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Cannibalism in smooth snakes, *Coronella austriaca*

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Cannibalism is a widespread behavioural trait in nature and snakes are no exception. In smooth snakes (*Coronella austriaca*) it has only been visibly observed in captive individuals or known from faecal/stomach content analyses. Between 2009 and 2018 one incidence of cannibalism, determined from a faecal sample, and one sighting, were recorded in wild smooth snakes in Wareham Forest plantations, UK. Analysis of faecal samples and visual encounter surveys were used to estimate its frequency. Both records occurred in early autumn and our results suggest that its incidence in wild smooth snakes in southern England is low (0.1-0.3 %) and may be the result of low body condition. The circumstances resulting in cannibalism in the smooth snake may also be relevant to other animal species where cannibalism has been reported.

Keywords: body condition, carrion cannibalism, intraspecific predation, maternal predation, ophiophagy, predatory cannibalism

Cannibalism (consumption of a conspecific), is a widespread natural process influencing population structure, life history, competition for both resources and mates and behaviour (Polis, 1981; Mitchell, 1986), and occurs in a wide diversity of organisms e.g. bacteria, protozoa, invertebrates and vertebrates (Polis, 1980; Fox, 1975). In reptiles cannibalism has been observed in crocodilians, lizards, snakes and turtles (Mitchell, 1986; Mitchell & Walls, 2008; Maritz, Alexander & Maritz, 2019).

Most cannibalistic predators take a wide variety of prey species causing cannibalism rates to vary within and between years, something that may be influenced by changes in the availability of prey species (Fox, 1975). The accurate assessment of the number of cannibalised individuals in a species' diet is difficult and may require a relatively large number of faecal samples collected over a long period of time (Fox, 1975).

Although the occurrence of cannibalism in wild snakes has attracted interest for many years (Schöland, 1895), records are often anecdotal with most observed instances recorded in captive animals (Mitchell, 1986; Lourdais et al., 2005; Göçmen, Werner & Elbeyli, 2008; Mociño-Deloya et al., 2009) which probably reflects both its rarity and the difficulty of observing snake behaviour in the field (Mitchell, 1986). The confined and unnatural conditions under which captive snakes are kept, and where the ability of potential conspecific prey to escape is restricted, may be a factor resulting in cannibalistic behaviour. This may be particularly true in snakes following prolonged periods of fasting (Mitchell, 1986; Martinez-Freiría, Brito & Lizana-Avia, 2006; Göçmen et al., 2008), though the effects of high density are often confounded with those of food shortage (Fox, 1975).

The smooth snake (*Coronella austriaca*) is a diurnal, secretive colubrid, widely distributed in continental Europe (Arnold & Burton, 1978) but restricted to the lowland heaths of southern England in the UK (Boughey, 2017). Typically they feed on a range of small prey, typically lacertid lizards, shrews and nestling rodents, whose relative abundance in the diet varies according to their availability (Goddard, 1984; Luiselli, 2006; Moreira et al., 2011; Brown, Ebenezer & Symondson, 2014 Reading & Jofré, 2013). Ophiophagy (Rugiero et al., 1995; Reading & Jofré, 2013; Strugariu et al., 2014; Groen, 2018) and cannibalism (Drobenkov, 1995, 2000; 2014; Luiselli, 2006) have also been reported for the smooth snake.

Until now cannibalism in *C. austriaca* has only been visibly observed in captive individuals (Street, 1979) where information concerning its possible causes e.g. snake body size, body condition and sex, is lacking (Mitchell, 1986). Although the diet of smooth snakes has been studied widely across their geographic range (Goddard, 1984; Rugiero et al., 1995; Moreira et al., 2011; Brown, Ebenezer & Symondson, 2014; Reading & Jofré, 2013; Reading & Jofré, 2018) evidence of cannibalism has only been obtained from a few studies in which faeces or stomach content were analysed (Drobenkov, 1995; 2000; 2014; Luiselli, Capula & Shine, 1996), suggesting that it could be uncommon.

Following a field observation of an adult male *C. austriaca* eating an adult female *C. austriaca*, our objective was to assess the occurrence of cannibalism in smooth snakes inhabiting commercial pine plantations in southern England, and attempt to explain the factors resulting in this behaviour.

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MATERIALS AND METHODS

Sixteen reptile surveys were completed annually between the last week of April and the second week of October 2009 – 2018 (a total of 160 surveys), in conifer plantations within Wareham Forest, southern England (50˚44'N, 2˚08'W) using refuge arrays, each comprising 37 sheets of corrugated steel spaced 10 m apart in a hexagonal pattern (see Reading, 2012; Jofré, Warn & Reading, 2016 for a detailed description of survey methods). The annual number of arrays surveyed varied between years (2009: 20; 2010-2013: 22; 2014: 25; 2015-2018: 28). All captured *Coronella austriaca* were sexed, measured (snout-vent length (SVL)), weighed (gm) and individually marked using passive integrated transponder tags (PIT-tags). The abdomen of all captured snakes was massaged, anterior to posterior, to encourage defecation and faeces were collected in Eppendorf tubes and preserved in 70 % ethanol prior to analysis under a binocular dissecting microscope (60-250x magnification: see Reading & Jofré, 2013).

The body condition of all *C. austriaca* captured in Wareham Forest pine plantations, including those involved in cannibalism, were estimated using a regression analysis of $\log_{10}$ body mass plotted against $\log_{10}$ SVL in Minitab 18.

RESULTS

Between April 2009 and October 2018 a total of 145,040 refuges were lifted during 2,056 hours of field work. A total of 998 *Coronella austriaca* were encountered from 883 refuges, consisting of 235 individuals.

Diet analysis

Between 2009 and 2018 a total of 69 individual male (SVL range: 21.5 – 49.7 cm) and 58 individual female *C. austriaca* (SVL range: 15.7 - 55.7 cm) provided 155 and 139 faecal samples respectively from which the remains of 329 prey items were identified (Table 1). One faecal sample, from an adult female (SVL: 40.4 cm; tail: 7.6 cm; mass: 25 gm) captured on 2nd October 2015 contained the remains of a single new-born smooth snake (determined from the size of the frontal head scale: length = 3.1 mm; width = 2.1 mm).

As only a single instance of cannibalism was detected its contribution to the overall diet of smooth snakes was negligible (0.3 %) compared to the total contribution of lacertids (53.5 %), small mammals (39.8 %) and slow-worms (6.1 %) (Table 1). However, in 2015, the percentage of the total annual dietary intake for larger females (SVL ≥30 cm), accounted for by cannibalism was 6.25 %, compared to 43.75 % by lacertids, 43.75 % by small mammals, and 6.25 % by slow-worms.

Field observation

On 16 September 2018 (13:15 hrs; air temperature: 23.3˚C) two adult *C. austriaca* were found tightly coiled around each other (Fig. 1a) and were initially assumed to be mating. However, it transpired that the male had started to swallow the live female head first (Fig. 1b). On capture, their sex, body length and body mass were recorded (male: SVL: 44.2 cm; tail: 12.1 cm; mass: 40 gm; female: SVL: 43.1 cm; tail: 8.3 cm; mass: 24 gm). Although the male was untagged, the female was first captured in June 2018 when she was gravid and weighed 37 gm. The body condition of both the female and male were outside, and below, the 95 % confidence interval

Table 1. Number of prey items identified in smooth snake (*C. austriaca*) faecal samples, according to snake sex and SVL. All samples were collected between late April and mid-October 2009 to 2018. Lacertid lizards (*Lacerta agilis*, *Zootoca vivipara*); Slow worm (*Anguis fragilis*); Small mammals (*Sorex minutus*, *S. araneus*, *Apodemus sylvaticus*, *Microtus agrestis*). The percentage of the diet represented by each prey type is shown in parenthesis.

Prey type	Males		Females		Total
	SVL <30 cm	SVL ≥30 cm	SVL <30 cm	SVL ≥30 cm	
Lacertid lizards	18	85	15	58	176 (53.5 %)
Slow-worms	1	12	0	7	20 (6.1 %)
Smooth snakes	0	0	0	1	1 (0.3 %)
Small mammals	3	59	2	67	131 (39.8 %)
Invertebrates	0	0	1	0	1 (0.3 %)
Total	22	156	18	133	329

Figure 1. Male smooth snake (*C. austriaca*), SVL: 44.1 cm, eating a conspecific adult female (SVL: 43.1 cm), in Wareham Forest, Dorset, UK in 2018.

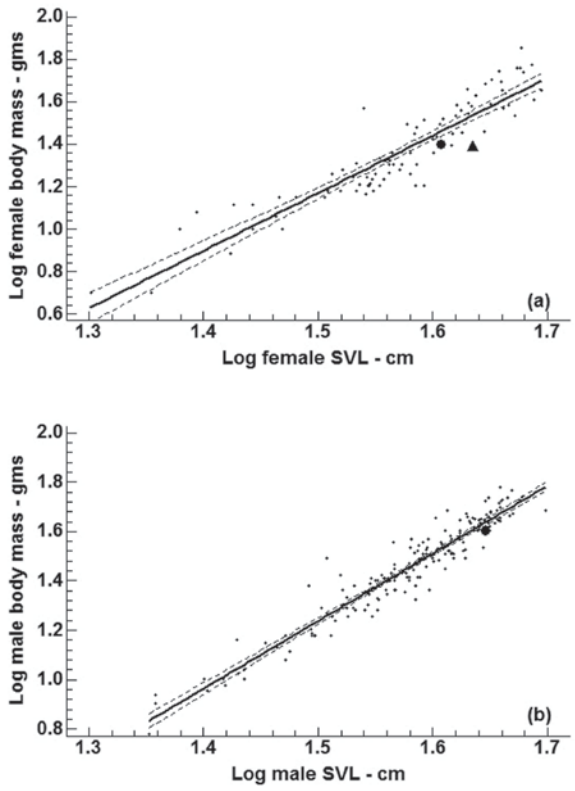

Figure 2. Regression analysis of female **(a)** and male **(b)** $\log_{10}$ body mass against $\log_{10}$ SVL with 95 % confidence intervals (---) for plantation smooth snakes. ●- Cannibal; ▲- Prey. **Female:** $\text{Log}_{10}\text{Mass} = -2.893 + 2.709\ \text{Log}_{10}\text{SVL}$; $r^2 = 84.4$ %; $P < 0.001$; $n = 88$. **Male:** $\text{Log}_{10}\text{Mass} = -2.864 + 2.735\ \text{Log}_{10}\text{SVL}$; $r^2 = 91.8$ %; $P < 0.001$; $n = 170$.

for snakes of their respective mass and SVL occurring in plantations (Fig. 2). The estimated rate of cannibalism over ten years, derived from direct observation, is approximately 0.1 %.

DISCUSSION

To our knowledge, this is the first reported direct (witnessed as opposed to inferred from faeces/stomach content analysis), observation of predatory cannibalistic behaviour in wild *Coronella austriaca*. There are, however, two reported field observations of ophiophagy in adult female smooth snakes, one preying on a juvenile grass snake (*Natrix natrix*; Strugariu et al., 2014) and one on a juvenile adder (*Vipera berus*; Groen, 2018), in which the predation showed a similar pattern to our observation: gripping the prey's head, coiling around the posterior part of their body, constricting them, and swallowing them head first.

Most observations of cannibalism in snakes can be explained by differences in size, e.g. large individuals taking smaller individuals (Göçmen et al., 2008) or females sometimes eating smaller males after mating e.g. green anaconda *Eunectes marinus*, (Rivas & Owens, 2000). In contrast, our field observation involved an adult male smooth snake eating an adult female of a similar body size. This apparent reversed form of sexual cannibalism may reflect opportunistic foraging, which, for example, has been observed in amphipod crustaceans (*Gammarus* sp.), where males may attack females when alternative prey items are scarce (Dick, 1995).

Although the two events of cannibalism we report may have different explanations, both snakes had a body condition below the average estimated for *C. austriaca* inhabiting pine plantations in Wareham Forest (Reading & Jofré, 2018) suggesting that they may have been experiencing food stress.

'Optimal Foraging Theory' predicts that an animal's diet will generally become more diverse when resource availability decreases (Emlen, 1966; MacArthur & Pianka, 1966; Shoener, 1971). Consequently, during periods of reduced food availability, predators are expected to expand their diet to include previously ignored prey (Polis, 1980; 1981). Hunger may also trigger a series of behavioural changes that increase the probability of intraspecific contact and predation, e.g. increasing foraging activity, lowering the attack threshold and increasing vagility leading to an expansion of the search area. Increased activity may also leave animals deprived of food, weaker and increasingly vulnerable to cannibalism (Polis, 1981).

The cannibalistic event observed in 2018 occurred in a 17 year old plantation with high tree canopy cover (mean ± SD = 78.91 % ± 40.96 %), a habitat not usually favoured by reptiles (Jofré, Warn & Reading, 2016). This was supported by the observed lack of resident *C. austriaca* at this site since early 2014. Their subsequent presence in this 'unsuitable' plantation in 2018, along with seven new *C. austriaca*, may have been the result of nearby forest management activities causing disturbance and resident snakes in those areas to disperse (Jofré, 2018).

It was not possible to determine whether the female *C. austriaca* that ate a conspecific new-born had killed and eaten another female's live offspring (predatory cannibalism), one of its own offspring (maternal predation), or if the juvenile was already dead when eaten (carrion cannibalism). Female snakes producing young in captivity frequently ingest their own undeveloped ova and stillborn offspring e.g. the Colombian rainbow boa, *Epicrates cenchria maurus* (Lourdais et al., 2005) and the Mexican lance-headed rattlesnake, *Crotalus polistictus* (Mociño-Deloya et al., 2009). In the wild a late parturition leaves snakes, that feed infrequently when gravid (Luiselli, Capula & Shine, 1996; Reading & Davis, 1996; Reading & Jofré, 2013) a shorter time to forage before the next hibernation or reproductive event and may increase the pressure towards cannibalism (Mociño-Deloya et al., 2009).

The frequency of cannibalism in *Coronella austriaca* in this study was 30–34 times lower than that estimated from stomach content analyses in Belarus (9.1 –10.3 %; Drobenkov, 1995; 2014) and 6–21 times lower than in that estimated from faeces and stomach content analysis in the Carnic Alps, Italy (Luiselli, Capula & Shine, 1996) where cannibalism accounted for 1.7 % of the overall diet; increasing to 6.25 % in larger females (SVL≥30 cm). However, the data from both Belarus and Italy were based on relatively small sample sizes (n = 29, 55 and n = 118 respectively) compared to our study (identified prey: n = 329; refuges revealing snakes: n = 883) and

may, therefore, have over-estimated the cannibalism rates in these locations. Indeed, the cannibalism rates for Wareham Forest may also be over-estimated if no further incidents occur whilst the number of refuges turned, or faecal samples analysed, increases. Conversely, an additional incidence of cannibalism may double the estimated rate but it would still remain lower than those for Belarus and Italy. The problems associated with very small sample sizes, when attempting to estimate cannibalism rates must, and should, be recognised and acknowledged.

Our results suggest that cannibalism in Wareham Forest *C. austriaca* is a rare behavioural trait that may occur when an individuals' body condition is low, possibly due to periods of food shortage. The conditions leading to cannibalism may also apply to other species where cannibalism has been reported.

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