



Anurophagy by the Brown-banded Watersnake, Helicops angulatus (Squamata: Colubridae): A Review with New Records

Juan Manuel Acosta-Ortiz^{1,2} and Vincent A. Vos³

¹Grupo de Divulgación e Investigación Herpetológica, 500001, Villavicencio, Meta, Colombia (juan.acostaherp@gmail.com) ² Programa de Biología, Universidad de los Llanos, 500017, Villavicencio, Meta, Colombia ³Instituto de Investigaciones Forestales de la Amazonía, Universidad Autónoma del Beni José Ballivián, Riberalta, Beni, Bolivia

viven their high population densities and protein intake, Jwhich are the result of their efficiency in converting ingested energy into biomass (Wells 2007), amphibians represent an important food resource for various groups of vertebrates and invertebrates. Among the groups of invertebrates that engage in anurophagy are flatworms, annelids, gastropods, arachnids, crustaceans, and insects (Wells 2007). Regarding vertebrates, various records indicate that all groups consume amphibians, including other amphibians (Wells 2007; Sierra-Rueda and Acosta-Ortiz 2020). Likewise, eggs, larval, juvenile, and adult amphibians often are prey of snakes, with amphibians being one of the main items in the diets of some species (e.g., Elaphe quadrivirgata, Thamnophis sirtalis, Thamnodynastes strigatus) (White and Kolb 1974; Bernarde et al. 2000; Wells 2007; Mori and Nagata 2016).

The Brown-banded Watersnake, Helicops angulatus (Linnaeus 1758), is a semiaquatic snake that is widely distributed in South America with records in Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname, Trinidad, and Venezuela (Nogueira et al. 2019). This snake usually inhabits areas with little human disturbance but also occupies disturbed habitats, where it can be seen in lotic and lentic bodies of water, such as ponds for fish production and temporary pools formed after rains (Martins and Oliveira 1998; Ford and Ford 2012; Acosta-Ortiz and Pardo-Moreno 2019). Due to its semi-aquatic habits, the diet of this snake is comprised mainly of animals associated with bodies of water, such as fish and anurans, although it also may include lizards and invertebrates (Martins and Oliveira 1998; Teixeira et al. 2017; Acosta-Ortiz et al. 2020). However, despite being a frequently encountered and widely distributed species, relatively few dietary records exist for *H. angulatus*.

Herein we present a review of publications addressing the diet of *H. angulatus* in which anurans were reported as prey. We conducted searches using the keywords "Helicops

angulatus diet" in Google Scholar and ResearchGate and reviewed the first 200 publications in each search engine and the literature cited in those publications. We prepared a list of the documented species, adjusting for taxonomic changes according to Frost (2021). In addition, we report three species of anurans for the first time as prey of H. angulatus in natural conditions, constituting the first documented records for Bolivia, French Guiana, and Suriname.

We found descriptions of 22 species of anurans reported as prey items of *H. angulatus* (Table 1). The families with the highest number of prey species were Hylidae and Leptodactylidae, with 14 of the 22 species recorded. The genus with the greatest number of species was Rhinella, with six of the 22 species. Eighteen of the 23 available records were from Brazil. In one record from Colombia, Acosta-Galvis et al. (2022) reported Leptodeira annulata preying on Elachistocleis tinigua; however, according to the image presented with this record, the predator was H. angulatus.



Fig. 1. Record of predation on the Bolivian Major Toad (Rhinella major) by the Brown-banded Watersnake (Helicops angulatus) in Riberalta, Bolivia. Photograph by Ruben Layme Cruz.

Table 1. Anuran species recorded in the diet of the Brown-banded Watersnake (*Helicops angulatus*). Type of report: PE = predation event;GC = gut content; RE = regurgitation.

Species	Locality	Туре	Authority
Aromobatidae			
Brilliant-thighed Poison Frog	Serra do Navio, Amapá, Brazil	GC	Costa-Campos et al. 2017
(Allobates femoralis)			
Bufonidae			
North Coastal Granular Toad			
(Rhinella beebei)	Villavicencio, Meta, Colombia	GC	Acosta-Ortiz and Agudelo-González 2021
Bolivian Major Toad			
(Rhinella major)	Riberalta, Beni, Bolivia	PE	This study
South American Common Toad			
(Rhinella margaritifera)	Salvador, Bahia, Brazil	GC	Reis et al. 2010
Cane Toad			
(Rhinella marina)	Barcelos, Amazonas, Brazil; Pará, Brazil	GC	Kaefer and Montanarin 2011; Teixeira et al. 2017
Miranda Ribeiro's Toad			
(Rhinella mirandaribeiroi)	Pará, Brazil	GC	Teixeira et al. 2017
Granular Toad			
(Rhinella merianae)	Carbet Toukan, Cayenne, French Guiana	PE	This study
Hylidae			
Rusty Treefrog			
(Boana boans)	Pará, Brazil	GC	Teixeira et al. 2017; dos Santos-Costa et al. 2022
Rattle-voiced Treefrog			
(Boana crepitans)	Piranhas, Goiás, Brazil	GC	da Silva et al. 2003
Map Treefrog			
(Boana geographica)	Manaus, Amazonas, Brazil	GC	Martins and Oliveira 1998
Emerald-eyed Treefrog			
(Boana xerophylla)	Boven Saramacca, Sipaliwini, Suriname	PE	This study
Manaus Slender-legged Treefrog	L		
(Osteocephalus taurinus)	Manaus, Amazonas, Brazil	RE	Martins and Oliveira 1998
Paradox Frog			
(Pseudis paradoxa)	Pará, Brazil	GC	Teixeira et al. 2017
Common Snouted Treefrog			
(Scinax ruber)	Pará, Brazil	GC	Teixeira et al. 2017
Leptodactylidae			
Dark-spotted Thin-toed Frog			
(Adenomera hylaedactyla)	Laranjal do Jari, Amapá, Brazil	GC	Tavarez-Pinheiro et al. 2019
Lineated Frog	j		
(Leptodactylus fuscus)	Laranjal do Jari, Amapá, Brazil	GC	Tavarez-Pinheiro et al. 2019
Cei's White-lipped Frog			
(Leptodactylus macrosternum)	Caseara, Tocantins, Brazil	GC	Fadel et al. 2019
Lutz's Natal Frog			
(Leptodactylus natalensis)	Cruz do Espírito Santo, Paraíba, Brazil	GC	Albuquerque et al. 2013
Ceara White-lipped Frog			1
(Leptodactylus pustulatus)	Caseara, Tocantins, Brazil	GC	Fadel et al. 2019
Cuvier's Foam Froglet			·
(Physalaemus cuvieri)	Brazil	GC	Scartozzoni 2009
Fischer's Dwarf Frog		-	
(Physalaemus fischeri)	Villavicencio, Meta, Colombia	PE	Acosta-Ortiz and Pardo-Moreno 2019
Microhylidae	· ·		· · ·
Tinigua Oval Frog			
(<i>Elachistocleis tinigua</i>)	La Macarena, Meta, Colombia	PE	Acosta-Galvis et al. 2022
(Luunsioneis inniguu)	La iviacatella, ivicta, COlOIIIDIà	T L	

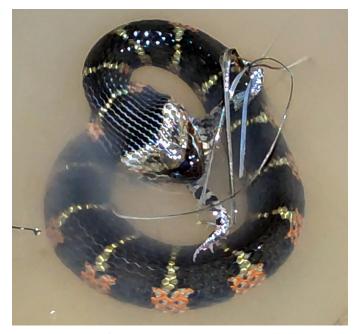


Fig. 2. First record of predation on the Granular Toad (*Rhinella merianae*) by the Brown-banded Watersnake (*Helicops angulatus*) at Carbet Toukan, French Guiana. Photograph by Vincent Prémel.

New records include an unsexed *H. angulatus* approximately 50 cm in total length found consuming a Bolivian Major Toad (Rhinella major) (Fig. 1) at 2357 h on 28 February 2020 at the beginning of a trail in degraded várzea forest on the outskirts of Riberalta in the northern part of the Department of Beni, Bolivia (-11.024644 S, -66.082303W; elev. 136 m asl; WGS 84). Both H. angulatus and R. major are among the most commonly encountered species along this trail (VAV, pers. obs.). In this case, the snake was on the edge of a small pool about 2 m in length, 30 cm in width, and to 10 cm in depth. The pool was in the middle of the small trail, near the edge of the várzea vegetation and more open secondary vegetation established in this area after local deforestation to start urbanization. The snake, which had already ingested at least half of the toad when we made the observation, responded to our presence by entering the shallow water without being able to submerge completely. The toad was being swallowed head first and had a slightly inflated body when initially encountered.

On 17 June 2022 in Carbet Toukan, in Kourou Commune, Cayenne District, French Guiana (5.236528 N, -52.763361 W; elev. 9 m asl; WGS 84), two predation events of *H. angulatus* on the Granular Toad (*Rhinella merianae*) (Figs. 2, 3) were observed between 2120 and 2142 h along a trail cleared by passing construction machinery. The first snake was floating in a pool approximately 20 cm deep, where it had captured its prey by the head and wrapped its body around it, which served to facilitate ingestion. Some 100 m farther down the trail, another snake was preying on another Granular Toad in a pond with a maximum depth of about 10 cm. The snake had captured the toad by its back and ingested



Fig. 3. Second record of predation on the Granular Toad (*Rhinella merianae*) by the Brown-banded Watersnake (*Helicops angulatus*) at Carbet Toukan, French Guiana. Photograph by Magali Portal.

it directly. In both cases, the toads had inflated their bodies to resist being swallowed. Nevertheless, complete ingestion did not exceed two minutes in either case.

Despite the fact that the genus *Rhinella* has parotoid glands that produce and store poisons as a deterrent against predators (Gadelha and Soto-Blanco 2012), no evidence of intoxication was observed in any of the three snakes.

At about 2200 h on 31 May 2019 in Boven Saramacca, Sipaliwini District, Suriname (4.582406 N, -55.604783 W; elev. 127 m asl; WGS 84), we observed an *H. angulatus* preying on an Emerald-eyed Treefrog (*Boana xerophylla*) in a pool not exceeding 5 cm in depth next to an open trail (Fig. 4). The snake had captured the frog by its left leg. The



Fig. 4. Record of predation on the Emerald-eyed Treefrog (*Boana xero-phylla*) by the Brown-banded Watersnake (*Helicops angulatus*) in Boven Saramacca, Suriname. Photograph by Dick Lock.

frog inflated its body and made erratic movements trying to free itself while vocalizing. After approximately five minutes the frog's body was no longer inflated and movements ceased. The snake swallowed the frog body first (head last). The snake subsequently remained completely submerged. Complete ingestion took about eight minutes.

Many anurans inflate their bodies to deter ingestion by a predator (Wells 2007; Toledo et al. 2011). In response, snakes can pierce and deflate the lungs. However, especially when the prey is large, inflation can hinder ingestion. Consequently, snakes typically ingest prey head first to reduce the resistance of the body (Brown et al. 2003). Acosta-Ortiz and Pardo-Moreno (2019) had noted this behavior in H. angulatus but two of the new observations described above suggest that where the prey is initially grasped and possibly the size of the prey can be more important. Also, head-first ingestion can lead to the prey escaping if it is not accompanied by the rapid injection of venom (Mori 1993; Brown et al. 2003; Mori 2006). Although H. angulatus is moderately venomous, it does not have a fast-acting venom, which can increase the risk of its prey escaping (Estrella et al. 2012), further suggesting that H. angulatus captures its prey in whatever manner enhances retention and subsequent ingestion.

All the records correspond to species of anurans with indirect development, which may facilitate the encounters with *H. angulatus*, given their dependence on water to complete their life cycle. This favors the snake, since it feeds not only on adults, but also on eggs and larvae (Martins and Oliveira 1998). In addition, this explains the particular susceptibility of the tree frogs (Hylidae, with the exception of *Pseudis paradoxa*) registered as prey of these snakes (Table 1), although these frogs are distributed vertically on the vegetation, during their reproductive season some species perform their calls from the ground or descend in search of pools to lay their eggs (Lynch and Suarez-Mayorga 2001; Wells 2007).

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