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Herpetology Notes

Published: 17/01/2023

Publisher's PDF, also known as Version of record

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):

Major, T., Bracegirdle, R., Gandini, A., Limia Russel, G., Pozzi, A., Morgan, R., Mulley, J., & Wüster, W. (2023). Mate today, gone tomorrow: male-on-female cannibalism in *Zamenis longissimus* (Laurenti, 1768) in North Wales. *Herpetology Notes*, 16, 51-54.

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Mate today, gone tomorrow: male-on-female cannibalism in *Zamenis longissimus* (Laurenti, 1768) in North Wales

Tom Major^{1,*}, Rebecca Bracegirdle¹, Antonio Gandini¹, Guillem Limia Russell¹, Andrea V. Pozzi¹, Rhys Morgan², John F. Mulley², and Wolfgang Wüster¹

Cannibalism is widespread in animals, but the consumption of adult females by adult males is considered rare and difficult to explain because eating an adult female represents the loss of a potential mate (Glaudas and Fento, 2021). Because of the secretive nature of snakes, and the paucity of information on the specific dietary requirements of many species, this phenomenon may be truly rare or simply under-reported, making observations of male-on-female cannibalism particularly valuable (Polis, 1981).

The Aesculapian Snake, *Zamenis longissimus* (Laurenti, 1768), lives in mainland Europe with a range extending from eastern Spain to Azerbaijan (Geniez, 2018). Sexual dimorphism is present, with males reaching up to 200 cm total length and females reaching 140 cm (Corti et al., 2011; Kreiner, 2007). The species is mainly diurnal but may become crepuscular during the hottest months of the year (Kreiner, 2007). It lives predominantly in mixed forests (Gomille, 2002), with lowland populations preferring more humid microhabitats and highland populations preferring drier and more sun-exposed habitats (Corti et al., 2011). *Zamenis longissimus* are cryptic, making them difficult to spot even when basking (Kreiner, 2007). Females lay eggs in late summer, often in communal sites. These sites can be used by multiple species (Corti et al., 2011), such as *Natrix helvetica* (Lacépède, 1789) and *Hierophis viridiflavus* (Lacépède, 1789).

Zamenis longissimus is considered a generalist predator, but although they incorporate a wide variety of prey into their diet (Capula and Luiselli, 2002), they are not known to be snake-eaters. The species displays an ontogenetic shift in diet, with neonates and juveniles feeding mainly

on lizards and juvenile micromammals (e.g., voles, mice, shrews) and occasionally on amphibians and invertebrates (Naulleau and Bonnet, 1995; Najbar 2007; Lelièvre et al., 2012). In adults, most of the diet consists of terrestrial micromammals, birds, and bird eggs. Some cases of chiropterophagy by adult *Z. longissimus* have been reported (Barti et al., 2019).

The observation described here was made during a radiotelemetry study of a *Z. longissimus* population in Colwyn Bay, North Wales. This population originated as an accidental introduction in the 1970s and is outside the species' modern natural range. In 2021, we tracked nine adult snakes as part of our study investigating movement patterns, space use, and habitat use of this population.

M137 is an adult male (Fig. 1B) captured on 10 May 2021 after being found beneath a black tarpaulin in the garden of a local resident. He weighed 512 g and measured 1178 mm in snout-vent length (SVL) with a tail length (TL) of 280 mm. A radio transmitter was implanted on 1 June 2021 and the snake was released on 2 June 2021. F159 is an adult female (Fig. 1A) that was initially captured on 11 June 2021 while basking in a hedgerow. At the time of capture, she weighed 266 g and measured 845 mm in SVL with TL of 173 mm. Transmitter insertion was performed on 17 June 2021 and the snake was released on 18 June 2021. Both snakes were fitted with Holohil BD2-T transmitters, with F159 receiving a 1.6-g transmitter and M137 a 1.9-g transmitter. Transmitters were implanted following Reinert and Cundall (1982), with isofluorane anaesthesia and butorphanol analgesic. Following release, the snakes were tracked twice daily throughout the active season, at approximately 10:00 h and 14:00 h.

From 17 August 2021 both snakes were suspected to be in a similar area, in or close to the grounds of an old country house. However, by this time the battery of F159's transmitter was running out, making it difficult to pinpoint her exact location. On 8 September 2021 during regular tracking, both M137 and F159 seemed to be inside a large rhododendron bush. RB spotted a snake inside the bush and caught it. The snake was discovered

¹ Molecular Ecology and Evolution at Bangor, Bangor University, Bangor, Gwynedd, LL57 2UW, United Kingdom.

² School of Natural Sciences, Bangor University, Bangor, Gwynedd, LL57 2UW, United Kingdom.

* Corresponding author. E-mail: tom.major@bangor.ac.uk

to be M137. The frequencies for both M137 and F159 were found to emanate from the same snake, with two radio transmitters inside M137. The only logical explanation was cannibalism – M137 had eaten F159. It is unclear whether F159 was predated or whether she died, and the carcass was subsequently eaten. M137 was released on 8 September 2021.

The cannibalistic individual, M137, was recaptured on 19 June 2022 and was found to weigh 502 g and appeared to be in excellent body condition. We confirmed that the female's radio transmitter was no longer inside his body by using a magnetic stud finder, and we believe the female's transmitter had either passed through the male's gastrointestinal tract or was expelled via vomiting.

Ophiophagy, the consumption of snakes as prey items, is a widespread trait among serpents and is found in species of most snake families (Jackson et al., 2004). From an energetic point of view, snakes as prey items represent a significant resource to other snakes, allowing them to ingest elongated prey and thus overcome their mouth gape constraint (Cundall and Greene, 2000; Wiseman et al., 2019). In fact, x-rays have shown that snakes are able to ingest prey exceeding their length, by the predator folding the prey's spine into curves inside the gastrointestinal tract (Jackson et al., 2004). What seems odd from an evolutionary perspective is the fact that the cannibalised individual was a female while the predator was a male. In fact, the presence of reproductive females is usually a limiting factor in most reproductive systems and feeding on a female could be perceived as damaging to future mating opportunities. Glaudas and Fuento (2022) highlighted the rarity of this kind of male-on-female cannibalistic event and discussed the

potential ecological and evolutionary reasons behind this phenomenon. They stated that even considering this behaviour as maladaptive, predation upon a conspecific female would still provide a male with significant energy intake, especially if the female is not seen as a potential mate at the time of predation. Shankar and Whitaker (2013) observed multiple adult male king cobras, *Ophiophagus hannah* (Cantor, 1836), feeding on female conspecifics. They noted that this behaviour occurred outside the breeding season and hypothesised that hormones associated with mating suppress appetite in males during the breeding season, but they return to snake-eating, including cannibalism, later in the year.

Predominantly ophiophagic snakes are absent in Europe, but there are a few species, such as European whipsnakes (genus *Hierophis*), Montpellier snakes (genus *Malpolon*), and the smooth snake, *Coronella austriaca* Laurenti, 1768, known to commonly feed on other snakes and even conspecifics (Safaei-Mahroo et al., 2017; Di Nicola et al., 2020; Jofré and Reading, 2020). Such cannibalistic behaviour has historically been perceived as odd and mostly confined to the captive environment (Jofré and Reading, 2020). Nevertheless, recent studies have highlighted a strong underappreciation of this phenomenon, which is rarely observable but may have significant ecological implications. For example, a recent investigation of the feeding habits of the Cape Cobra, *Naja nivea* (Linnaeus, 1758), revealed that conspecifics represented up to 4% of all the ingested prey items and that this behaviour might have led to young specimens feeding in different areas than adults to avoid predation (Maritz et al., 2019).

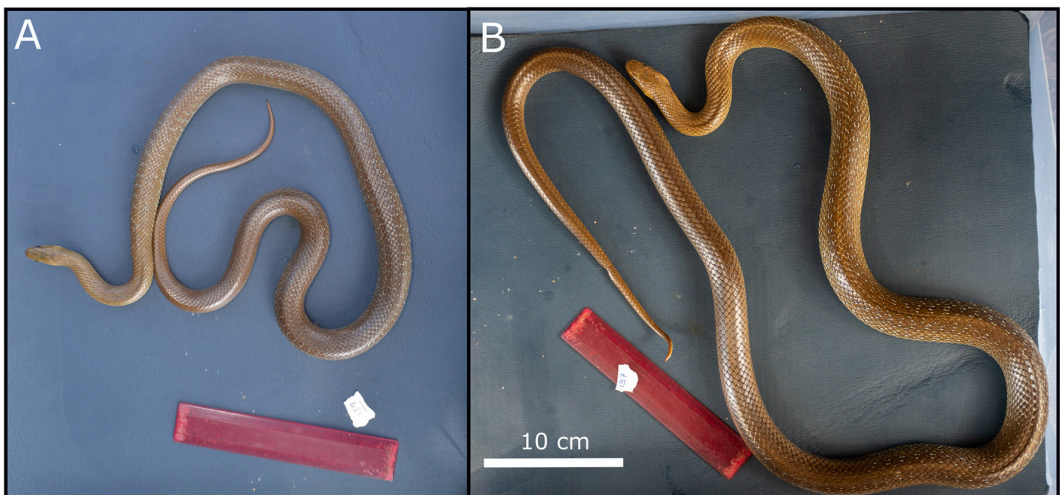


Figure 1. Two adult *Zamenis longissimus* from Colwyn Bay, Wales. The female individual (A) was eaten by the male (B).

The reasons underlying the observed behaviour may be various. Firstly, cannibalistic behaviours are often correlated with the decline or absence of suitable prey, especially in the case of generalist predators (Polis, 1981; Jofré and Reading, 2020). It is possible that there is limited prey availability in the restricted range of the Welsh *Z. longissimus* population, although we would expect a healthy population of rodents due to the close proximity to the Welsh Mountain Zoo, where lots of animal feed is present. Cannibalism among snakes may also be associated with high population density, where the high encounter rate among conspecifics could favour cannibalism (Faraone et al., 2020).

We strongly suspect that the cannibalised female laid eggs before the event, for a few reasons. Firstly, she was coiled up with a male snake when initially captured, suggesting she may have mated. She also made an uncharacteristic long-distance movement during July, which we interpret as a foray to find a suitable ovipositioning site. This was reinforced by her apparent weight loss immediately thereafter. It is plausible that the potentially emaciated and smaller female simply represented a significant source of energy intake for the male. Moreover, *Z. longissimus* is characterised by strong sexual dimorphism, with males growing significantly larger than females (Kreiner, 2007; Corti et al., 2011). Taking this trait into consideration, our observation fits into an asymmetric cannibalism context, with cannibalism frequently exhibited by relatively large individuals in populations with high size variance (Polis, 1981).

Cannibalism is a complex behavioural trait whose underlying causation may be hard to explain. In this case, in a very small introduced range of only a few square kilometres, bounded by roads and housing estates, it seems likely that encounter rates between individuals would be high, increasing the potential for cannibalism. Further telemetric study of this species and others may reveal that male-on-female cannibalism is less rare than we think.

Acknowledgements. This work was supported by the Knowledge Economy Skills Scholarships (KESS II – case number 80815) and the Welsh Mountain Zoo. We are very grateful to the numerous keepers and other staff of the Welsh Mountain Zoo for their continued help, support, and advice. This work took place with approval from the Bangor University Animal Welfare and Ethics Review Board. Telemetry procedures were conducted under Home Office project licence PC44793B6.

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