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NOTE AND RECORD

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Ophiophagy and cannibalism in African vine snakes (Colubridae: *Thelotornis*)

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1 | INTRODUCTION

Cannibalism, the consumption of conspecifics, occurs throughout the animal kingdom (Polis, 1981). The ingestion of one's own kind is hypothesised to arise as a by-product of intraspecific competition and/or through the added benefit of energetic gains from the meal (Van Allen et al., 2017). In snakes, cannibalism has been documented in several lineages (Polis & Myers, 1985) including elapids (Maritz, Alexander, & Maritz, 2019), colubrids (Göçmen, Werner, & Elbeyli, 2008), lamprophiids (Shine, Branch, Harlow, Webb, & Shine, 2006) and viperids (Funk, 1965). However, instances of cannibalism are rarely recorded in wild animals, leading to these events being dismissed as rare and of little ecological importance (Maritz, et al., 2019). This is particularly true for African snakes for which detailed dietary studies are often lacking or incomplete.

African vine snakes (*Thelotornis* spp.) are a group of venomous colubrids that include five distinct taxa which inhabit savannah and forested regions across sub-Saharan Africa (Broadley, 2001; Uetz, Freed, & Hošek, 2019). Members of the genus are largely arboreal but the inclusion of terrestrial prey in their diet suggests they occasionally come to ground to feed (Akani, Luiselli, & Angelici, 2002; Shine, Harlow, Branch, & Webb, 1996). Only southern vine snakes (*T. capensis capensis*) and forest vine snakes (*T. kirtlandii*) have been subjected to detailed dietary analysis (Akani et al., 2002; Shine et al., 1996). These two studies found that vine snakes eat a diet dominated by arboreal vertebrates, particularly geckos, agamas and chameleons, but that birds are relatively scarce in their diets. Notably, both species are occasionally ophiophagous (i.e., consume snakes) but importantly, neither study detected incidents of cannibalism.

Here, we report on the first case of cannibalism in *Thelotornis*. Then, given that cannibalism is potentially more likely to arise in ophiophagous lineages, we review the instances of ophiophagy within the genus.

2 | METHODS

The Museu de História Natural de Maputo (Mozambique) is in the process of having its collection upgraded and digitised. The herpetological collection includes mostly historical material (pre-1970), but also some recently collected material (Conradie et al., 2016; Jones et al., 2017; Portik, Mulungu, Sequeira, & Mcentee, 2013). In April 2019, W. Conradie was invited to identify specimens in the herpetological collection. During examination of preserved snake material, an adult eastern vine snake (*T. mossambicanus*) was discovered that had been preserved in the process of consuming a conspecific (bottle no. 42).

We additionally reviewed diet data for *Thelotornis* derived from published (scientific and grey) literature and from photographic records shared via Facebook. Most Facebook feeding records were collected using the public group 'Predation Records—Reptiles and Amphibians (sub-Saharan Africa)' (https://www.facebook.com/groups/888525291183325). Taxonomic assignments within the genus *Thelotornis* have been subjected to several changes in the last 50 years (Broadley, 1979, 2001). Within our review, we treat species assigned to *T. kirtlandii capensis* or *T. capensis capensis* from

outside of western Zimbabwe or southern Mozambique as *T. mossambicanus*. In localities where two species of *Thelotornis* potentially coexist, we treat diet records conservatively by assigning them only at the genus level.

3 | RESULTS AND DISCUSSION

While inspecting the reptile collection at the Museu de História Natural de Maputo (Mozambique), a specimen of an eastern vine snake (*Thelotornis mossambicanus*) was discovered that had been preserved in the process of ingesting a conspecific (Figure 1). The identification of the cannibalistic individual was based on the uniform unpatterned dorsal head scales and temporal shields with fine black stippling (Broadley, 1979, 2001) (Figure 1b). For the prey, the main identifying features were not visible due to the inseparability of the two specimens. However, we assume the ingested snake was a conspecific because *T. mossambicanus* does not occur in sympatry with any other members of the genus (Broadley, 2001). The specimens were collected in Mozambique, but a precise collection locality was not catalogued when they were deposited. However, *T. mossambicanus* occurs predominantly north of 20°S. Little information was stored with specimens at the time of preservation limiting our understanding of the specifics of the situation.

The cannibalistic individual was identified as a female with a total length of 1,100 mm (snout-vent length: 700 mm and tail length: 400 mm). At the time of preservation, the female had ingested one-third of the conspecific with the remaining portion protruding from the mouth. The prey was identified as a male, based on an enlarged tail base (where the hemipenes are stored), with an approximate total length of 570 mm. Although undocumented in snakes, post-copulatory sexual cannibalism would provide an energetic supply to the female to aid with egg provisioning. Alternatively, the event may have occurred independently of copulation, rather being motivated by opportunism or intraspecific competition. Combative behaviour has been observed in southern vine snakes (*T. c. capensis*) (Uys, 2011), which could allow for opportunistic cannibalism. Notably, among cannibalism events in wild snakes, females consume both sexes (Franch & Sebastián, 2013; Göçmen et al., 2008; Krey, O'Shea, Farajallah, Setiadi, & Suryobroto, 2015) suggesting cannibalism may occur under several circumstances.

Our review revealed that all *Thelotornis* species include snakes in their diet (Table 1). Several of the snake species recorded in the diet of *Thelotornis* are highly venomous including black mamba (*Dendroaspis polylepis*) and boomslang (*Dispholidus typus*) both of which exhibit arboreality. Interestingly, three of the taxa (*sans T. c. oatesii*) include green snakes (*Philothamnus* spp.) in their diet and these records represent 47.8% of observations of ophiophagy in the wild (Table 1). Much like *Thelotornis*, many *Philothamnus* species are expert climbers but can also be found occupying terrestrial habitats (FitzSimons, 1962). Notably, the only study on the behavioural ecology of *T. c. capensis* found that they frequently inhabit the shrub-tree interface (<1.5 m) during the warmest months where they are hypothesised to lay awaiting potential prey (Jacobsen, 1982). Thus, this microhabitat interface may provide the platform for the majority of *Philothamnus–Thelotornis* interactions.

Cannibalism has never been reported in the genus *Thelotornis* despite their appetite for snakes (Table 1; Figure 2). Although cannibalism may occur infrequently, rare prey types can be important food sources and have significant fitness benefits for the predator (Wiseman, Greene, Koo, & Long, 2019). No studies to date have examined the diet of *T. mossambicanus*, partially due to the recent description of the species. However, Akani et al. (2002) examined the diet of *T. kirtlandii* in southern Nigeria (N_{prey} = 62) and revealed that snakes represent only 1.6% of prey items. Additionally, Shine et al. (1996) investigated the diet of *T. c. capensis* using museum specimens (N_{prey} = 50) and found that snakes constitute 8.0% of their diet. With the addition of new data from social media and published ad hoc observations, snakes make up 13% of all prey items reported for *T. c. capensis* (data not shown). Although a bias towards photographs of ophiophagy in our social media dataset is a concern, we found no significant difference between the proportion of snakes ingested in the museum dataset versus the social media dataset (χ^2 = 3.14, p = .076). Notably, the collection of snake diet data is not trivial and the resulting limited sample sizes may contribute to the apparent absence of cannibalism within other *Thelotornis*. Further investigation into the cannibalistic tendencies within this clade is warranted.

Among the tribe Dispholidini (to which *Thelotornis* belongs), ophiophagy is only known from boomslang (*Dispholidus typus*) (Haagner, 1990; Smith, Layloo, Maritz, & Maritz, 2019) and African vine snakes (see Table 1; this study). Importantly, these are the only lineages from which cannibalism is known suggesting ophiophagy

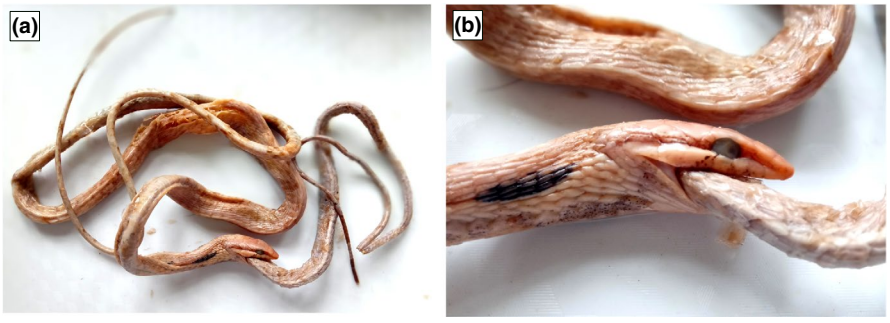

FIGURE 1 Cannibalism in the eastern vine snake (*Thelotornis mossambicanus*). (a) A museum record of a female *Thelotornis mossambicanus* swallowing a conspecific male. (b) The unpatterned dorsal head scales and temporal shields with fine black stippling are indicative of *T. mossambicanus*

TABLE 1 Recorded observations of ophiophagy in the genus *Thelotornis*

Snake species	Prey species (no. recorded)	Reference
Thelotornis capensis capensis	Colubridae	Shine et al. (1996)
	Dispholidus typus	Haagner and Clarke (1992)
	Duberria lutrix	Shine et al. (1996)
	Lycodonomophus rufulus	Shine et al. (1996)
	Philothamnus hoplogaster	Shine et al. (1996)
	Philothamnus natalensis	Mckibbin (2017)[a]
	Philothamnus occidentalis (2)	de Klerk (2018)[a]; Vollet, Vollet, and Ping (2015)[a]
	Philothamnus semivariegatus (2)	Maritz and Barends (2017)[a]; Kinsella and Maritz (2016)
	Psammophis subtaeniatus	de la Harpe-Parker (2017)[a]
Thelotornis capensis oatesii	*Aparallactus lunulatus*	McDonald (2018)
	Dendroaspis polylepis	Gartner and Theart (2018)[a]
	Dispholidus typus	Vrdoljak and Perry (2019)[a]
	Psammophis subtaeniatus	Nobrega (2018)[a]
	Serpentes	Shine et al. (1996)
Thelotornis kirtlandii	*Hapsidophrys smaragdina*	Akani et al. (2002)
	Philothamnus carinatus	Bogert (1940)
	Philothamnus sp. (2)	Akani et al. (2002)
Thelotornis mossambicanus	*Afrotyphlops mucruso*[b]	Loveridge (1923)
	Philothamnus angolensis (2)	Loveridge (1953)
	Thelotornis mossambicanus	This study
Thelotornis sp.[c]	*Crotaphopeltis torneri*	Barbour and Loveridge (1928)
	Dasypeltis atra[b]	Barbour and Loveridge (1928)
	Natriciteres olivacea[b]	Barbour and Loveridge (1928)
	Philothamnus hoplogaster[b]	Barbour and Loveridge (1928)

[a]Facebook observation.
[b]In captivity.
[c]Recorded as *Thelotornis kirtlandii* but refers to either *T. mossambicanus* or *T. usambaricus*.

FIGURE 2 Ophiophagy in African vine snakes (*Thelotornis* spp.). African vine snakes eat a diversity of snakes in the wild including (a) *Philothamnus natalensis* (Photograph: Richard Mckibbin), (b) *Aparallactus lunulatus* (Photograph: Sean McDonald) and (c) *Psammophis subtaeniatus* (Photograph: Sean de la Harpe-Parker)

may contribute to cannibalistic tendencies (This study; FitzSimons, 1962). Although other members of Dispholidini (*Xyelodontophis*, *Thrasops* and *Rhamnophis*) do not display ophiophagy or cannibalism (Spawls, Howell, Hinkel, & Menegon, 2018), few detailed diet studies on these genera exist, which can lead to an underrepresentation of rare, but important, predation events.

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DATA AVAILABILITY STATEMENT

Data are available upon reasonable request from the authors.

REFERENCES

Akani, G. C., Luiselli, L., & Angelici, F. M. (2002). Diet of *Thelotornis kirtlandii* (Serpentes: Colubridae: Dispholidini) from southern Nigeria. *Herpetological Journal*, *12*, 179–182.

Barbour, T., & Loveridge, A. (1928). A comparative study of the herpetological faunae of the Uluguru and Usambara mountains, Tanganyika Territory with descriptions of new species. *Memoirs of the Museum of Comparative Zoology at Harvard College*, *50*, 85–265.

Bogert, C. M. (1940). Herpetological results of the Vernay Angola Expedition. *Bulletin of the American Museum of Natural History*, *77*, 1–107.

Broadley, D. G. (1979). Problems presented by geographical variation in the African vine snakes, genus *Thelotornis*. *South African Journal of Zoology*, *14*, 125–131. https://doi.org/10.1080/02541858.1979.11447661

Broadley, D. G. (2001). A review of the genus *Thelotornis* A. Smith in eastern Africa, with the description of a new species from the Usambara Mountains (Serpentes: Colubridae: Dispholidini). *African Journal of Herpetology*, *50*, 53–70. https://doi.org/10.1080/21564574.2001.9635451

Conradie, W., Bittencourt-Silva, G., Engelbrecht, H. M., Loader, S. P., Menegon, M., Nanvonamuquitxo, C., … & Tolley, K. A. (2016). Exploration into the hidden world of Mozambique's sky island forests: New discoveries of reptiles and amphibians. *Zoosystematics and Evolution*, *92*, 163–180. https://doi.org/10.3897/zse.92.9948

de Klerk, M. (2018, January 26). *Predation Records - Reptiles and Frogs (Sub-Saharan Africa)*. Retrieved from https://www.facebook.com/groups/888525291183325/permalink/1544106182291896

de la Harpe-Parker, S. (2017, April 14). *Predation Records - Reptiles and Frogs (Sub-Saharan Africa)*. Retrieved from https://www.facebook.com/groups/888525291183325/permalink/1289391751096675

FitzSimons, V. F. M. (1962). *Snakes of southern Africa*. Cape Town, South Africa: Purnell and Sons.

Franch, M., & Sebastián, O. S. (2013). A case of cannibalism by and extra large female of *Malpolon monspessulanus* (Montpelliar snake) in the Iberian Peninsula. *Herpetology Notes*, *6*, 379–380.

Funk, R. S. (1965). Food of *Crotalus cerastes laterorepens* in Yuma County, Arizona. *Herpetologica*, *21*, 15–17.

Gartner, U., & Theart, F. (2018, March 6). *Predation Records - Reptiles and Frogs (Sub-Saharan Africa)*. Retrieved from https://www.facebook.com/groups/888525291183325/permalink/1580585058644008

Göçmen, B., Werner, Y. L., & Elbeyli, B. (2008). Cannibalism in *Dolichophis jugularis* (Serpentes: Colubridae): More than random? *Current Herpetology*, *27*, 1–7. https://doi.org/10.3105/1345-5834(2008)27%5B1:CIDJSC%5D2.0.CO%3B2

Haagner, G. V. (1990). Life history note: *Dispholidus typus typus* (boomslang): Ophiophagy. *Journal of Herptological Association of Africa*, *37*, 47. https://doi.org/10.1080/04416651.1990.9650263

Haagner, G. V., & Clarke, C. H. (1992). Life history note: *Thelotornis capensis capensis* (southern vine snake): Ophiophagy. *Journal of Herpetological Association of Africa*, *41*, 45. https://doi.org/10.1080/04416651.1992.9650358

Jacobsen, N. H. G. (1982). *The ecology of the reptiles and amphibians in the Burkea africana – Eragrostis pallens savanna of the Nylsvley Nature Reserve*. (Master's thesis, University of Pretoria). Retrieved from http://hdl.handle.net/2263/29218

Jones, S. E. I., Clause, J. K., Geeraert, L., Jamie, G. A., Sumbane, E., Van Berkel, T., & Jocque, M. (2017). *The Njesi Plateau expedition: a biological assessment of Mt Chitagal, Mt Sanga and the Njesi Plateau in Niassa Province, Mozambique*. Biodiversity Inventory for Conservation *(BES 6.3)*. Retrieved from https://www.binco.eu/wp-content/uploads/2016/08/BES6.3_25_10_2017.pdf

Kinsella, K., & Maritz, B. (2016, February 15). *Predation Records - Reptiles and Frogs (Sub-Saharan Africa)*. Retrieved from https://www.facebook.com/groups/888525291183325/permalink/963714023664451

Krey, K., O'Shea, M., Farajallah, A., Setiadi, D., & Suryobroto, B. (2015). *Micropechis ikaheka* (Elapidae) in Papua, Indonesia: A study of diet and cannibalism. *Herpetology Notes*, *8*, 323–328.

Loveridge, A. (1923). Notes on east African snakes, collected 1918–1923. *Proceedings of the Zoological Society London*, *93*, 871–897.

Loveridge, A. (1953). Zoological results of a fifth expedition to east Africa III Reptiles from Nyasaland and Tete. *Memoirs of the Museum of Comparative Zoology at Harvard College*, *110*, 143–322.

Maritz, B., Alexander, G. J., & Maritz, R. (2019). The underappreciated extent of cannibalism and ophiophagy in African cobras. *Ecology*, *100*(2), e02522. https://doi.org/10.1002/ecy.2522

Maritz, B., & Barends, J. (2017, March 4). *Predation Records - Reptiles and Frogs (Sub-Saharan Africa)*. Retrieved from https://www.facebook.com/groups/888525291183325/permalink/1278640175505166

McDonald, L. (2018, September 28). *Predation Records - Reptiles and Frogs (Sub-Saharan Africa)*. Retrieved from https://www.facebook.com/groups/888525291183325/permalink/1824174280951750

Mckibbin, R. (2017, October 16). *Predation Records - Reptiles and Frogs (Sub-Saharan Africa)*. Retrieved from https://www.facebook.com/groups/888525291183325/permalink/1453285314707317

Nobrega, J. D. (2018, May 04). *Predation Records - Reptiles and Frogs (Sub-Saharan Africa)*. Retrieved from https://www.facebook.com/groups/888525291183325/permalink/1638986202803893

Polis, G. (1981). The evolution and dynamics of intraspecific predation. *Annual Review of Ecological Systematics*, *12*, 225–251. https://doi.org/10.1146/annurev.es.12.110181.001301

Polis, G. A., & Myers, C. A. (1985). A survey of intraspecific predation among reptiles and amphibians. *Journal of Herpetology*, *19*, 99–107. https://doi.org/10.2307/1564425

Portik, D. M., Mulungu, E. A., Sequeira, D., & Mcentee, J. P. (2013). Herpetological surveys of the Serra Jeci and Namuli

massifs, Mozambique, and an annotated checklist of the southern Afromontane archipelago. *Herpetological Review*, *44*, 394–406.

Shine, R., Branch, W. R., Harlow, P. S., Webb, J. K., & Shine, T. (2006). Biology of burrowing asps (Atractaspididae) from southern Africa. *Copeia*, *2006*, 103–115. https://doi.org/10.1643/0045-8511(2006)006%5B0103:BOBAAF%5D2.0.CO%3B2

Shine, R., Harlow, P. S., Branch, W. R., & Webb, J. K. (1996). Life on the lowest branch: Sexual dimorphism, diet, and reproductive biology of an African twig snake, *Thelotornis capensis* (Serpentes, Colubridae). *Copeia*, *1996*, 290–299. https://doi.org/10.2307/1446845

Smith, C. C. D., Layloo, I., Maritz, R. A., & Maritz, B. (2019). Sexual dichromatism does not translate into sex-based difference in morphology or diet for the African boomslang. *Journal of Zoology*, *308*(4), 253–258. https://doi.org/10.1111/jzo.12670

Spawls, S., Howell, K., Hinkel, H., & Menegon, M. (2018). *A field guide to east African reptiles* (2nd ed.). London, UK: Bloomsbury.

Uetz, P., Freed, P., & Hošek, J. (2019). *The reptile database*. Retrieved from http://www.reptile-database.org

Uys, W. (2011, September 30). *iSpot: Vine snakes fighting*. Retrieved from https://www.ispotnature.org/communities/southern-africa/view/observation/335830/vine-snakes-fighting

Van Allen, B. G., Dillemuth, F. P., Flick, A. J., Faldyn, M. J., Clark, D. R., Rudolf, V. H. W., & Elderd, B. D. (2017). Cannibalism and infectious disease: Friends or foes? *American Naturalist*, *190*, 299–312. https://doi.org/10.1086/692734

Vollet, R., Vollet, S., & Ping, T. J. (2015, August 25). *Predation Records - Reptiles and Frogs (Sub-Saharan Africa)*. Retrieved from https://www.facebook.com/groups/888525291183325/permalink/888904307812090

Vrdoljak, P., & Perry, M. (2019). *African Reptiles and Venom*. Retrieved from https://www.facebook.com/AfricanReptilesAndVenom/posts/1385071861633974

Wiseman, K. D., Greene, H. W., Koo, M. S., & Long, D. J. (2019). Feeding ecology of a generalist predator, the California kingsnake (*Lampropeltis californiae*): Why rare prey matter. *Herpetological Conservation and Biology*, *14*, 1–30.

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