



The Smooth Snake is not a threat to the Meadow Viper: predator–prey interactions of a reptile specialist snake

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Abstract

Ecological data on the Smooth Snake (*Coronella austriaca*) remains limited. Previous studies report that it mainly consumes lizards, but also mammals and snakes. Its habitat selection remains poorly understood, especially regarding prey availability. As there is limited data on the diet of this species from Central Europe, and it was considered a potential predator of the endangered *Vipera ursinii rakosiensis* (Hungarian Meadow Viper), we conducted a study concerning the diet of *C. austriaca* in one of the largest *V. ursinii* habitats in Hungary. We also tested if the availability of prey species affects its occupancy. Smooth Snake individuals were captured to collect faecal samples, in which the remains were identified. In the obtained samples, we found remains of lizards (65%, namely *Lacerta viridis*, *Podarcis tauricus* and *Lacerta agilis*), mammals (20%), insects (12.5%) and Smooth Snake (2.5%). We found no remains of *V. ursinii* in the samples. We used two-species occupancy modelling to test if the occupancy of *C. austriaca* is linked to the presence of prey species in the area. We found interactions between *C. austriaca* and its lizard prey, as occupancy of the Smooth Snake had a higher probability when these species were present. We found no interaction between the Smooth Snake and *V. ursinii*. Our results support that *C. austriaca* mainly preys on lizards and its occupancy depends on prey availability. Importantly, we found no evidence that *C. austriaca* consumes *V. ursinii*, further supported by the lack of interaction between the occupancy of *C. austriaca* and *V. ursinii*.

Keywords *Coronella austriaca* · Prey–predator interactions · Occupancy modelling · *Vipera ursinii rakosiensis* · Reptile ecology · Diet analysis

Introduction

By understanding the interactions between species, we can acquire crucial information about the life history of species, food webs and communities (Christensen et al., 2014). Studying the diet of a predatory species can not only provide information about the predator's food habits, it also helps to gain insight into prey availability, evolutionary changes, coevolution of species and the forming of ecosystems (Buren et al., 2012; Yoshida et al., 2007). Understanding predator–prey relationships can contribute to the conservation of both the predator and the prey species, and research on food webs can help detect ecosystem problems (Mizsei et al., 2019; Tylanakis et al., 2010). Research about trophic interactions can help maintain biodiversity both on a smaller and larger scale (Stouffer & Bascompte, 2010).

Even though they account for a large portion of terrestrial vertebrate diversity, the global conservation status of reptiles has rarely been assessed (Böhm et al., 2013). As of 2013,

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19% of all reptiles were threatened (IUCN categories: Critically Endangered, Endangered and Vulnerable), 7% were near threatened, with an additional 20% falling into the IUCN category Data Deficient (Böhm et al., 2013; Tingley et al., 2016). The most important factors threatening reptile populations worldwide are habitat destruction and fragmentation due to agriculture, logging or urbanisation and invasive or problematic native species (Böhm et al., 2013). The conservation of snakes is made more challenging by their negative public image (Williams, 2009), the increased demand in illegal trade (Hierink et al., 2020) and a recently appeared fungal infection (Lorch et al., 2016).

The conservation status of snakes is not favourable, and more research would be necessary to address existing gaps in knowledge (Christensen et al., 2014; Williams, 2009). Even though some aspects of the behavioural ecology of snakes (e.g. reproductive biology) are rather well studied, literature on other topics, such as trophic interactions remain scarce (Shine, 2003; Williams, 2009). The importance of understanding trophic interactions for conservation is often overlooked, even though prey availability can have a strong effect on the population dynamics of snakes (Fitzgerald et al., 2004; Madsen et al., 2006). Trophic links of snakes can not only provide information about the diet of the species, but they can also offer important insight into spatial ecology, life history and dynamics of populations (Wasko & Sasa, 2012).

Predation by native predators can pose a huge threat to threatened populations, even though its effects are often overlooked (McLoughlin & Owen-Smith, 2003). The Hungarian Meadow Viper (*Vipera ursinii rakosiensis*, further referred to as Meadow Viper) was once common in the steppe meadows of the Carpathian Basin, however, its global population size possibly declined to just a few hundred individuals (Korsós, 2002; Péchy et al., 2015) mainly due to habitat loss (Mizsei et al., 2018). According to more advanced recent estimations, its population size in the Kiskunság is approximately 9000 individuals (Mizsei et al., unpublished data). In the last two decades, huge conservation efforts have been allocated to save this subspecies from extinction. Currently, mortality due to predation is considered to be the most important threat (Móré et al., 2022). The Meadow Viper is mostly preyed upon by native predators in Central Hungary, most importantly the European Badger (*Meles meles*), the Red Fox (*Vulpes vulpes*) and several avian predators, such as the European Buzzard (*Buteo buteo*) or the short-toed eagle (*Circus gallicus*) (Móré et al., 2022; Tisza et al., 2024).

During the monitoring of conservation actions implemented to enhance the conservation status of the Meadow Viper, we frequently observed individuals of the Smooth Snake (*Coronella austriaca*) among other reptiles. Even though it is widespread in Europe and Western Asia, little

is known about the ecology of this species (Goddard, 1984). Papers available about its diet are mainly from areas where the snake is rather rare and locally endangered (Drobenkov, 2014; Luiselli et al., 1996). According to various studies, the Smooth Snake is a reptile specialist predator (Brown et al., 2014; Capizzi et al., 1995; Luiselli et al., 1996). It feeds mostly on lizards, but it is also known for its frequent snake (Drobenkov, 2014), and occasional viper predation (Di Nicola et al., 2020; Escalante et al., 2023; Johansen, 2024). We identified 18 publications concerning the food habits of the Smooth Snake (Table 1). Most of them identified lacertid lizards (mainly *L. agilis* and *Z. vivipara*) as the main food source of the snake, but consumption of small mammals such as rodents and shrews and Slow Worms (*Anguis sp.*) were also common. There were some cases of Oligochaeta, insect and amphibian predation as well as consumption of snakes, with frequent cases of cannibalism. Vipers were identified as prey items of the Smooth Snake in 7 cases, the consumed viper species were *Vipera berus*, *V. aspis* and *V. seoanei* (Table 1).

There is limited information available on the habitat selection of the Smooth Snake with most studies covering the Northern extent of its range; however, literature data suggests that this species prefers the diversity of available microhabitat types (Köntopp, 2009; Volkl & Meier, 1988). It generally prefers rocky and open areas (Böhme, 1993; Köntopp, 2009; Volkl & Meier, 1988) and more complex habitat structure (Reading & Jofré, 2015). The influence of prey availability on the habitat selection of the Smooth Snake has rarely been studied; however, Ceirans and Nikolajeva (2017) found that it prefers sites with a higher density of its prey item, the Slow Worm (*Anguis fragilis*).

Considered a reptile specialist predator, and because its habitat and activity largely overlap with that of the Meadow Viper, it was suspected that the presence of the Smooth Snake can pose a threat to the Meadow Viper population. To assess this, we conducted a dietary study about the Smooth Snake to determine the composition of its diet in the study area and whether it preys on the Meadow Viper. Furthermore, we tested whether the habitat occupancy of the Smooth Snake is conditional or not on the occupancy of other reptile species in the Meadow Viper habitats in Central Hungary.

Methods

Study area

The sampling areas were designated in grassland habitats of the 'Felső-kiskunsági Turjánvidék' and 'Bócsa-bugaci homokpuszta' Natura 2000 SCI priority conservation areas (coded HUKN20003 and HUKN20024, respectively) of the

Table 1 Overview of the diet of *Coronella austriaca* and the proportion and taxonomic identity of prey items (to the lowest level reported) based on the literature

Country	Sample size (n)	Prey item	Percentage	Study
Norway	3	<i>Natrix natrix</i>		Johansen (2024)
		<i>Vipera berus</i>		
Belarus	57	<i>Zootoca vivipara</i>	43.6	Drobenkov (2014)
		<i>Coronella austriaca</i>	9.1	
		<i>Talpa europaea</i>	5.5	
		<i>Lacerta agilis</i>	16.4	
		<i>Anguis colchica</i>	7.3	
		<i>Microtus arvalis</i>	9.1	
		<i>Sorex araneus</i>	3.6	
		<i>Apodemus agrarius</i>	5.5	
Poland	12	Reptilia	77.4	Najbar (2001)
		Mammalia	21.3	
		Insecta	1.3	
Poland	1	<i>Coronella austriaca</i>		Kolanek (2020)
The Netherlands	1	<i>Vipera berus</i>		Groen (2018)
Great Britain	47	Small mammals	59.57	Goddard (1984)
		<i>Zootoca vivipara</i>	53.19	
		<i>Anguis fragilis</i>	2.13	
Great Britain	226	<i>Zootoca vivipara</i>	15	Reading & Jofré (2013)
		<i>Lacerta agilis</i>	7.1	
		Lacertidae	26.1	
		<i>Anguis fragilis</i>	5.7	
		<i>Natrix helvetica</i>	0.4	
		<i>Bufo bufo</i>	0.4	
		<i>Sorex minutus</i>	16.4	
		<i>Sorex araneus</i>	5.8	
		Soricidae	9.7	
		<i>Apodemus sylvaticus</i>	2.2	
		<i>Microtus agrestis</i>	3.1	
		Muridae	8	
Great Britain	329	Lacertidae	53.5	Jofre (2020)
		<i>Anguis fragilis</i>	6.1	
		<i>Coronella austriaca</i>	0.3	
		Small mammals	39.8	
		Invertebrates	0.3	
Germany	17	<i>Lacerta agilis</i>	18	Zimmermann (1988)
		<i>Podarcis muralis</i>	77	
		<i>Anguis fragilis</i>	3	
		<i>Apodemus spp.</i>	2	
Germany	1	<i>Coronella austriaca</i>		Rowland and Nöllert (2021)
Romania	1	<i>Natrix natrix</i>		Strugariu (2014)
France, Switzerland	2	<i>Coronella austriaca</i>		Zdunek (2023)
Italy	44	Coleoptera	2.27	Rugiero (1995)
		<i>Podarcis muralis</i>	43.18	
		<i>Podarcis siculus</i>	6.81	
		<i>Podarcis sp.</i>	09.08	
		<i>Lacerta viridis</i>	09.08	
		Lacertidae	13.63	
		<i>Anguis fragilis</i>	2.27	
		<i>Vipera aspis</i>	2.27	
		<i>Apodemus sp.</i>	09.08	

Table 1 (continued)

Country	Sample size (n)	Prey item	Percentage	Study
Italy	118	Oligochaetes	0.85	Luiselli (1996)
		Orthoptera	2.54	
		<i>Anguis fragilis</i>	19.49	
		<i>Zootoca vivipara</i>	68.64	
		<i>Coronella austriaca</i>	1.69	
		<i>Vipera berus</i>	0.85	
		<i>Apodemus sylvaticus</i>	5.93	
Italy	3	<i>Hierophis viridiflavus</i>		Di Nicola (2020)
Spain	28	<i>Vipera aspis</i>		Galan Regalado (1988)
		<i>Microtus lusitanicus</i>	3.57	
		Small mammals (indet.)	7.14	
		<i>Podarcis bocagei</i>	46.43	
		<i>Lacerta schreiberi</i>	3.57	
		Lacertidae(indet.)	10.71	
		<i>Chalcides striatus</i>	7.14	
		<i>Anguis fragilis</i>	14.29	
		<i>Coronella austriaca</i>	3.57	
		Carabidae	3.57	
Spain	1	<i>Vipera seoanei</i>		Pardavila (2012)
Spain	1	<i>Vipera aspis</i>		Escalante (2023)

Table sorted based on reptile species richness according to Sillero et al. (2014)

Kiskunság National Park Directorate (Fig. 1). These sites hold the largest populations of *Vipera ursinii* in Hungary. The sites are characterised by Pannonic sand steppes (6260), priority habitat type of the EU Habitats Directive, which is a mosaic of dry sandy grasslands, mesophile grasslands and marsh meadows. The grasslands are managed mostly by extensive cattle grazing as conservation management; however, mowed hayfields and combined use of grazing and mowing are also present in some parts of the area (Mizsei et al., 2023a). Apart from the Smooth Snake and the Meadow Viper, the other reptile species found here are the Eastern Green Lizard (*Lacerta viridis*), the Balkan Wall Lizard (*Podarcis tauricus*), the Sand Lizard (*Lacerta agilis*), the Viviparous Lizard (*Zootoca vivipara*), the Grass Snake (*Natrix natrix*) and the European Pond Turtle (*Emys orbicularis*).

Reptiles—including Smooth Snakes and Meadow Vipers—are regularly monitored in both study sites. The sampling design was developed to assess the effect of conservation actions of the LIFE HUNVIPHAB “Viability improvement of Hungarian meadow viper populations and habitats in the Pannonian region” LIFE project (LIFE18 NAT/HU/000799). The monitored areas include reference state primary grasslands, secondary grasslands in a semi-natural state impacted by conservation actions of the project (habitat diversification through plant seeding; wild boar

exclusion; predator control) and not impacted seminatural secondary habitats. The selected habitat patches consisted of the most common grassland types of the study areas and thus can be considered representative of all terrestrial reptile species occurring in the study area. We performed a spatially balanced stratified random sampling and designated $n = 70$, 0.25 ha (50 × 50 m) quadrats for the surveys. Exact sampling sites are not shown for conservation purposes.

Occupancy surveys

We used the following monitoring protocol to assess reptile occupancy by surveying the sampling quadrats in eight consecutive survey seasons, during spring (April–May) and autumn (September–October) between 2020 and 2023. Each spring and each autumn survey season constitutes a primary survey season. In each primary survey season, all quadrats were surveyed 10 times (secondary surveys) between 7 am and 6 pm. Duration of secondary surveys varied from 5 to 30 min, depending on the number of observations to record and habitat complexity, with longer surveys conducted in denser vegetation. The secondary surveys covered the whole area of the quadrat. We recorded the GPS coordinates, time and individual data (species, sex, age) of detected individuals using the OpenBioMaps smartphone application, including the metadata of the surveys (start and end time, tracklog,

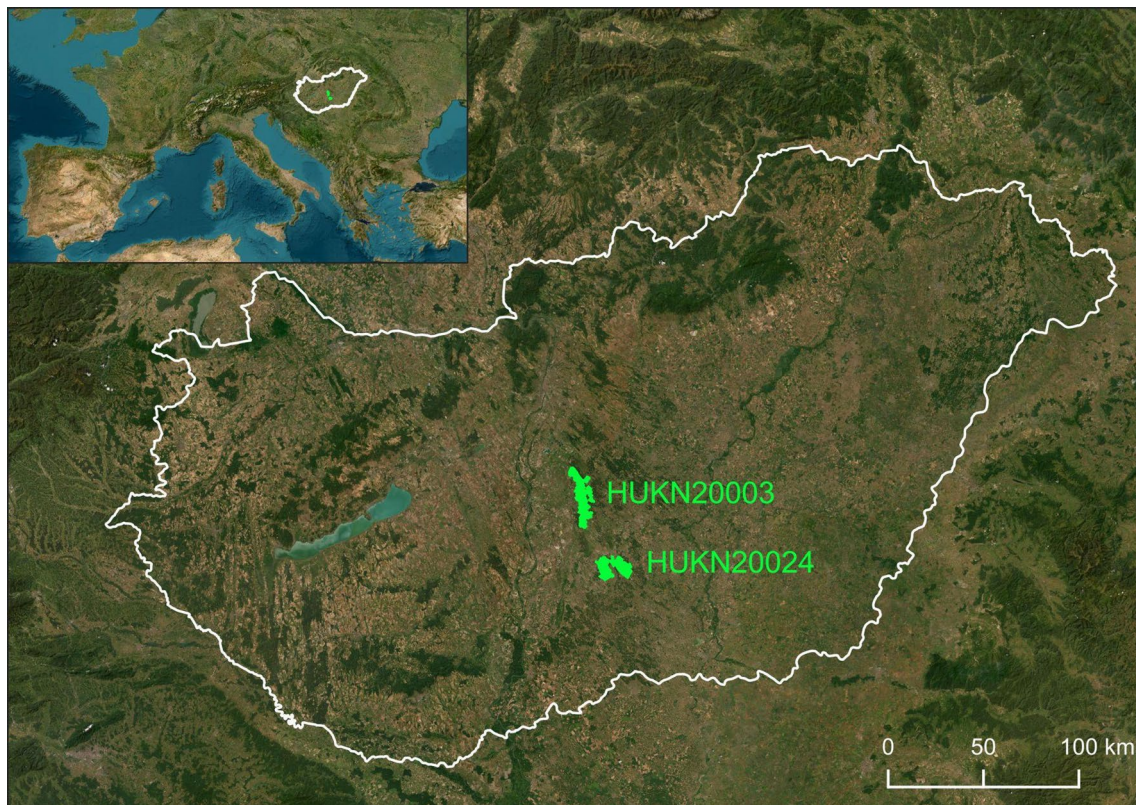


Fig. 1 Location of the sampled Natura 2000 sites (green polygons). The white line indicates the border of Hungary

surveyor ID) and stored in an OpenBioMaps database (Bán et al., 2022). Furthermore, as weather fundamentally influences the activity of reptiles, to account for detection probability, we measured operative temperature during the surveys as described in (Mizsei et al., 2023b). In summary, we conducted $n = 10$ secondary surveys in $n = 70$ sampling quadrats in $n = 8$ primary survey seasons resulting in $n = 5600$ surveys to record reptile observations.

Faecal samples

We characterised the diet of the Smooth Snake by visual analysis of faecal samples collected at the ‘Felső-kiskunsági Turjánvidék’ site (HUKN20003, Fig. 1). Visual analysis has several advantages such as the simplicity of sample collection, storage and processing, and the possibility of obtaining information on the species identity, life stage, age or sex of prey and the number and relative abundance of prey consumed, and is thus still widely used in dietary studies and monitoring programmes (Mizsei et al., 2019; Nielsen et al., 2018; Vacheva & Naumov, 2024).

Smooth Snakes were captured during the occupancy surveys in 2021 and 2022, and we also captured snakes in July–August 2020 and 2021. That time of the year was included because neonates of both the Meadow Viper and

the Smooth Snake are born during that period and literature suggests that Smooth Snakes are more likely to prey on neonate vipers (Di Nicola et al., 2020; Groen, 2018). We recorded sex, snout-vent length (SVL), date of capture and GPS coordinates. The captured individuals were kept in separate textile bags for 2–4 days (min. 1 day, max. 7 days) in a building near the habitats that had continuously open windows to equilibrate with outside air temperature, ensuring the snakes were kept at ambient conditions to allow them to produce faecal samples. The snakes were checked every day for faecal samples. After measurements, we released all individuals at the exact site of their capture. Faecal samples were stored in 96% ethanol.

We investigated the faecal samples under a stereomicroscope to find and identify all remains of potential prey specimens. Visual examination of the faecal samples allows the detection of bones and teeth of vertebrates, non-digestible hair of mammals, feathers of birds, scales of reptiles, chitinized cuticles of arthropods and other body parts (e.g. earthworm bristles), and usually also allow species-level identification of prey items (Angelici et al., 1997; Mizsei et al., 2019; Pérez-Mellado et al., 1991; Shine et al., 1998). We identified the partly digested remains found in the samples to the lowest taxonomic level possible, following the methodology described by (Luiselli & Amori, 2016).

Statistical analyses

The diet composition of the Smooth Snake was characterised by calculating the relative frequency of occurrence (%O or RFO). %O highlights the presence of rare or small and soft-bodied prey found in small quantities. The prey remains were grouped to class (Mammalia), order (Orthoptera, Coleoptera) or family level (Lacertidae) in the case of lizards, and species (*C. austriaca*) in the case of snakes, based on the accuracy of the identification and the focus of this study. %O was calculated for SVL groups (< 20 cms, 21–31 cms, 31–40 cms, 41–50 cms, 50 < cms) and by sex of adult snakes.

To make an inference on the habitat occupancy of the Smooth Snake whether it is dependent on other potential prey reptile species present in the study area, we applied occupancy models. Occupancy models allow us to account for the imperfect detection probability of a species in surveys and to determine the probability of the true presence or absence of a species at a site (MacKenzie et al., 2002). These dynamic or multiseason occupancy models were developed to provide estimates of occupancy of a focal species by modelling detection probability using the detection/non-detection data of secondary surveys and include the probability of changes in occupancy through time (colonisation, extinction) along the primary survey seasons (Hines et al., 2014). An extension of these models was developed to include the detection/non-detection data of two or more species to assess occupancy dependence among species such as competition or predator–prey interactions (Devarajan et al., 2020; Rota et al., 2016).

Models were fitted separately for the Smooth Snake with each potential reptile prey species (*P. tauricus*, *L. agilis*, *L. viridis*, *V. ursinii*). Detection/non-detection histories along the surveys were constructed based on the secondary surveys recorded in each primary survey for each species. Individual observation numbers were summed up for each secondary survey for each species and truncated to 0 or 1, where 0 marked secondary surveys when a given species was not detected and 1 if it was detected regardless of the number of individuals observed. In each species pair, we ran a model including species interaction and another without interaction, while the rest of the model parameterization was the same. We assumed that each species has a different detection probability (p) depending on the weather, however, the p of one species is independent of the occupancy or detection of the other. In each model, we included the mean operative temperature (the ambient temperature available to the individual during thermoregulation) of a secondary survey as the explanatory variable of p (Shine & Kearney, 2001). Operative temperature was measured using $n = 8$ thermometers (BTP-06 temperature sensors connected to a BEL-06 ecologger unit, Boreas Ltd., Hungary) placed in copper

tubes that were painted to mimic the viper's pattern, $n = 4$ were placed in full sun and $n = 4$ were partially shaded by grass. The logger recorded the operative temperature values at 2 min intervals (Mizsei et al., 2023b). Occupancy probability (ψ) was estimated of both species dependent on habitat type, while colonisation probability (γ) and extinction probability (ϵ) were estimated by a constant (null) model. We expected that the ψ of the Smooth Snake may interact with the habitat occupancy of some of the potential prey species. If there is no interaction between the two species, based on the estimates of species interaction factor (SIF) then their occupancy patterns are independent, meaning ψ of the Smooth Snake (species B) is the same when a potential prey reptile species (species A) is absent or present ($\psi_B = \psi_{BA}$). The calculation of SIF is

$$\text{SIF} = \psi_A \times \psi_{BA} / \psi_A(\psi_A \times \psi_{BA} + (1 - \psi_A) \times \psi_B)$$

where ψ_A is the probability of occupancy for species A, ψ_{BA} is the probability of occupancy for species B, given species A is present, and ψ_B is the probability of occupancy for species B, given species A is absent (Richmond et al., 2010). A SIF > 1 suggests the species are more likely to occur together than expected. The SIF was considered empirically supported if the model including species interaction had a lower AIC value than the model without species interaction parameter.

All data processing and analysis were conducted in the R statistical environment (R 4.1.3, R Core Team 2022). Survey data was processed using the hunviphab package (Mizsei et al. 2022) and to fit the occupancy models, we used the RPresence 2.13.49 package (MacKenzie & Hines, 2023). R scripts are available upon request from the corresponding author.

Results

We captured $n = 85$ individuals of the Smooth Snake ($n = 15$ juveniles, $n = 52$ adult males, $n = 18$ adult females) and collected faecal samples from 53 (62.3%). The remaining 32 individuals produced no faecal sample in 7 days and were released at their sites of capture. In the collected faecal samples, we detected 40 prey items, of which 2.5% were beetles, 10% were orthopterans, 65% were lacertid lizards, 2.5% were colubrid snakes and 20% were mammals (Table 1). We were unable to identify all reptile remains to species level, however, the lacertid lizard prey items which were identifiable ($n = 8$), belonged to Eastern Green Lizard ($n = 5$), Balkan Wall Lizard ($n = 2$) and Sand Lizard ($n = 1$). Only one prey item was identified as a snake, a subadult Smooth Snake consumed by a large adult male. Meadow Viper remains were not found in any of the samples (Fig. 2).

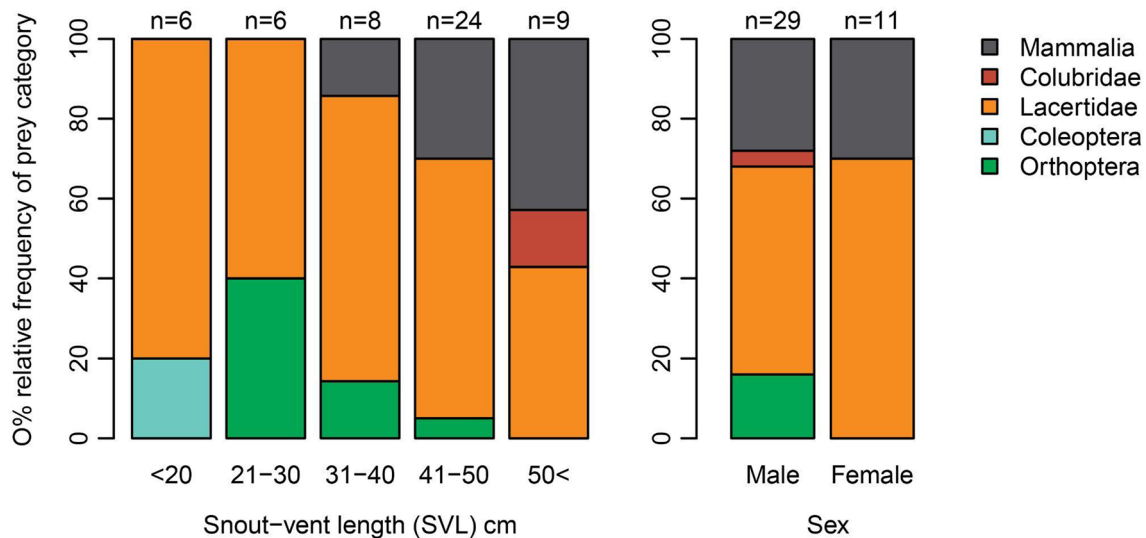


Fig. 2 Variation in diet composition of *Coronella austriaca* by SVL and sex of adult individuals. The number on the top of the bars indicates the number of sampled *C. austriaca* individuals in a given category

Table 2 Occupancy of potential prey species (ψ_A) of *Coronella austriaca*, its conditional occupancy whether a potential prey is present (ψ_{BA}) or absent (ψ_{Ba}), and SIF of a potential prey and the Smooth Snake

Potential prey species	ψ_A	ψ_{BA}	ψ_{Ba}	SIF
<i>Podarcis tauricus</i>	0.614	0.12	0.057	1.254*
<i>Lacerta agilis</i>	0.611	0.106	0.092	1.057*
<i>Lacerta viridis</i>	0.847	0.093	0.087	1.01*
<i>Vipera ursinii rakosiensis</i>	0.356	0.244	0.239	1.015

Asterisks indicate that SIF is empirically supported by model selection based on AIC values

During the data collection for the occupancy modelling, we detected Smooth Snakes in $n=81$ surveys, Meadow Vipers in $n=93$ surveys, Balkan Wall Lizards in $n=780$ surveys, Sand Lizards in $n=499$ surveys, Eastern Green Lizards in $n=1148$ surveys and Viviparous Lizards in $n=3$ surveys. The latter species was not included in the analyses. Mean naive occupancy across the survey seasons was 0.102 for the Smooth Snake, 0.146 for the Meadow Viper, 0.454 for the Balkan Wall Lizard, 0.361 for the Sand Lizard and 0.645 for the Eastern Green Lizard. The two-species occupancy models revealed interaction between the Smooth Snake and its lizard prey: the Balkan Wall Lizard, the Sand Lizard and the Eastern Green Lizard, indicating a higher occupancy probability of the Smooth Snake at sites where these potential prey species occur, however, no interaction was found between the Smooth Snake and the Meadow Viper (Table 2).

Discussion

Faecal analysis of the Smooth Snake in Central Hungary revealed that their diet primarily consisted of reptiles, with lacertid lizards (> 65%) being the dominant prey group. The Eastern Green Lizard and the Balkan Wall Lizard were the most commonly identified lizard prey. Small mammals (20%) and insects (Orthoptera and Coleoptera, 10%) were also consumed, although less frequently. Notably, no Meadow Viper remains were found in the sampled individuals ($n=85$). Occupancy modelling indicated an interaction between the Smooth Snake and its potential lizard prey (*P. tauricus*, *L. agilis*, *L. viridis*), but not between the Meadow Viper and the Smooth Snake.

Our findings align with the general trend observed in previous studies, characterising the Smooth Snake as a reptile specialist predator (Brown et al., 2014; Capizzi et al., 1995; Drobenkov, 2014; Luiselli et al., 1996). Most research identified the Smooth Snake as a predator primarily feeding on Lacertid lizards (Brown et al., 2014; Capizzi et al., 1995; Drobenkov, 2014; Luiselli et al., 1996). This is further supported by the dominance of lizards in the diet, suggesting that the Smooth Snake actively targets these reptiles. Small mammals constituted the second most common prey item found in the faecal samples (20%), which aligns with the established knowledge of adult individuals exhibiting opportunistic feeding behaviour on small mammals. However, an exception was reported by Goddard (1981), who found a higher rate of small mammal consumption compared to lizard consumption. Spellerberg and Phelps (1977) found that adults mainly feed on rodents, while juveniles are nearly exclusively reptile eaters. It is

important to note that in their study, both prey categories were present in over 50% of the collected faecal samples, suggesting opportunistic feeding on both lizards and mammals. As a difference from previous studies, we found a notably larger proportion of insects, primarily orthopterans in the faecal samples, mainly in those from juvenile snakes. This might be because the area hosts a diverse community of orthopterans and the majority of animals included in the study were captured in late summer and fall, the season in which orthopteran activity peaks. It might be possible that the found orthopteran remains in the samples originate from secondary predation (Käsewiter, 2002; Sheppard et al., 2005) and the snakes consume orthopterans only through their lizard prey. However, we find this explanation unlikely, as most orthopteran remains were found in faecal samples in which no lizard remains were detected.

The lizard remains identified in our study belonged to Eastern Green Lizards, Balkan Wall Lizards and Sand Lizards. Previous studies also reported the Viviparous Lizard as a frequent prey items of the Smooth Snake (Brown et al., 2014; Capizzi et al., 1995; Drobenkov, 2014; Luiselli et al., 1996). Interestingly, while this species is present in our study area, it was not found in the faecal samples. However, the extreme rarity of *Z. vivipara* in our study area, being primarily restricted to wetlands where Smooth Snake individuals are rarely observed, likely explains its absence from the diet of the snakes.

The Smooth Snake is known to frequently display cannibalism both in the wild (Galán, 1988; Phelps, 1978; Zdunek et al., 2023) and in captivity (Uysal et al., 2019). In some Smooth Snake populations, where population density is relatively high, it can account for around 10 per cent of the diet of the snakes (Drobenkov, 2014). In most cases, it involves adult snakes consuming juveniles or subadults (also reported here) (Drobenkov, 2014; Galán, 1988; Luiselli et al., 1996), but the Smooth Snake is also known to attack conspecifics of similar or larger size (Kolanek & Bury, 2020; Zdunek et al., 2023). There are reports of the Smooth Snake consuming Grass Snakes (*Natrix natrix*) (Johansen, 2024; Najbar, 2001; Strugariu, 2014), however, we did not detect this species in the faecal samples.

Understanding predator–prey interactions is a cornerstone of ecology, informing critical conservation strategies (Agrawal et al., 2007; Andrewartha & Birch, 1954; Krebs, 1972). This study exemplifies this principle. Occupancy modelling revealed a positive interaction between habitat occupancy of the Smooth Snake and its preferred lizard prey (*P. tauricus*, *L. agilis*, *L. viridis*). This aligns with established ecological knowledge: prey availability shapes predator distribution patterns (Christensen et al., 2014; Tylanakakis et al., 2010). In simpler terms, areas with abundant lizard populations support a higher presence of the

Smooth Snake, as occupancy probability correlates with abundance.

The current study provides valuable insights, but limitations are acknowledged. Expanding the sample size for faecal analysis and incorporating complementary dietary assessment methods, such as DNA metabarcoding, could enhance the robustness of future investigations. Additionally, focusing solely on the habitats of the Meadow Viper restricts the generalizability of these findings on the dietary niche of the Smooth Snake to regions with distinct or more diverse reptile assemblages. Furthermore, limited sample sizes precluded a thorough analysis of seasonal dietary patterns. Future research should prioritise quantifying prey selection by incorporating prey availability data alongside faecal analysis to assess the preference of the the Smooth Snake towards specific prey categories. This would provide a more comprehensive understanding of the long-term feeding patterns of the snake. Additionally, investigating the factors influencing prey selection across different regions and examining the potential impact of the Smooth Snake on its preferred lizard prey populations would further contribute to our understanding of the predator–prey dynamics within this reptile community.

In conclusion, this study confirms the Smooth Snake as a reptile specialist predator in Central Hungary, with lacertid lizards as the dominant prey. While previous research documented viper consumption by the Smooth Snake elsewhere (Capizzi et al., 1995; Di Nicola et al., 2020; Escalante et al., 2023; Groen, 2018; Johansen, 2024; Luiselli et al., 1996; Pardavila et al., 2012), no evidence of predation on the Meadow Viper was found in our diet analysis. This, coupled with the positive interaction between the habitat occupancy of Smooth Snake and its preferred lizard prey in occupancy modelling, suggests that encounters with vipers are likely much less frequent than encounters with lizards. Furthermore, the dominance of lizards in the diet underscores their critical role as a primary food source for the Smooth Snake in this region. These findings emphasise the importance of holistic conservation strategies that consider the entire reptile community (Reading & Jofre, 2020). Managing habitats to sustain stable lizard populations would not only benefit the Smooth Snake by ensuring a readily available food source but also potentially alleviate predation pressure on the vulnerable Meadow Viper. It is important to acknowledge that viper predation by the Smooth Snake can potentially occur. However, based on our findings, such events are likely negligible compared to the predation pressure exerted by established viper predators like the Eurasian Badger (*Meles meles*), the Red fox (*Vulpes vulpes*), and the Common Buzzard (*Buteo buteo*) (Móré et al., 2022; Tisza et al., 2024).

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Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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