2004). Most have terrestrial and semi-fossorial habits, with a few species associated with aquatic habitats (e.g. *M. lemniscatus* and *M. surinamensis*) (Almeida et al. 2016). Depending on the species, true coral snakes can be diurnal and/or nocturnal, though most are more active during the rainy season (Almeida et al. 2016). Regarding their diet, elongated vertebrates (snakes, amphisbaenians, caecilians, and fish), lizards and invertebrates (onychophorans) are eaten by *Micrurus* species (Roze 1996; Marques & Sazima 1997; Martins & Oliveira 1998; Campbell & Lamar 2004). In a recent review of the biology of Brazilian species, Almeida et al. (2016) found that snakes and amphisbaenians are the main prey items, followed by gymnophthalmid lizards, caecilians, other lizards, fish, and invertebrates.

The aquatic coral snake, *Micrurus surinamensis*, occurs in the Amazon regions of Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname, and Venezuela (Nogueira et al. 2019). *Micrurus surinamensis* is considered to be associated with aquatic habits, showing both diurnal and nocturnal activity, and occurring in various types of aquatic environments in forest, open, and disturbed areas (Martins & Oliveira 1998; Bernarde & Abe 2006). It may reach 1,400 mm in total length (Silva-Haad 1994) and is the most robust species within *Micrurus* (Campbell & Lamar 2004). It feeds mainly on fish (*Callichthys callichthys*, *Gymnotus carapo*, *Sternopygus macrurus*, and *Synbranchus marmoratus*) (Silva-Haad 1994; Martins & Oliveira 1998; Morais et al. 2011; Almeida et al. 2016; Corrêa et al. 2018; Sierra-Rueda et al. 2020; Tavares-Pinheiro et al. 2021) and occasionally on lizards (Martins & Oliveira 1998), with a single record in the literature of a snake (*Erythrolamprus reginae*; Pinto et al. 2011).

Micrurus surinamensis has longer temporal and quadrate bones and thus has a more kinetic skull than other *Micrurus*, and its wider gape size allows it to feed on larger and wider prey, contrasting with other

congeneric terrestrial species, which feed mainly on elongated prey, such as snakes, amphibiaenians, and caecilians (Almeida et al. 2016; Silva et al. 2018). Another adaptation observed in *M. surinamensis* refers to the composition of its venom, which shows enzymatic activities differing from other *Micrurus*, having higher toxicity to fish than to other prey types (snakes, amphisbaenians, and caecilians) (Silva & Aird 2001). Here we present information about the foraging activity and abundance of *M. surinamensis* in terra firme and várzea forests of the western Brazilian Amazonia.

Materials and methods

Observations in nature were carried out from September 2019 to January 2023 in three locations in the municipalities of Cruzeiro do Sul and Tarauacá, Acre state, Brazil (Figure 1). The state of Acre is located in the western Brazilian Amazonia, and shows a tropical, hot, humid climate with an average annual temperature of 22–24°C (Acre 2010). The annual rainfall in the region varies between 1,140 mm and 2,700 mm with the relative humidity always above

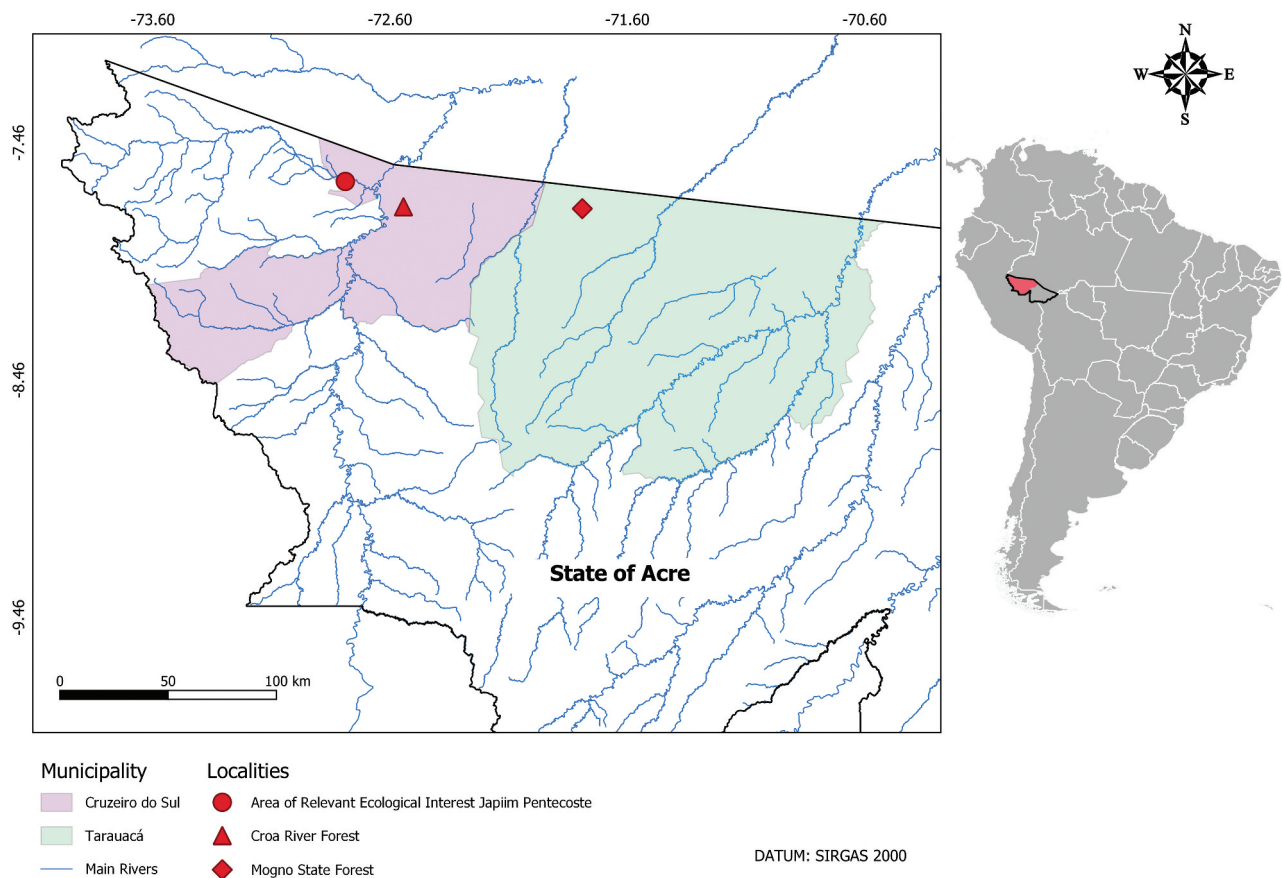


Figure 1. Map with the location of the three study locations in the state of Acre, western Brazilian Amazon.

60%, with the driest period between June and September (Duarte 2006).

The first locality was the Japiim-Pentecoste Area of Relevant Ecological Interest (AJP; 07°37'S, 72°47' W, 189 m a.s.l.). It consists of an area of floodplain forest seasonally flooded by the lakes adjacent to the Moa River, located in Cruzeiro do Sul. The second locality was the Mogno State Forest (MSF; 7°50'S, 71°48' W, 265 m a.s.l.), which consists of an area of terra firme forest, located in Tarauacá. The third locality was Croa River Forest (RCF; 7°43'S, 72°32'W, 190 m a.s.l.), which consists of a floodplain forest seasonally flooded by the Croa River, located in Cruzeiro do Sul.

Regular monthly searches for snakes were carried out between August 2021 and January 2023 at ARIE Japiim-Petenconste and at Mogno Forest. We used time-constrained searches during the day and at night (Campbell & Christman 1982), which consists of walking slowly along a transect in search of snakes visually exposed in the environment. This method allows the observation of habitat use and activity patterns in the field. The sampling effort in these two locations was carried out as follows: (1) From August 2021 to July 2022: 48 person-hours of search at night and 24 during the day (in the morning) were carried out monthly in each location, totaling 576 person-hours of search at night and 288 during the day, making up 864 search person-hours per location. (2) From August 2022 to January 2023: only night searches were carried out (24 person-hours per month), totaling 144 person-hours. In addition to the regular search for snakes, incidental observations were made in the three locations between September 2019 and July 2021.

Three specimens were collected (SISBIO permit number: 12178) and deposited in the Herpetological Collection of the UFAC Campus Floresta (Vouchers: UFACF 4709, 4761, and 4809). Video recordings were deposited (catalog numbers ZUEC-VID 1047 and 1048) at Fonoteca Neotropical Jacques Viellard in

Campinas, São Paulo, Brazil (FNJV), which is available online (<https://www2.ib.unicamp.br/fnjv/>).

Results

Eleven individuals of *M. surinamensis* were observed in nature during the night, four of them moving (quickly), four hunting in ambush posture (stationary, with the body partially out of the water, with the head on the surface), and three actively hunting (moving slowly and inspecting the substrate) (Table 1; Figure 2). Most snakes (eight) were observed during the rainy season (October to April) and three during the dry season (July and September). Most specimens (ten) were observed in aquatic environments (temporary puddles and streams, streams, and lakes), with only two records on the forest floor.

An individual of *M. surinamensis* was observed on 10th December 2022, in a stream (approximately 1 m wide and 40 cm deep) in the Mogno Forest. It was stationary with the tip of its mouth next to the water, performing quick tongue flicking, and with the rest of the body on a substrate of fallen branches in the stream, next to an armored catfish (Siluriformes: Loricariidae) (Figure 3A–B). The snake made slow movements with its head toward the rippling of the water caused by the fish. On a sudden move by the armored catfish, the snake struck toward it and another fish (Characiformes) that was nearby, without success. After these attempts, it returned to its initial ambush position, with the tip of its mouth close to the surface of the water, eventually making head movements and tongue flicking. After approximately 50 minutes of foraging by ambush, it began to forage actively, moving slowly in the water, inspecting the environment with its head and flicking its tongue. It was observed for another 50 minutes and during this period it moved (going back and forth) for about 4 meters along the stream. This same individual (recognized by its natural

Table 1. Field observations of *Micrurus surinamensis* active in western Brazilian Amazonia.

Size (cm)	Locality	Date	Time	Substrate	Activity	Obs. Time	Fig.
120	AJP	18/09/2019	20:13	ground	Active foraging	3 min	2A
80	AJP	15/01/2020	20:56	water puddles	Active foraging	3 min	2B
100	RCF	17/02/2021	21:08	river	Ambush foraging	30 min	2C
75	AJP	07/07/2021	20:50	water puddles	Ambush foraging	25 min	2D
70	AJP	28/10/2021	20:10	lake	Moving	1 min	–
70	AJP	11/11/2021	20:30	temporary stream	Active foraging	5 min	–
32.2	AJP	24/04/2022	20:43	water puddles	Moving	1 min	–
50.6	AJP	26/07/2022	18:25	temporary stream	Moving	1 min	–
50	AJP	26/10/2022	19:40	ground	Moving	1 min	–
87.8	MSF	13/11/2022	18:57	temporary stream	Ambush foraging	2 min	–
100	MSF	10/12/2022	21:15	temporary stream	Ambush foraging	50 min	3A–B
100*	MSF	05/01/2023	21:40	temporary stream	Ambush foraging	30 min	3C–D

AJP, ARIE japiim-Pentenconste; MSF, Mogno State Forest; RCF, Rio Croa forest. * same individual as previous observation.

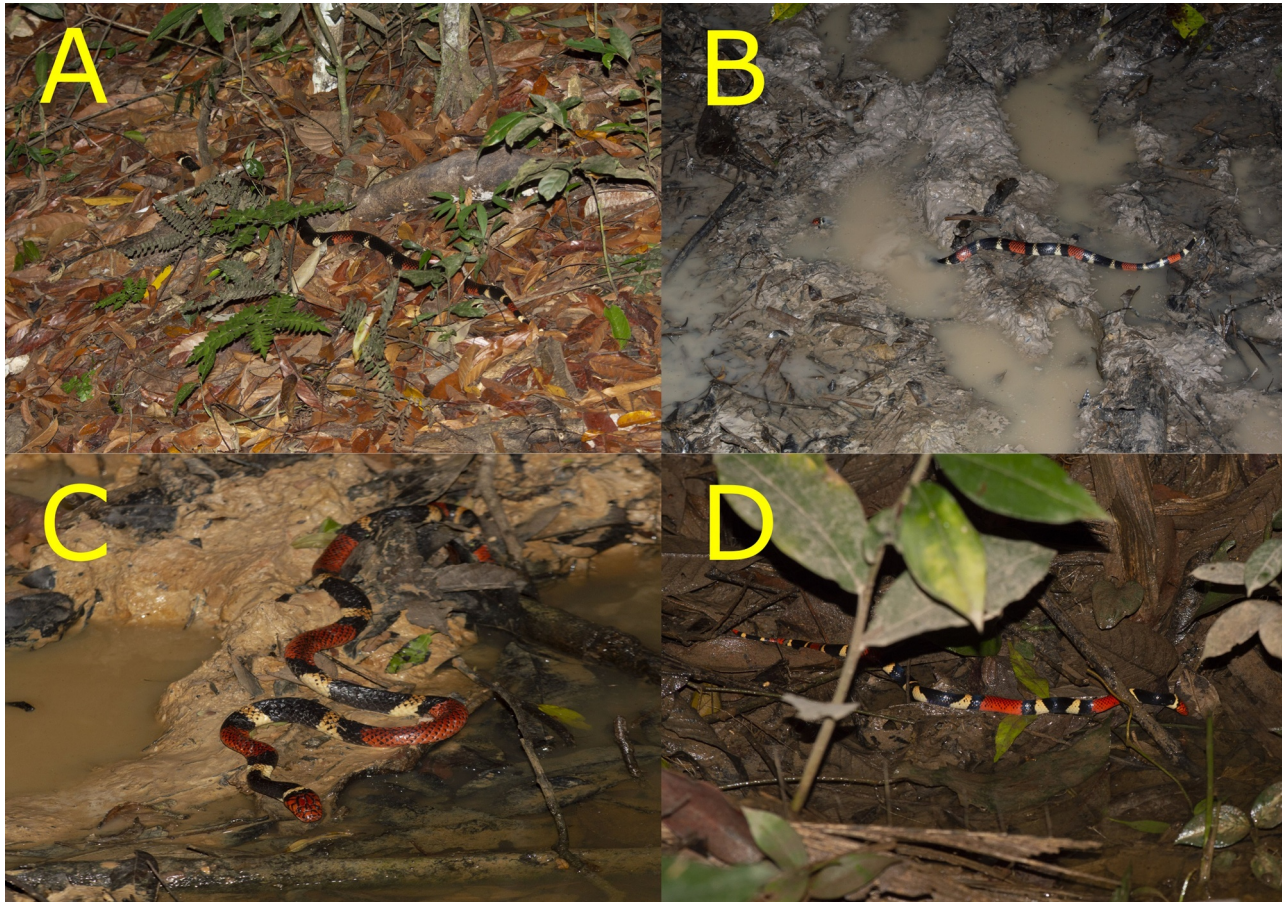


Figure 2. Photographs of some observed individuals: (A) an individual performing active foraging on the ground; (B) an individual actively foraging in temporary pools; (C) an individual foraging by ambush at the riverbank; (D) an individual foraging by ambush in temporary pools; Photos by M. R. N. Almeida.

marks) was observed again exhibiting the same hunting behavior the following month in the same stream.

At várzea forest (AJP) five individuals of *M. surinamensis* were recorded during a regular search for snakes, making up 3.2% out of 156 individuals of 32 species found. At terra firme forest, *M. surinamensis* corresponded to 1.6% out of 124 individuals of 38 species found. Other sympatric species of *Micrurus* recorded were *M. lemniscatus* (five individuals) on várzea forest, and *M. bolivianus* (one), *M. ortonii* (two), and *M. obscurus* (one) on terra firme forest.

Discussion

Most elapid species forage actively for their prey by searching the environment (Shine 1980; Webb & Shine 1997), and this was the only foraging pattern described for species of *Micrurus* (Greene 1984; Martins & Oliveira 1998; Almeida et al. 2016). Here we show that *M. surinamensis* may also forage by ambushing, besides searching for its prey actively. This behavior may be associated with its diet based

on fish, considering that ambush is a strategy used by other piscivorous snakes among natricines and dip-sadines (e.g. *Helicops angulatus*, *Nerodia clarkii*, *N. rhombifer*, *N. sipedon*, *Mesotes strigatus*, and *Thamnophis atratus*) (Martins & Oliveira 1998; Mario-da-Rosa et al. 2020), subfamilies in which active foraging is also widespread (Mushinsky 1987; Martins & Oliveira 1998; Glaudas et al. 2019). Indeed, foraging by ambush seems to be an efficient strategy to capture moving fish in aquatic environments.

The fish species recorded in the diet of *M. surinamensis* belong to different taxonomic groups: Gymnotiformes (*Gymnotus carapo* and *Sternopygus macrurus*), Siluriformes (*Callichthys callichthys*), and Synbranchiformes (*Synbranchus marmoratus*) (Martins & Oliveira 1998; Almeida et al. 2016; Tavares-Pinheiro et al. 2021). These fish are nocturnal and active foragers (Nanjappa et al. 2000; Brejão et al. 2013; Zuanon et al. 2015), which may explain why *M. surinamensis* may choose to wait for these fish to approach in an ambush position. These fish are usually

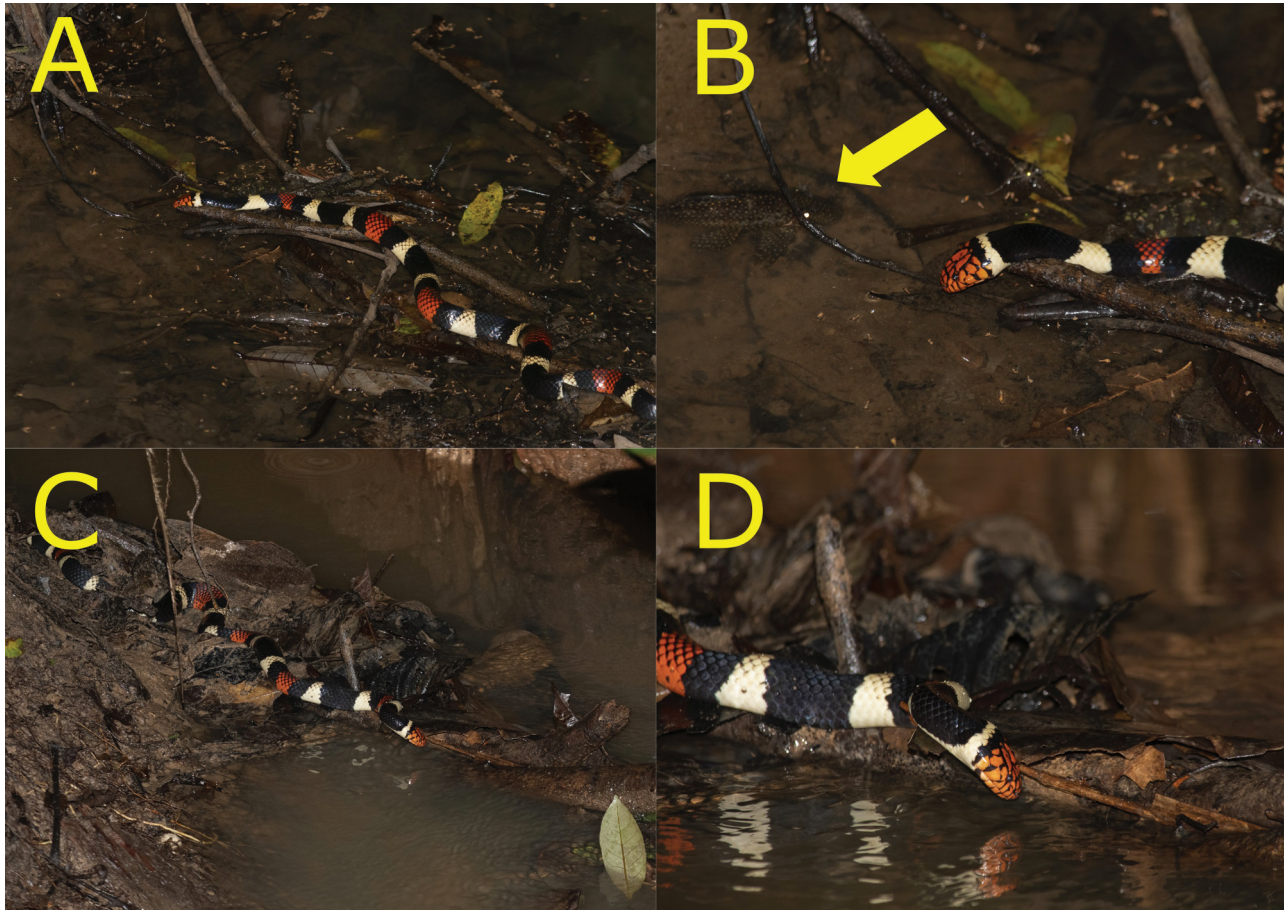


Figure 3. Photograph of a 100 cm-sized individual observed in the MSF: (A and B) the specimen foraging by ambush in a temporary stream; note in (B) the armored catfish (indicated by the arrow) near the snake; (C and D) the same individual observed again the following month hunting from ambush in the same stream. Photos by M. R. N. Almeida.

abundant and occur in various habitats (Kramer et al. 1978; Crampton 1998; Zuanon et al. 2015), which explains the occurrence of *M. surinamensis* in various types of aquatic environments, and the fact that, in this study, it was more commonly found in the (flooded) várzea forest (AJP), where these environments and fish are common.

Another characteristic shared by these fish, with the exception of *S. macrurus*, is that all of them present facultative air breathing, going to the surface to engulf air, and are able to move in terrestrial environments (*C. callichthys* and *S. marmoratus*) and use humid galleries in the soil during the dry season (*S. marmoratus*) (Graham 1997). Surface breathing may make these fish more susceptible to predation by *M. surinamensis* when foraging by ambush. In a previous study at AJP, Silva et al. (2020) recorded five individuals of *M. surinamensis* moving at night on the forest floor, where they also recorded a specimen of *C. callichthys* moving on land. The records of *M. surinamensis* in terrestrial activity may be associated

with actively searching for prey, either fish, lizards, or snakes (e.g. Martins & Oliveira 1998; Pinto et al. 2011). Várzea forests are more unstable ecosystems than terra firme forests, being seasonally flooded and characterized by temporary aquatic environments, with a seasonal reduction in oxygen concentration due to the decomposition of organic matter, favoring air-breathing fish (Chellappa et al. 2005; Carvalho-Freitas et al. 2018; Val 2019). It is reasonable to hypothesize that *M. surinamensis* has greater availability of these air-breathing fish (*C. callichthys*, *G. carapo*, and *S. marmoratus*) in várzea forests.

The knifefish, *S. macrurus*, is the least common fish species observed in *M. surinamensis* diet records, with only two records (Corrêa et al. 2018; Tavares-Pinheiro et al. 2021). Tavares-Pinheiro et al. (2021) recorded a specimen of *M. surinamensis* preying on a *S. macrurus* on the ground, on the bank of a stream in eastern Amazonia. As this fish does not breathe air (Garlick et al. 1979) and does not migrate through the terrestrial environment, it is possible that the

individual of the event recorded by Tavares-Pinheiro et al. (2021) was captured inside the creek and taken to the bank to be ingested.

Interestingly, despite the great diversity of fish in Amazonia (Dagosta & Pinna 2019), the diet of *M. surinamensis* basically consists of the four aforementioned fish species (Martins & Oliveira 1998; Almeida et al. 2016; Tavares-Pinheiro et al. 2021). Another sympatric Amazonian water snake that is nocturnal and piscivorous, *Helicops angulatus*, shows a broader diet composed of more than 20 species of fish, in addition to amphibians and lizards (Carvalho-Teixeira et al. 2017). Analyzing the diet of three species of *Helicops* in eastern Amazonia, Carvalho-Teixeira et al. (2017) observed that *H. angulatus* has a more generalist diet, *H. hagmanni* more specialized (more than 50% composed of Cichliform fish), and *H. polylepis* occupies an intermediate position. Most species of fish that *Helicops* feed on are nocturnal (Carvalho-Teixeira et al. 2017), indicating that, as *M. surinamensis*, they hunt fish at night. *Helicops angulatus* are often much more abundant locally than *M. surinamensis* (e.g. Martins & Oliveira 1998). However, despite also preying on *C. callichthys*, *Gymnotus* sp., and *S. marmoratus*, most of its diet is made up of Characiformes (Carvalho-Teixeira et al. 2017). Even though Characiformes is the most abundant order of fish in Amazonia (Dagosta & Pinna 2019), it is not preyed by *M. surinamensis*, evincing the specialist character of this snake, which feeds on just a few types of prey.

Glaudas et al. (2019) showed that ambush foragers tend to be more opportunistic because they encounter prey less frequently and have a broader diet of prey types compared to active foragers. Apparently, this is not the case for *M. surinamensis*, which feeds mainly on a few species of fish (Martins & Oliveira 1998; Almeida et al. 2016). This is probably due to the abundance of these fish (*C. callichthys*, *G. carapo*, *S. macrurus*, and *S. marmoratus*) in the environments in which it forages and because it also uses active search for its prey.

In this study, most individuals of *M. surinamensis* were observed in aquatic environments. However, this snake can also be found on the forest floor (Silva et al. 2020) and there are two records of juveniles (255 and 400 mm) found on the vegetation (1.25 and 2.38 m in height, respectively) (Hartdegen & Aucone 2001; Dávila et al. 2014). Sleeth et al. (2021) suggested that, among the factors that may be related to the opportunistic arboreality of Australian terrestrial elapids may be the availability of prey, microhabitat for thermoregulation, refuge from flooding, and prevention of attacks by terrestrial predators. Some terrestrial species

of *Micrurus* (e.g. *M. altirostris*, *M. circinalis*, *M. diastema*, *M. distans*, *M. fulvius*, *M. nigrocinctus*, and *M. tschudii*), including both juveniles and adults, have also been recorded resting, foraging, and moving on the vegetation (Schmidt & Smith 1943; Carr 1994; Sajdak 2000; Campbell & Lamar 2004; Suazo-Ortuño et al. 2004; Machado et al. 2005; Valencia-Herverth et al. 2016; Getelina et al. 2018). Because these individuals of *M. surinamensis* found on vegetation by Hartdegen and Aucone (2001) and Dávila et al. (2014) are juveniles, and one of them has been recorded resting, we believe that this behavior may be to avoid terrestrial predators (see Martins 1993). Here we demonstrate that *Micrurus surinamensis* is nocturnal, and mostly found in aquatic environments (permanent or temporary streams, puddles, rivers, and lakes), apart from also being observed as active on the ground. Terrestrial activity may be related with searching for fish that can be found in this substrate (*C. callichthys* and *S. marmoratus*), and the search for water bodies according to the hydrological cycle of flooding and drought in temporary environments. When hunting, *M. surinamensis* uses both foraging modes, being able to search for its prey actively, or by ambushing, with the body partially off, and the head on the water surface. Due to the greater availability of aquatic environments and consequently its prey (fish), *M. surinamensis* is most often found during visual search in floodplain forest ecosystems in the western Brazilian Amazonia. Additional field observations may help in elucidating the biology of this ecologically differentiated species within the genus *Micrurus*.

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Disclosure statement

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Author contributions statement

MRNA: conception, data collection, analysis and writing of the document; JAFN: data collection; ESM: data collection; LGLM: data collection; WLF: data collection and analysis; PSB: analysis and writing of the document; MM: analysis, writing of the document, and translation. All authors reviewed and approved this paper.

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