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How does a lizard eat spaghetti? Predation by Peters's Lava Lizard, *Tropidurus hispidus* (Spix, 1805), on an amphisbaenian in northeastern Brazil

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The feeding behaviour of terrestrial tetrapods is a complex multifactorial biological phenomenon that encompasses foraging and capture strategies and a series of cyclical and synchronized movements of the mandibles and the hyolingual apparatus (Bels and Herrel, 2019; Bels et al., 2023). The process serves to advance the food bolus through the oral cavity to the oesophagus (Reilly and Lauder, 1990), culminating in the swallowing of the food. In lizards, feeding behaviour is greatly influenced by the anatomy of the hyolingual system, which defines how prey is captured, ingested, transported, processed, and swallowed (Schwenk, 2000). The sequence of stages during a feeding bout follows a pattern of jaw opening and closing movements (Bramble and Wake, 1985), which can be modulated by the characteristics of the prey or food (size, shape, texture; e.g., Herrel et al., 1996, 1997; Schaerlaeken et al., 2008; Montuelle et al., 2010; Taverne et al., 2022).

Most experimental studies that analyse and compare feeding behaviours in different species of lizards use only one or two types of prey (e.g., Smith, 1984; McBrayer and Reilly, 2002). Few studies have analysed the influence of different types of food on feeding processes, specifically in the stages of chewing and intraoral transport (Herrel et al., 2001). Properties such as texture, for example, alter the time and amplitude of jaw movements of species exposed to food samples with different particle masses and toughness indices but equivalent sizes and shapes (Herrel et al., 1999). Under controlled conditions, prey is generally small and short and rarely large and long. In these studies, food boluses are always represented graphically as a compact, relatively short mass that fits entirely in the predator's mouth (e.g., Bels et al., 1994: Fig. 4). Nevertheless, some lizard species can feed on very large and long prey (Schalk and Cove, 2018), such as earthworms, snakes, and other lizards (Baird, 2000; Karametade et al., 2015; Kasperoviczus et al., 2015; Pergentino et al., 2017; Picelli et al., 2019), which can measure up to three times the body length of the predator itself (Meyers et al., 2005). The processing and intraoral transport of elongated prey by iguanid lizard species that do not undertake inertial feeding may require a radical modulation of the feeding sequence, since several stages of feeding behaviour may overlap (Schwenk and Rubega, 2005) to complete the task of fully swallowing the food.

Lizards of the genus *Tropidurus* are sit-and-wait foragers and have a generalist and opportunistic diet, reflecting the availability of food (usually plants and arthropods) in the environment (Kolodiuk et al., 2010). In addition to small prey, *Tropidurus* lizards can catch relatively large prey, like other lizards (Pergentino et al., 2017). Generalist species are expected to have a more varied behavioural repertoire when faced with different types of food. Here we describe the predation by Peters's Lava lizard, *T. hispidus*, on an amphisbaenian and discuss biomechanical hypotheses regarding the intraoral transport of elongated prey in iguanid lizards.

A predation event on an unidentified amphisbaenian species (total length ca. 170 mm) by an adult *T. hispidus* (snout–vent length ca. 131 mm) was observed on 30 January 2022 in the backyard of a house in an urban area in Tamandaré Municipality on the south coast of Pernambuco State, Brazil (8.75842°S, 35.0965°W). This area is part of the Atlantic Forest domain, where the climate is tropical humid with an average annual rainfall of 1500 mm and an average temperature of 25°C.

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The entire predation process, from prey capture to complete ingestion, lasted 15 min and was recorded in a sequence of 112 photos later transformed into a video. The exact moment when the prey was first caught was not recorded. The lizard's body remained vertically oriented on a wall throughout the feeding event. Measurements of the lizard and the amphisbaenian were estimated using ImageJ v1.54h software (Schneider et al., 2012).

By analysing the sequence of photos, it was possible to identify five events in the predation process: (1) prey capture; (2) release of the prey; (3) recapture of the prey; (4) displacement and swallowing; (5) total swallowing (Fig. 1). At first, the lizard was seen in a vertical position with its head pointed down, holding the amphisbaenian by the head (Fig. 1A) and performing vigorous head shaking movements to stun or kill the prey. This behaviour was probably performed immediately after capturing the prey. In the second event, the lizard released the prey and the amphisbaenian continued to move immediately after being released (Fig. 1B). The lizard recaptured its prey 2 s later by grasping the amphisbaenian at the tail end. This movement placed the amphisbaenian into the right side of the lizard's mouth (Fig. 1C). The prey remained on that side of the mouth as it was being swallowed. During the fourth part of the process, the lizard began to move by initially resting parallel to the ground (Fig. 1D), then turning further to complete a 180° turn (Fig. 1E). With its head pointing up, the lizard climbed the wall to a height of approximately 1.80 m. During the entire process, no perceptible movements of the lizard's jaw were observed. At the final moment of ingestion, the lizard moved the prey to the left side of its mouth, then returned it to the right side (side-to-side movement) (Fig. 1F) and swallowed the amphisbaenian completely. The amphisbaenian was swallowed at a rate of 14 mm per minute.

This is the first record of a complete amphisbaenian predation event by a lizard. In this so far unique event, an adult *T. hispidus* managed to subdue and swallow an amphisbaenian without any perceptible chewing movements, while it clung to a vertical surface throughout the feeding process. According to Bramble and Wake's (1985) model, at the end of the SOII phase

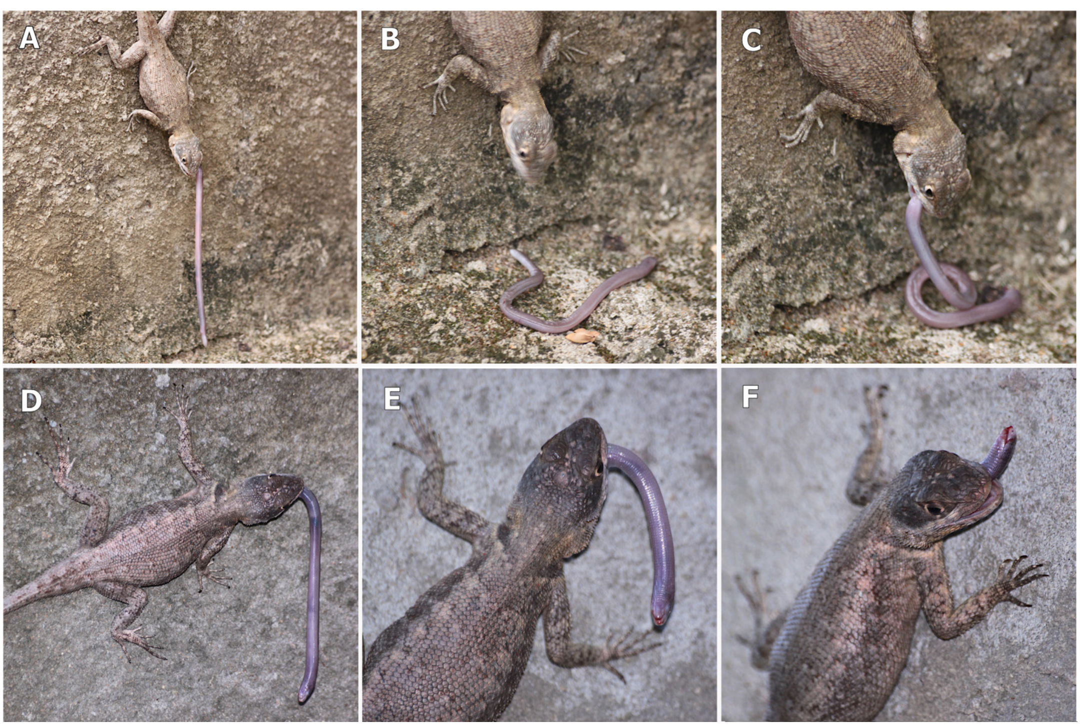

Figure 1. Feeding sequence of the predation process of an unidentified amphisbaenian by *Tropidurus hispidus* in the Tamandaré Municipality, Pernambuco State, Brazil. (A) Prey capture. (B) Prey release. (C) Prey recapture. (D, E) Displacement and swallowing. (F) total swallowing.

(the second of two slow opening phases when the jaw gape is kept constant), the jaw no longer holds the prey, which is instead held between tongue and palate in a behaviour called palatal crushing (McBrayer and Reilly, 2002). The lava lizard probably makes barely perceptible movements with its jaw, tightening and lessening pressure on the prey during the anteroposterior movements of the hyolingual apparatus, while forcing the amphisbaenian's body towards the oesophagus.

Although some stages in a feeding bout generally precede other stages, these do not always occur sequentially. For example, capture/subjugation and ingestion are sometimes combined into a single stage (ingestion), while the processing and transportation cycles occasionally alternate or overlap (Schwenk and Rubega, 2005). In our observation, it appears that subjugation, transportation, and ingestion take place more or less simultaneously. The synchronicity between rapid jaw relaxation and anteroposterior tongue movement may be a specific behavioural modulation of arboreal lizards that feed on elongated prey (Howland et al., 1990; Picelli et al., 2019), considerably reducing the risk of losing food due to the pull of gravity.

The ability to adjust feeding behaviour in response to different prey characteristics seems to be essential, as it can allow for more efficient food processing, especially in generalist species (Verwaijen et al., 2002; Schaerlaeken et al., 2011). Despite being predominantly insectivorous, *T. hispidus* is an opportunistic species with a generalist diet and can also feed on plant items and on small vertebrates (Pergentino et al., 2017; Mascarenhas-Junior et al., 2021; Sousa et al., 2021). Like many other iguanid lizard species (Meyers and Herrel, 2005), it feeds mainly on ants and termites (Gomes et al., 2015), which are common and abundant prey in their areas of occurrence at all times of the year (Ribeiro and Freire, 2011). *Tropidurus hispidus* is a species that normally depends on a relatively small set of prey types but can opportunistically capture a wide variety of prey that may appear in its microhabitats (Vitt et al., 1996; Ribeiro and Freire, 2011). Despite its sit-and-wait feeding strategy, *T. hispidus* can move quickly through its territory to detect and capture potential prey (Kolodiuk et al., 2010).

Walls and tree trunks are the substrates used most frequently by *T. hispidus* in urbanized environments in northeastern Brazil (Albuquerque et al., 2018; de Andrade, 2002). In open areas of urban environments, walls provide a thermal environment conducive to increasing the potential length of time for lizard activity. Walls with rough surfaces can provide environments comparable to rocky outcrops in natural areas where this species can be found (Vitt et al., 1996, de Andrade, 2002). Indeed, foraging and feeding in vertical environments may be a defensive strategy against predators present in the study area, such as the common marmoset *Callithrix jacchus* (Melo et al., 2018) or stray cats and dogs (Beltrão-Mendes and Pinto, 2022).

Although lizards commonly prey on relatively small prey, at least some species can subdue and ingest relatively large prey (Shine and Thomas, 2005). There are reports worldwide of iguanid lizards capable of swallowing elongated prey, particularly other squamates (Best and Pfaffenberg, 1987; Baird, 2000; Meyers et al., 2005; Karatema et al., 2015). In Brazil, Mascarenhas-Junior et al. (2021) reported the capture of *Amphisbaena vermicularis* by *T. hispidus* in an urban area but did not observe the entire feeding process. In a conserved area of the Caatinga biome, a legless lizard was found in the stomach of a specimen of *T. cocorobensis* (Oliveira and Nunes, 2020). In general, iguanid and agamid lizards need to chew less than autarchoglossan lizards presented with the same types of food (McBrayer and Reilly, 2002). This indicates that iguanids have a lower need for pre-digestion food processing or more efficient ingestion compared to other lizards. Future experimental studies on the ingestion, processing, and transport of elongated prey by iguanid lizards could provide interesting information on the evolution of feeding behaviour in lepidosaurs and even tetrapods as a whole. Overall, eating spaghetti whole without choking does not seem that complicated. Salamanders, for example, mostly do not chew their food yet often consume elongate prey (Schwartz et al., 2023).

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