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Does swallowing a toad require any specialisation? Feeding behaviour of the dipsadid snake *Philodryas nattereri* on the bufonid toad *Rhinella jimi*

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Snakes are one of the most diverse and widely distributed vertebrate groups on earth (Greene, 1997; Wallach et al., 2014; Uetz et al., 2018). Much of snakes' success can be explained by the unique adaptations of their body, especially those related to feeding mechanisms (Gans, 1961; 1983; Greene, 1997). However, detailed knowledge on feeding ecology and behaviour of many species are poorly understood, particularly for tropical and subtropical species of the Neotropics (e.g., Marques and Sazima, 1997; Marques and Puorto, 1998; Hartmann and Marques, 2005; Albuquerque et al., 2007; Alencar et al., 2013).

Philodryas nattereri Steindachner, 1870 is a common dipsadid snake widespread in open landscapes in Brazil and Paraguay, including the Caatinga, Cerrado, and Pantanal biomes (Vanzolini et al., 1980; Wallach et al., 2014; Guedes et al., 2014; 2018; Uetz et al., 2018). This semi-arboreal snake is an opportunistic predator, feeding on a wide variety of small vertebrates including small mammals, birds, lizards, and, occasionally, frogs and snakes (Vanzolini et al., 1980; Vitt, 1980; França et al., 2008; Mesquita et al., 2011; Guedes et al., 2014; Guedes, 2017; Marques et al., 2017). Most of what is known about the diet and feeding behaviour of this species is based on fortuitous observations (e.g., Mesquita and Borges-Nojosa, 2009; Godinho et al., 2012; Araújo et al., 2013; Menezes et al., 2013; Guedes, 2017) or gut content analyses of specimens collected in the field or housed in scientific collections (e.g., Vitt, 1980; Mesquita et al., 2011). The few descriptions of its feeding behaviour indicate that prey are swallowed head-first (e.g., Mesquita and Borges-Nojosa, 2009; Menezes et al., 2013; Guedes, 2017). Here we report two observations of *P. nattereri* behaviour while feeding on the bufonid toad *Rhinella jimi* (Stevaux, 2002) in the wild. The snakes and their prey were not collected, but the two feeding sequences were photographed, and these pictures are used herein to illustrate the preying behaviour.

On 21 April 2008 at 10:15 h, a *P. nattereri* adult (snout-vent length ~ 70 cm) was observed preying upon a juvenile "Cururu Toad" *Rhinella jimi* (total length ~ 12 cm) on the ground in a caatinga habitat at the municipality of Parnamirim, Pernambuco, northeast Brazil (8°79'00"S, 39°57'00"W). When spotted, the snake was already constricting and adjusting the puffed-up toad in the mouth (Figure 1A). Then the snake loosened its coil hold on the toad, which was positioned with its belly up (Figure 1B). After this, the snake started jaw movements along the prey until the posterior teeth punctured the prey's belly, which started to deflate a little (Figure 1C). The toad was swallowed belly up and head-first (Figure 1D). The feeding sequence lasted about 30 min.

The second event was recorded at 14:00 h on 3 March 2011, when another *P. nattereri* adult (snout-vent length ~ 75 cm, tail missing) was found on the ground preying upon a *R. jimi* juvenile (total length ~10 cm) in an disturbed area within the limits of the Seridó Ecological

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Figure 1. Feeding sequence of *Philodryas nattereri* adult manipulating and swallowing a *Rhinella jimi* juvenile in Parnamirim, Pernambuco, NE Brazil: A – The snake constricts and adjusts the puffed-up toad in the mouth; B – The snake loosens its coil hold on the toad, already positioned with its belly up; C – The snake starts jaw movements along the prey until the posterior teeth punctures the prey's belly, which starts to deflate a little; and D – The toad is swallowed belly up and head-first (Photos by Wanessa Almeida).

Station, in the municipality of Serra Negra do Norte, Rio Grande do Norte, NE Brazil (06º35'00"S, 37º20'00"W). The snake bit and held the toad by the head and was constricting the prey (Figure 2A). The snake spent some time adjusting the puffed-up toad in the mouth until positioning the prey (Figure 2B). The snake started jaw movements until the posterior teeth punctured the toad's belly, which slowly deflated it while being swallowed head-first and belly up. Duration of this second feeding sequence was not recorded.

Anurans (from eggs to adults) are an important prey item of several neotropical snakes (Haddad et al., 2013) and this is mostly due to their abundance, small to moderate size and soft skin (Duellman and Trueb, 1994). However, only a few snake species are specialized to feed on toads of the genus *Rhinella*, as these anurans are stocky, inflate their body in defence, and have parotoid venom glands placed dorsolaterally behind the eyes (Duellman and Trueb, 1994). For instance, *Xenodon merremii* (Wagler, 1824) is morphologically and behaviourally specialised to feed on *Rhinella* toads (Amaral, 1934; Vanzolini et al., 1980; Duellman and Trueb, 1994; Jordão, 1996). This snake has an elongated post-diastemal tooth on each side, and a short rotating maxilla (Kardong, 1979). Toads are already seized with belly up and before swallowing their puffed-up bodies are punctured by the large post-diastemal teeth, which makes ingestion easier or even possible (Amaral, 1934; Vanzolini et al., 1980; Jordão, 1996; Greene, 1997). The head-first and belly up swallowing of *R. jimi* toads by

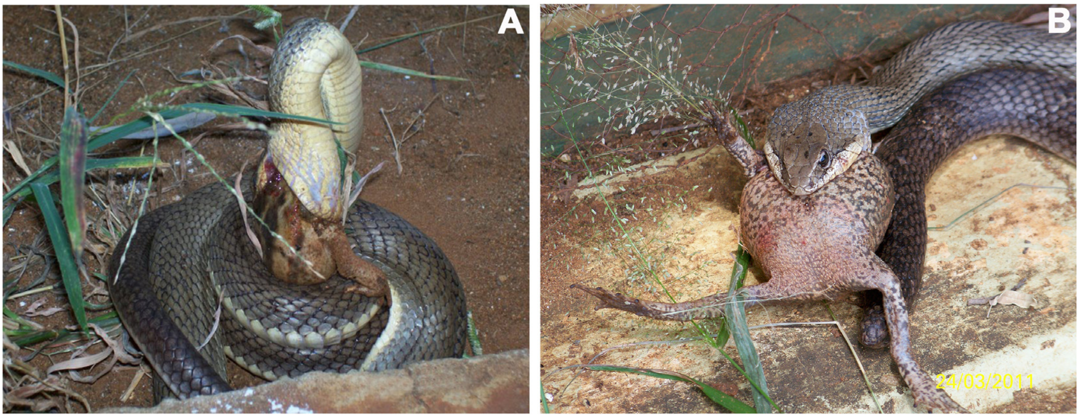

Figure 2. Feeding sequence of *Philodryas nattereri* adult manipulating and swallowing a *Rhinella jimi* juvenile in the Seridó Ecological Station, Serra Negra do Norte, Rio Grande do Norte, NE Brazil: A – The snake bites and holds the toad by the head and constricts the prey; B – The snake ends the adjustment of the toad belly up in the mouth, and begins to swallow the prey (Photos by Carlos Freire).

P. nattereri is similar to that recorded for *X. merremii* (Jordão, 1996). However, morphological data obtained from preserved specimens indicate that the length of posterior maxillary teeth of 10 *X. merremii* (Mean= 4.85 ± 1.47) almost doubles that of nine *P. nattereri* (Mean= 2.62 ± 0.48) and the observed difference is significant (t=4.05, P=0.0008). In light of these new data, it appears that the elongated posterior maxillary teeth specialisation is not as decisive to deflate and swallow a puffed-up toad as is the belly up positioning of prey before swallowing (see below). The large xenodontine snake *Hydrodynastes gigas* (Duméril, Bibron & Duméril, 1854) also has elongated posterior teeth (Glenn et al., 1992) and also swallow toads belly up (Strüssmann, 1992), and sometimes the prey deflates during adjustments before ingestion (C. Strüssmann; I. Sazima, pers. obs). However, *H. gigas* apparently swallow most puffed-up toads belly up without deflating them (C. Strüssmann; I. Sazima, pers. obs.) which likely depend on the toads' relative size and species, as the size of venom glands varies greatly within the genus *Rhinella* (Haddad et al., 2013). It should be noted that some xenodontines have undifferentiated maxillary teeth [e.g., *Erythrolamprus miliaris* (Linnaeus, 1758) and *E. poecilogyrus* (Wied-Neuwied, 1825)] and also may swallow toads belly up (A. Fellone and O.A.V Marques, pers. obs.).

An explanation for the belly up toad swallowing preference could be that this position prevents the prey from grasping on the substrate and makes its ingestion easier (Strüssmann, 1992; Jordão, 1996). An alternative explanation could be that swallowing a belly-up toad reduces the friction on, and compression of, the parotoid glands against the palate of the snake, thus avoiding venom liberation during the ingestion initial phases. As the elasticity of the ventral portion of the mouth would not compress the venom glands, the belly up position could be advantageous since the action of the venom could be more dangerous on the oral mucosa than in the digestive tract. *Rhinella jimi* belongs in the *Rhinella marina* (Linnaeus, 1758) complex of giant toads renowned for their large parotoid glands that secrete powerful venom (Toledo and Jared, 1995; Valinotto et al., 2010), which could partly explain the prey handling behaviour we described herein for *Philodryas nattereri*.

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