Food habits and substrate use by the South American xenodontine snake *Erythrolamprus frenatus*, with comments on its brightly-coloured venter

Silara F. Batista^{1,2,*}, Rodrigo R. Scartozzoni¹, and Otavio A. V. Marques^{1,2}

Most of the knowledge about the natural history of South American snakes has been elucidated from studies carried out in the last 30 years (e.g. Sazima, 1992; Martins and Oliveira, 1999; Marques and Sazima, 2004; Sawaya et al., 2008). Information on diet and reproduction of these snakes has largely been obtained from the dissection of preserved specimens from collections (e.g. Orofino et al., 2010; Marques et al., 2014; Stender et al., 2016). As a result, habitat use is among the least known aspects of Neotropical snake natural history, with data being scarce for many species. Habitat use and diet composition in snakes can be closely related, and some authors suggest that microhabitat preferences are linked to optimizing prey encounter rate (Reinert, 1993; Martins et al., 2002; Hartmann and Marques, 2005).

Erythrolamprus frenatus (Fig. 1) belongs to the family Dipsadidae (Dixon, 1989), and is distributed mainly within Cerrado areas of southeastern South America (Wallach et al., 2014). This species belongs to the tribe Xenodontini, which occupy a wide range of habitats (Pizzatto, 2003; Sawaya et al., 2008; Forlani et al., 2010; França et al., 2012). Although *E. frenatus* has been reported to have aquatic habits (Vaz-Silva et al., 2007; Marques et al., 2015), there are few published observations of habitat use. Here, we provide data on

² Instituto de Biociências, Letras e Ciências exatas,

substrate use in the field and describe the diet of *E*. *frenatus*, a poorly-known aquatic snake.

Information on substrate use was obtained from unpublished data provided by three other researchers in three different locations (see Table 1). We examined a total of 120 specimens to check for stomach contents, deposited in the following herpetological collections: Instituto Butantan (IBSP), Museu Nacional do Rio de Janeiro (MNRJ), Museu de Zoologia da UNICAMP (ZUEC), Museu de Zoologia da USP (MZUSP), and Coleção Zoológica de Referência da Universidade Federal do Mato Grosso do Sul (ZUFMS). The sampling covered the following Brazilian states in which the species occurs: Paraná, São Paulo, Mato Grosso do Sul, Mato Grosso and Goiás (northernmost sample: 18° 9'56.59"S/53° 3'46.39"W; southernmost sample: 25°24'29.97"S/54°35'37.67"W; westernmost sample: 22°35'34.90"S/55°43'16.97"W; easternmost sample: 21°35'37.45"S/48°4'13.25"W; see Appendix I). The following data were taken from each specimen: 1) snout-vent length (SVL), using a measuring tape along the venter and measured to the nearest millimetre; 2) sex, by making incisions at the base of the tail; 3) stomach and/or intestine contents, with mid-ventral incisions. All food items in the stomach were removed, identified to the lowest possible taxonomic level, and measured. The direction of prey ingestion was recorded whenever possible. All prey items were returned to the specimens of E. frenatus consulted.

Five specimens were observed in the water, while two others were found on land close to bodies of water (all observations are from the field; Table 1). No observations were obtained of *E. frenatus* away from water. Four prey items in four specimens were recorded from 120 specimens analysed, all of which were swamp eels of the family Synbranchidae (Table 2). One of these specimens contained a heavily digested prey item (vestiges of vertebrae and cranial bones) could not be

¹ Laboratório de Ecologia e Evolução, Instituto Butantan, São Paulo, Avenida Vital Brazil, 1500, 05503-900, São Paulo, SP, Brazil.

Universidade Estadual Paulista "Julio de Mesquita Filho" - UNESP, R. Cristovão Colombo, 2265, 15054-000, São José do Rio Preto, SP, Brazil.

^{*} Correspondence author. E-mail: silara_fatima@hotmail.com

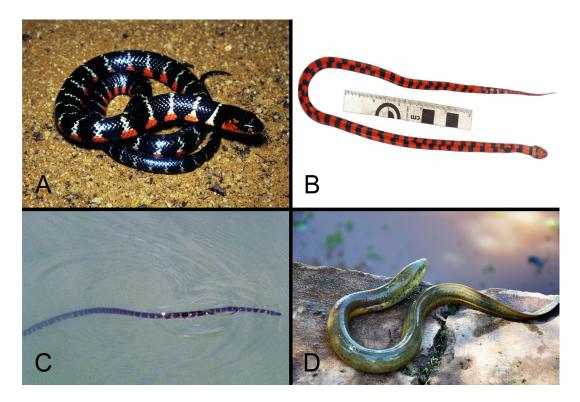


Figure 1. (A): A juvenile specimen of *Erythrolamprus frenatus* showing the extension of the bright red ventral colour onto lateral margins (Photo: Ivan Sazima); (B): view of the ventral side of a *E. frenatus* specimen deposited in Para La Tierra, Paraguay (Photo: Helen Pheasey); (C): specimen of *E. frenatus* moving on a river in UHE Rosana, municipality of Rosana, SP, Brazil (Photo: Giuseppe Puorto); (D): individual of *Synbranchus marmoratus*, prey of *E. frenatus* (Photo: Efraim Penãranda).

identified to the species level, but it was identified as a member of the Synbranchiformes. Relative prey size (prey SVL/snake SVL) was 0.22 (range 0.17–0.29, n = 3). The identification of the prey items was based on

the analysis of diagnostic characters of the skull and vertebrae, and was done by the ichthyologist Sandra Elisa Favorito, a specialist in Synbranchiformes.

Data on natural history for E. frenatus are scarce,

Table 1. Substrate use of *Erythrolamprus frenatus*. The abbreviations for the state names are as follows: GO = Goiás, SP = SãoPaulo.

Substrate description	Locality	N	Observer	
In the water, in stream	Catandúva - SP (21°08'16"S 48°58'22"W)	1	H. Ferrarezzi	
In the water in a flooded area (about 20 cm deep) of watercress plantation, next to stream	Catandúva – SP (21º08'16"S 48º58' 22"W)	2	H. Ferrarezzi	
Under a stone, at the edge of a stream	Catandúva - SP (21º08'16"S 48º58'22"W)		H. Ferrarezzi	
Dead on road, approximately 300 meters from a water body	Catandúva – SP (21°08'16"S 48°58'22"W)		H. Ferrarezzi	
Moving on the surface of a river	UHE Rosana, Rosana - SP (22°36'07"S 52°52'20"W)		G. Puorto	
On flooded ground, approximately 5 meters from the water.	Parque Nacional das Emas – GO (18°5'23"S 53°6'55"W)		C. Nogueira	

Table 2. Voucher, sex, snout-vent length (SVL) and prey found in stomach from specimens analysed; Direction of ingestion (DI) and relative length of prey (RLP).

Voucher	Sex	SVL	Prey	SVL (Prey)	DI	RLP
IBSP 8536	F	797mm	Synbranchus marmoratus	140mm	Head first	0.175
IBSP 19138	F	862mm	Synbranchus marmoratus	180mm	Head first	0.208
IBSP 61161	F	365mm	Synbranchus marmoratus	108mm	-	0.295
IBSP 46606	F	500mm	Synbranchiformes	Heavily digested	-	-

and our results partly fill this gap, providing important information on substrate use and diet of this species. The data on substrate use demonstrates that *E. frenatus* inhabit flooded areas and enter water bodies. The prey consumed (swamp eels) are often found in sludge caves of rivers, marshes and/or marshy areas (Graham and Baird, 1984). Thus, *E. frenatus* may search for such prey while moving through water bodies. Other semi-aquatic xenodontine snakes also feed on fish, but aquatic prey represents only a part of their diet (Marques and Souza, 1992; Scartozzoni, 2009).

Our limited data suggest that *E. frenatus* is a fish-eating snake, which seems to have a preference for elongated fishes. A closely related species from Amazonia, *E. breviceps*, has been observed active on the ground, but like *E. frenatus*, is also associated with water bodies (Martins and Oliveira, 1999). Besides feeding on swamp eels, *E. breviceps* also preys on earthworms and frogs (Beebe, 1946; Martins and Oliveira, 1999). Specialization on elongated fish, as may occur in *E. frenatus*, has been verified in snakes of the genus *Hydrops*, another xenodontine belonging to the tribe Hydropsini (Scartozzoni, 2009), and it is also reported in *Farancia erythrogramma*, a North American dipsadine that preys on eels almost exclusively (Richmond, 1945; Neill, 1964).

A marked characteristic of *E. frenatus* is the red venter with dark bands (Fig. 1; Dixon, 1989; Fernandes et al., 2002). Many aquatic or semi-aquatic dipsadids have bright colours and high-contrast patterns, such as stripes or bands, on the ventral region (e.g., *E. almadensis, E. reginae, Sordellina punctata, Helicops* spp., *Farancia* spp.) (Richmond, 1965; Martins, 1996; Giraudo, 2001; Marques et al., 2001, 2019; Marques and Sazima, 2004). Our data obtained for *E. frenatus* strengthen the association between aquatic habits and a brightly coloured venter in snakes (Martins, 1996; Marques and Sazima, 2004), although there are also terrestrial snakes with bright ventral patterns. The presence of a brightly coloured venter in many aquatic and/or semi-aquatic snakes from different lineages (*see* Zaher et al., 2019) may suggest that this pattern could have a defensive function that is useful for deterring predators that are likely to be encountered in aquatic environments. Additionally, a red venter with dark bands is similar to the colour pattern of venomous coral snakes (*Micrurus* spp.) and may also have an aposematic function, potentially causing avoidance by predators approaching the snake from below (Martins, 1996).

As suggested by Greene (1988), fishes are probably relatively unimportant in the evolution of defensive tactics in lizards and snakes, since few of these animals are aquatic. However, some small aquatic snakes may face strong predation pressure by large carnivorous fish (*e.g.* Bernini et al., 2006) and, thus, may have developed defensive adaptations directed at these potential predators. This hypothesis could be tested using plasticine replicas in aquatic environments, similar to experiments carried out in terrestrial environments (e.g. Brodie III, 1993; Brodie III and Janzen, 1995; Pfenning et al., 2001; Wüster et al., 2004).

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Appendix I. Specimens examined, organized alphabetically by Brazilian states. The abbreviations for the state names are as follows: GO = Goiás, MT = Mato Grosso, MS = Mato Grosso do Sul, PR = Paraná, SP = São Paulo.

MT: Alta Floresta (IBSP 41501); Unknown municipality (IBSP 50035).

MS: Unknown municipality (IBSP 19138, 61170); Maracajú (IBSP 19907); Ponta Porã (IBSP 41422, 43853, 18904, 37254); Ribeirão Claro (IBSP 7023); Campo Grande (IBSP 10080, 15656, 42977, 46254, 48940); Campo Grande (ZUFMSREP 1578); Campo Grande (MZUSP 10132).

PR: Itaipu (IBSP 44701, 44707, 44717); Foz do Iguaçu (IBSP 43023); Porecatu (IBSP 40532, 40554, 40558, 40562, 40566).

SP: Alberto Moreira (IBSP 9559); Aracatuba (IBSP 34405, 28295, 34153, 55704, 28294); Araçatuba (ZUEC 1063, 1064); Araraquara (IBSP 24652); Assis (IBSP 43771, 45732); Bauru (IBSP 29737, 50170, 54965); Bebedouro (IBSP 32126); Boa Esperança do Sul (IBSP 9890); Cândido Rodrigues (IBSP 16288); Catanduva (HF 09, 85, 165); Catanduva (IBSP 54791); Colina (IBSP 40544); Cosmorama (IBSP 22779); Cruzália (IBSP 27848, 27654); Dobrada (IBSP 59991); Fernandópolis (IBSP 32665, 32669, 41616, 41914, 41919, 41921); Garça (IBSP 17620); Guarantã (IBSP 23926); Guararapes (IBSP 30959); Ibarra (IBSP 8536); Iguarapava (IBSP 50586); Ilha Solteira (IBSP 36376, 35992, 36211); Jaú (IBSP 42552); Jurema (IBSP 10236); Lavínia (IBSP 63508); Lins (IBSP 5768, 46606, 25973, 49615); Maracaí (IBSP 32407, 33949); Mirassol (HF 365); Monte Alto (IBSP 18773); Morro Agudo (IBSP 50780); Nova Rubinéia (IBSP 35497); Paraguaçu (MZUSP 2816); Pádua Sales (IBSP 8924); Pindorama (IBSP 9833, 16709, 17313, 24614, 34406); Pirajuí (IBSP 42748, 9941, 42748); Pontal (IBSP 12558); Porto Martins (IBSP 5677); Presidente Prudente (IBSP 37265); Pedreira (IBSP 27653); Quatá (IBSP 41451); Rincão (IBSP 42343); Santa Sofia (IBSP 11008, 16911); São José do Rio Preto (IBSP 30301, 40038, 42257, 18370, 40026, 78129); São José do Rio Preto (HF 364, 314); Terra Roxa (IBSP 10481, 17148); Santa Adélia (IBSP 31336, 27320); Unknown municipality (IBSP 40005, 7124, 5916, 41818, 41858, 8522, 8509, 7635, 7699, 10193).

GO: UHE Aporé (MNRJ 14351). Unknown origin: (IBSP 61161).