

There is a first for everything: feet-first feeding by a Snouted Night Adder, *Causus defilippii* (Jan, 1863), on a Shovel-footed Squeaker, *Arthroleptis stenodactylus* Pfeffer, 1893, the first live predator-prey interaction reported for these genera and species and the first for Mozambique

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Natural observations of predator-prey interactions between snakes and their prey remain elusive because of the secretive nature of many snake species and a general avoidance by much of the photo-shooting public (e.g., Kery, 2002; Knight, 2008; Willson et al., 2011; Ward et al., 2017). This is especially true for some snake species in some regions, where research efforts have been limited, but as Maritz and Maritz (2020) have pointed out, this may be improving dramatically with the help of social media posts.

The African viper genus *Causus* ranges through most of sub-Saharan Africa and currently comprises seven species, of which two, *C. defilippii* (Jan, 1863) and *C. rhombeatus* (Lichtenstein, 1823), have been reported from Mozambique (e.g., Branch, 1998; Branch et al., 2005; Ceriaco et al., 2021; Marais, 2022). Dietary information on these snakes is relatively scarce, and research efforts have been biased towards species occurring in western and southern parts of Africa, where more studies have been conducted (e.g., Akani et al., 2002; Ineich et al., 2006; Devaney, 2022; Pauwels

et al., 2022). Based on available studies, it has been reported that members of the genus *Causus* primarily feed on anurans (Luiselli et al., 2004; Ineich et al., 2006; Luiselli, 2006; Branch, 1998, 2016; Maritz and Maritz, 2020; Marais, 2022).

The Snouted Night Adder, *Causus defilippii*, has a widespread geographic distribution with a somewhat disjunct range across parts of western and southern Africa. It has a relatively short and stout body (maximum snout-vent length 43 cm; Marais, 2022) with medium-sized eyes and round pupils, and the tip of snout is distinctly upturned. This last characteristic gives the species its common name and distinguishes it from the similar, often syntopic *C. rhombeatus* (Lichtenstein, 1823). The head is triangular, distinctly wider than the neck, and covered with large scales that bear a distinct dark V-pattern. The greyish-brown to reddish-brown colouration and the darker dorsal and lateral markings make these snakes well camouflaged in their habitat (Branch, 2016; Marais, 2022). In our experience, *C. defilippii* is primarily nocturnal. Data on the natural history of *C. defilippii* is still very scarce, and the only prior reports on the prey items of this species were provided by Loveridge (1955), Broadley (1966), and Ineich et al. (2006).

On 4 March 2019 at 17:20 h the first author observed a Snouted Night Adder, *Causus defilippii*, in the process of ingesting a Shovel-footed Squeaker, *Arthroleptis stenodactylus* (Fig. 1) in Musseia, Pebane, Gilé National Park, Zambesia Province, northern Mozambique (16.7030°S, 38.7974°E; Fig. 2). The encounter occurred in Miombo woodland on a humid day after a light rain, with temperatures around 25–27°C. Despite the well-camouflaged activity of predator and prey in the leaf litter, the frog emitted several distress calls that caught the first author's attention. During the observation, the frog was still alive even though it would have been

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envenomated, and it had puffed itself up in order to appear larger. Nevertheless, the snake had begun to swallow it, feet-first. The event unfolded on moist leaf litter, a typical microhabitat for both species.

While the consumption of anuran prey has been documented repeatedly for species in the genus *Causus* (e.g., Luiselli et al., 2004; Ineich et al., 2006; Luiselli, 2006; Maritz and Maritz, 2020), swallowing frogs feet-first has not been documented. This ‘reverse ingestion’ has been reported previously (e.g., *Heterodon* – Kroll, 1976; *Rhabdophis* – Mori and Vincent, 2008) and several additional accounts exist across several snake groups and their respective prey (e.g., *Nerodia sipedon* preying on *Lithobates catesbeianus* – Michael, 2010; *Hebius pryleri* on *Buergeria japonica* – Miller, 2018; *Rhabdophis tigrinus* on *Pelophylax nigromaculatus* – GeoAsia, 2019; *Natrix natrix* on *Rana temporaria* – Raleigh, 2021). Thus, this process may be relatively common, not only for night adders but for snakes in general, but it may not get publicised to the extent it may deserve (David Cundall, *in litt.*, 2023; Rick Shine, *in litt.* 2023).

Feet-first ingestion would appear to be less efficient from the perspective of snake feeding mechanics, and it can increase prey-handling time, and consequently

vulnerability to predators (Greene, 1976; Cundall and Greene, 2000). This type of feeding may be mechanically disadvantageous, since a long narrow body part of the prey has to be ingested before the main body can be grasped by the jaws. Even with this functional constraint, it is almost certain to occur with some regularity among frog-eating snakes, whose capability to turn and strike rapidly (“fast systems” *sensu* Cundall and Greene, 2000) may result in a strike at the posterior-most body part of a fleeing frog: the elongated legs in mid-jump. Anurans are not particularly harmful prey items for snakes (Kornilev et al., 2022) and some viperid species do not release anuran preys after the initial strike (Martins et al., 2002). Holding and beginning to ingest prey at the initial bite site may therefore contribute to the occurrence of reverse ingestion. Unexpectedly, reverse ingestion has been reported as a regular behaviour in the neotropical snake *Erythrolamprus aesculapii* (Linnaeus, 1758), which feeds on harmless colubrids and usually swallows its prey while the snakes are still alive (Braz and Marques, 2016). Feet-first feeding encounters appear to be rather cruel to the prey, which is alive while it is slowly pulled into the snake’s maw, and those encounters between snakes and frogs available for viewing on YouTube have



Figure 1. *Causus defilippi* feeding on an *Arthroleptis stenodactylus* feet-first, in Miombo woodland habitat in Gilé National Park, northern Mozambique. Photo by Avelino Miguel.

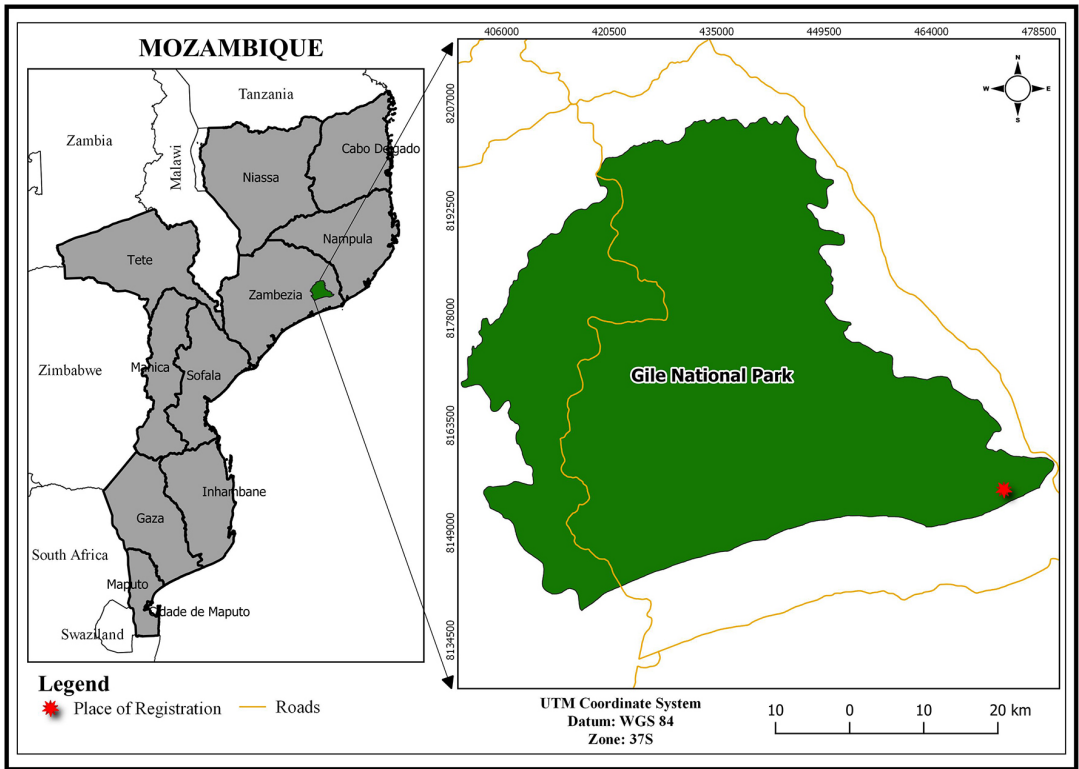


Figure 2. Map of Mozambique, showing the position of Gilé National Park and the locality where the interaction was observed (red star).

generated many comments and hundreds of thousands of views. It would be interesting to collect as much evidence as possible about feet-first ingestion from a broad taxonomic spectrum of snakes to determine how common this phenomenon is in nature.

Reports on the diet of *Causus* vipers have listed taxonomically diverse anuran prey, including species in the families Arthroleptidae, Brevicipitidae, Bufonidae, Hyperoliidae, Phrynobatrachidae, Ptychadenidae, Pyxicephalidae, Ranidae, and Rhacophoridae (Loveridge, 1955; Luiselli et al., 2004; Ineich et al., 2006). More specifically, Loveridge (1955) reported on a collection from Tanganyika Territory (now Tanzania) and listed *Arthroleptis stenodactylus*, *Sclerophrys regularis* (Reuss, 1833) (as *Bufo r. regularis*), *Phrynobatrachus acridoides* (Cope, 1867), and *Spelaophryne methneri* Ahl, 1924 as prey of *C. defilippii*, while Broadley (1966) listed *Breviceps mossambicus* Peters, 1854 as prey for the species in Mozambique. Our report is the second documented consumption of a member of the genus *Arthroleptis* by any night adder species – and it is also the first predator-prey interaction for these species and genera

in Mozambique. Clearly, documentation and reporting of these types of interaction is important and relevant to our knowledge of food webs throughout the Afrotropics, especially given the uncertainty posed by direct, human-initiated habitat loss (Furaca et al., 2021) and the impact of strong cyclones (such as the recent devastating Cyclones Idai and Freddy; Charrua et al., 2021) and the dire need for conservation action.

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