Review of ophiophagy in neotropical cat-eyed snakes, genus Leptodeira, with the first report of ophiophagy in L. ornata (Bocourt, 1884)

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Leptodeira is a genus of currently 18 species (Barrio-Amorós, 2019; Torres-Carvajal et al., 2020; Costa et al., 2022a, b) with a complex and still incompletely resolved taxonomic history. The feeding habits of these snakes have been reported in some detail, and Leptodeira species appear to have a preference for anurans (including highly poisonous toads) and their eggs, as well as lizards, fish, and even some insects, crabs and non-arthropod invertebrates (e.g., Duellman, 1958; Vitt, 1996; Savage, 2002). However, there are not many reports of Leptodeira preying on other snakes.

Ophiophagy by Leptodeira. We were able to locate eight literature records of ophiophagy in the genus Leptodeira, of which six were observed in nature (Table 1). Wright and Wright (1957) appear to have been the first to mention snakes as prey for the genus Leptodeira but these authors did not provide any specific examples or citations. Skehan (1959) reported an example of a cat-eyed snake of 50.2 cm in total length (probably L. rhombifera Günther, 1872) that was offered and consumed an 18-cm-long juvenile Lampropeltis triangulum (Lacépède, 1789) in captivity (reported as L. doliatus triangulum; taxonomy according to Ruane et al., 2014). Cantor and Pizzato (2008) reported two

Montalbán Huidobro and Aréchaga Ocampo (2010) reported on a female L. maculata (Hallowell, 1861) in Guerrero, Mexico, that had a male of its own species in its stomach. This was not only a case of ophiophagy but also the first case of cannibalism for the genus Leptodeira. McKelvy et al. (2013) observed a cat-eyed snake in Tortuguero, Costa Rica (listed as L. septentrionalis and now considered "L. aff. ornata 3" by Costa et al., 2022) that regurgitated tail-first a still living Ninia sebae (Duméril et al., 1854) that died 2 h later. In Guerrero, Mexico, Palacios-Aguilar et al. (2020) reported a Salvadora mexicana (Duméril et al., 1854) as prey of L. maculata, which expelled it tail-first, evidencing that it was swallowed head-first. Finally, in Costa Rica, Escalante et al. (2021) observed a cat-eyed snake (listed as Leptodeira sp. and now considered "L. aff. ornata 3" by Costa et al., 2022) that regurgitated a juvenile Chironius flavopictus (Werner, 1909), but did not mention whether the snake had been eaten head- or tail-first. We here report a further case of ophiophagy by a member of the genus Leptodeira, the first assigned to L. ornata sensu stricto, based on the range of this taxon relative to the clade called L. aff. ornata 2 by Costa et al. (2022).

Ophiophagy by *Leptodeira ornata*. On 8 August 2023 we observed an Ornate Cat-eyed Snake, *L. ornata*, preying on a juvenile Chocoan Parrot Snake, *Leptophis bocourti* Boulenger, 1909, in a remnant of

cases of ophiophagy for *L. annulata* (Linnaeus, 1758) in Brazil, one involving *Oxyrhopus guibei* Hoge and Romano, 1977 and the other *Atractus zebrinus* (Jan, 1862). It is interesting to note that while the *A. zebrinus* was consumed tail-first, the *O. guibei* was consumed head-first, as is common for almost all ophiophagous snakes with the exception of members of the genus *Erythrolamprus sensu stricto* that consume their snake prey tail-first (Greene, 1976, 1997; Marques and Puorto, 1994; Hartmann et al., 2009; Braz and Marques, 2016).

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Table 1. Listing of ophiophagy observed in cat-eyed snakes of the genus *Leptodeira*. We provide the species of the *Leptodeira* predator, the prey species, the direction (Dir) of ingestion (head-first – HF, tail-first – TF, mid-body – MB, not reported – NR), and the reference. The asterisk (*) indicates the only known case of cannibalism in the genus.

Species	Prey	Dir	Reference
annulata	Oxyrhopus guibei	HF	Cantor and Pizzato, 2008
annulata	Atractus zebrinus	TF	Cantor and Pizzato, 2008
*maculata (as L. cussiliris)	Leptodeira maculata	NR	Montalbán Huidobro and Aréchaga Ocampo, 2010
maculata	Salvadora mexicana	HF	Palacios-Aguilar et al., 2020
ornata	Leptophis bocourti	MB	this paper
aff. ornata (as L. septentrionalis)	Ninia sebae	TF	McKelby et al., 2013
aff. ornata (as Leptodeira sp.)	Chironius flavopictus	NR	Escalante et al., 2021
cf. rhombifera (as L. doliatus triangulum)	Lampropeltis triangulum	NR	Skehan, 1959

humid Chocó rainforest in Bosque Protector La Perla, a protected forest in La Concordia, Santo Domingo de los Tsáchilas, Ecuador (0.0242°S, 79.3867°W; elevation 246 m). The cat-eyed snake was coiled along the stem of a plant about 60 cm high, maintaining an upright position with its head raised and resting at the junction of two branches. It held its prey towards the

posterior end of the middle third of its body (Fig. 1A), presumably injecting venom, while the parrot snake attempted to defend itself by writhing and repeatedly biting its predator. Despite the defensive behaviours, the cat-eyed snake remained motionless for about 30 min until its prey stopped defensive movements; all movements of the parrot snake had ceased by the



Figure 1. (A) An Ornate Cat-eyed Snake, *Leptodeira ornata*, seen holding its prey, a Chocoan Parrot Snake, *Leptophis bocourti*, by its midbody. The parrot snake can be seen defending itself by biting the cat-eyed snake. (B) The cat-eyed snake holding its limp, dead prey. (C) The cat-eyed snake shown with the nearly completely ingested parrot snake, which it had swallowed beginning at midbody and ending at the head. Photos by Amanda B. Quezada.

40-min mark of the observation. The cat-eyed snake then began to swallow the parrot snake at the bite site, without adjusting the position of its head on the prey's body (Fig. 1B). The regular jaw movements of the cateyed snake pulled the parrot snake in, resulting in a folding of the prey's body. Thus, the parrot snake was devoured with its body folded and, based on the slightly posterior position of the bite site and the fold, the head was the last part of the parrot snake that disappeared (Fig. 1C). The entire ingestion process took about 1 h. During ingestion, the cat-eyed snake moved with its prey through the branches to the opposite side of the plant, maintaining an upright position but with its head facing downward. After completing ingestion, the cateyed snake remained suspended from the branches, and we discontinued our observation. The cat-eyed snake measured approximately 60 cm in total length, and the parrot snake approximately 40 cm. Leptophis bocourti was identified by having small black spots on the back of the head and along the body, and by the absence of a loreal scale (Torres-Carvajal and Terán, 2021; Albuquerque and Fernandes, 2022).

In sum, members of the genus *Leptodeira* are generalist feeders that mainly consume anurans and their eggs. However, these snakes exhibit a varied diet that includes a diverse selection of small animals, such as lizards, invertebrates, crabs and, sometimes, other snakes. Cat-eyed snakes are not specialist feeders, and as the emerging body of knowledge demonstrates, during ophiophagy they may capture their prey by any part of the body before proceeding with ingestion, head-first, tail-first, or even beginning at midbody.

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