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Research article

Dietary adaptations along the northern limit of distribution: what does the smooth snake *Coronella austriaca* eat in Norway? Metabarcoding of stomach content and visual analysis of faeces

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Understanding how species survive at their poleward limits of distribution is of interest in species conservation, particularly in light of global warming and predictions of shifting distributions of both predators and prey species. How species adapt to high latitudes and to future climate changes will be impacted both by direct interactions with the environment, such as changing heat tolerances, but also indirectly through biotic interactions with prey and predators. The smooth snake *Coronella austriaca* in Norway provides an interesting case study of biotic interactions at range limits. The number of potential prey species of *C. austriaca* is lower in Norway than in southern latitudes. To investigate trophic adaptations at its poleward range limit we used metabarcoding sequencing to identify prey species in stomach samples of a museum collection of 17 preserved *C. austriaca* from Agder in southern Norway. Eight prey species were detected, four reptiles and four mammals. Field vole *Microtus agrestis* and common shrew *Sorex araneus* were the most common prey species, while bank vole *Myodes glareolus* and wood mice *Apodemus sylvaticus* were eaten by only a few smooth snakes. Slow worm *Anguis fragilis* was found in five samples and common lizard *Zootoca vivipara* in only three samples. DNA was also recovered from grass snake *Natrix natrix* in all but one sample, and DNA from European adder *Vipera berus* in one sample, indicating the role of ophiophagy. Visual analysis of 75 faeces from the Oslo region showed that *A. fragilis* was the most common prey species, followed by shrews. The main conclusion is that *C. austriaca* in Norway have a higher proportion of mammalian prey and snakes in their diet compared to populations in more southern latitudes.

Keywords: *Coronella austriaca*, diet, faecal visual analysis, metabarcoding, Norway

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Introduction

Understanding species adaptation and survival in high latitudes is interesting in respect to species conservation, especially with global warming affecting prey species abundance and food availability. Species living near their poleward limit of distribution are supposed to have a higher risk of extinction, making it essential to understand ecological roles. Basic knowledge of ecological needs assists in understanding the impact of changing environments on individual species and broader ecological interactions. Dietary studies are an important topic in this area, as feeding habits of a species influence its environmental exploitation.

The smooth snake *Coronella austriaca* is particularly interesting to explore in terms of trophic interactions across a wide latitudinal gradient. The geographical distribution of *Coronella austriaca* extends from Iran in the east, to southern and western Europe, and north to the Nordic countries (Speybroeck et al. 2016), with a preference for a body temperature of 27–33°C (Fog et al. 1997). In the Nordic countries, *C. austriaca* is found only in Norway, Sweden, and some of the Åland Islands (Fog et al. 1997). Compared to occupying higher elevations in warmer areas of southern Europe, in relatively cooler Norway, *C. austriaca* are mainly observed in open, sunny, and often south-facing areas that include rock piles or stone walls, mainly around the coastal areas and warm inland valleys in the south of the country (Sørensen 2014, Speybroeck et al. 2016, Artsobservasjoner 2022).

Various factors influence the value of potential prey to predators like *C. austriaca*, including food availability, as this is often limiting and can affect growth, reproduction, space use, movement patterns, and winter survival. Food energetics are also important, especially for ectotherms living in northern latitudes in colder climate. Small mammals are considered ideal prey for terrestrial snakes, providing more calories than reptile or insect prey (Forsman and Lindell 1993, Shine 1993, Capula and Luiselli 2002, Brito 2004, Luiselli 2006). The number of small vertebrate species decreases towards the Arctic, thus limiting prey options for *C. austriaca* to a few species of reptiles, shrews, and small rodents. In the UK, *C. austriaca* are only found in a small range in the heaths of southern England where the densities of common lizards *Z. vivipara* and sand lizards *Lacerta agilis* are the highest in the country (Braithwaite et al. 1989, Brown et al. 2014).

Studies of stomach and gut contents of *C. austriaca* across their range have revealed they prey mainly on reptiles, including legged lizards and slow worm *Anguis fragilis* (Drobenkov 1995, 2000, Rugiero et al. 1995, Luiselli et al. 1996, Najbar 2001, Völkl and Käsewieter 2003, Brown et al. 2014, Speybroeck et al. 2016). Reading and Jofré (2020) even found that lizard abundance was controlled by *C. austriaca* numbers. *Coronella austriaca* are thought to consume all life stages of reptiles, including eggs (Werner 1897, Saint-Girons 1955, Moreira et al. 2011, Lunghi et al. 2015), and even exhibit cannibalistic behaviour (Jofré and Reading 2020), though this is challenging to quantify. Reports of *C. austriaca* predating on other snake species are rare and sporadic (Andrén and Nilson 1976). Juvenile *C. austriaca* often prey on young lizards, while larger specimens incorporate small mammals into their diet, exhibiting an ontogenetic shift (Goddard 1984, Strijbosch and van Gelder 1993, Luiselli et al. 1996, Reading and Jofré 2013, Brown et al. 2014). Nestling birds (NCC report 1983) and bird eggs (Johansen and Flaatten 2021) have also been reported in the diet of *C. austriaca*.

Amphibians and invertebrates appear in diet analyses (NCC Report 1983, Beebee and Griffiths 2000, Brown et al. 2014), although they are not regarded as preferred prey for *C. austriaca* (Völkl and Käsewieter 2003) and are thought to be consumed as secondary prey (Rugiero et al. 1995).

The conservation status of *C. austriaca* is unfavourable in several countries (EIONET 2020), especially in the northern parts of its range where subpopulations are fragmented (Speybroeck et al. 2016). Local Red Lists in Portugal, Switzerland, and Poland have categorised *C. austriaca* as Vulnerable (VU) (ICNF 2005, Monney and Meyer 2005, ISAP 2016) and in Norway it is Near Threatened (NT) (Artsdatabanken 2021). Because of the importance of sunlight in the northern habitats in particular, overgrowth by bush and forest is having a negative effect, as well as construction, since people and *C. austriaca* seek the same sunny areas along the southern coast of Norway. Consequences of climate warming may result in increased adult mortality because of a less isolating snow cover on hibernation sites (Elmberg et al. 2024). At the same time, warmer summers give earlier parturition dates (Johansen et al. 2022), which result in a longer feeding period for postgravid females before hibernation, which may increase fat layer and thus winter survival. Climate warming may also result in changes in available prey due to invasive species, or increased mortality due to invasive predator species. Introduced species may outcompete native prey species, such as the new introduction of the greater white-toothed shrew *Crocidura russula* in Norway (van der Kooij and Nyfors 2023). Snake fungal disease (SFD) in Europe (Franklinos et al. 2017) is a new threat to the snakes themselves. Because of new invasive species and infectious diseases, knowledge of the basic ecology of native species is crucial for future conservation work.

In recent years, molecular methods such as metabarcoding have proven useful for reptile diet analysis (Brown et al. 2012, 2014, Mondino et al. 2022, Scholtz 2022, Swinehart et al. 2023), yielding comparable results from stomach contents and faeces (Snider et al. 2022). Natural history museum collections represent a treasure chest of material for research, especially for species that are rare, difficult to find, and Red Listed, as is *C. austriaca* in Norway. This study used metabarcoding on the stomach contents of 17 preserved *C. austriaca* from Agder in southern Norway, and visual inspection of faeces from 61 live individuals from inner Oslo fiord, to identify prey species. Our aim was to gain insight into the diet of *C. austriaca* near the poleward limit of their European range where the diversity of potential prey species is low. While reptiles dominate their diet in southern Europe, only two native lizard species occur in Norway, which would make a heavily reptile-dominated diet a risky strategy. Notably, *C. austriaca* in Norway are particularly large (Sørensen 2023), suggesting they may incorporate larger prey into their diet as well. We hypothesize that Norwegian populations adopt a more opportunistic feeding strategy, preying on a broad range of species depending on availability.

Material and methods

Stomach and faeces collection

Faeces from 61 live *C. austriaca* at eight different locations around the inner Oslo fiord were collected during 1983 to 2013 for a visual study of *C. austriaca* prey choice. This region is at the northernmost range of *C. austriaca* distribution in Norway, at 59°54′47″N (Fig. 1). In total, 75 samples were used in the visual analysis. Faecal samples were air dried and stored in paper envelopes. Potential prey reptiles and mammals found dead in the study areas were collected for comparison. The samples were made moist by adding water and then examined under a binocular microscope to identify reptile scales, hair, feathers or skeletal remains. A microscope was further used to distinguish shrew hairs from rodent hairs. Reptile prey animals were identified to species by observing scale size and shape, and mammal prey animals were identified to order Rodentia or genus *Sorex* by comparing sample material with hairs from potential prey species. Small hairs from nestling mammals could not be identified to order level. Wing feathers that were not fully developed were identified as passerine nestling.

Agder county is the southernmost region in Norway, with its main city of Kristiansand located at 58°9′35″N, situated ca 300 km south-west of the capital Oslo. A collection of 33 preserved *C. austriaca* from the Natural History Museum and Botanical Garden, University of Agder (UiA), had been found dead by the public in southern Norway and stored in a −20°C freezer at the museum between 1995 and 2021. These were described morphologically, measured, gendered, and sorted into three age groups (adult, subadult, and juvenile). As snakes often have empty stomachs, stomach and gut contents were isolated from the 17 individuals with visible content, and preserved individually in 2 ml Eppendorf tubes, and stored at −20°C in 70% ethanol for subsequent analysis. The 17 *C. austriaca* consisted of 10 adults (8 males and 2 females), 4 subadults (32–52 cm total length), and 3 juveniles of one year (one winter survival, less than 32 cm total length) (Supporting information). The places of origin of the faeces and stomach samples are shown in Fig. 1, thus this study covers *C. austriaca* diet from its northernmost and southernmost ranges in Norway.

DNA isolation

DNA was extracted from 250 mg of homogenized gut material (or all material for samples < 250 mg) using the QIAamp PowerFecal DNA Kit (Qiagen), following the manufacturer's protocol. DNA concentration and quality were confirmed with a NanoDrop One (Thermo Scientific) spectrophotometer.

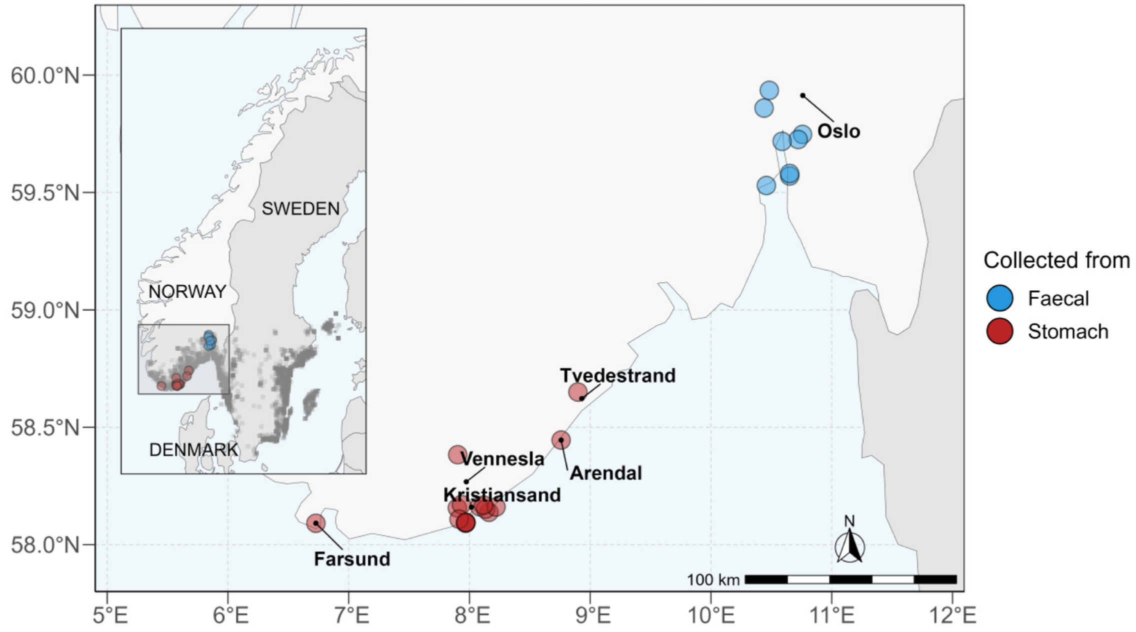

Figure 1. Map showing the locations in southern Norway of 17 dead *Coronella austriaca* individuals collected for metabarcoding of stomach content (red dots), and eight study areas of 75 visually inspected faeces located around the inner Oslo fiord (blue dots). When dots overlap, the colour becomes more intense. Inset: map of Scandinavia showing the distribution of *C. austriaca* as grey squares. Map created with 'ggplot2' (Wickham 2016) using R (ver. 4.2.1, www.r-project.org) in RStudio (ver. 2023.12.0, build 369), and distribution data downloaded from GBIF.Org User (2025).

Table 1. DNA degenerated sequence of the universal PCR primer pairs (fwhF2+fwhR2n). W: A or T. Y: C, T, U. R: A, G. H: A, C, T, U.

Primer name	Sequence (5′-3′)	Reference
fwhF2	GGD ACW GGW TGA ACW GTW TAY CCH CC	Vamos et al. (2017)
fwhR2n	GTR ATW GCH CCD GCT ARW ACW GG	Vamos et al. (2017)

Amplification and sequencing of DNA samples

PCR was performed using the Veriti® 96-Well Fast Thermal Cycler (Applied Biosystems). In each PCR, a 2 µl DNA sample was combined with a mixture comprising 10 µl of 2× Phusion High-Fidelity (HF) PCR Master Mix (Thermo Scientific), 6 µl PCR-grade water, and 1 µl each forward and reverse primers (10 µM) (Table 1). Thermo profile: an initial denaturation at 98°C for 30 s, followed by 40 cycles of 98°C for 20 s, 58°C for 30 s, and 72°C for 30 s, followed by a final extension at 72°C for 7 min. PCR products were visualized on 1.5% agarose gel and amplicons of approximately 200 bp were excised from the gel and purified with Quick Gel Extraction and PCR Purification Combo Kit (Invitrogen) following the manufacturer's protocol. Purified amplicons were stored at −20°C until sequencing. Samples were sequenced at a commercial facility (Novogene, Cambridge, UK) on an Illumina NovaSeq, 250 PE.

Bioinformatics and data analysis

Bioinformatic data processing was conducted in Qiime2 ver. 2022.2.0 (Bolyen et al. 2019). Sequences from the pooled samples were demultiplexed to separate out sequence reads from each individual snake using the in-line barcodes and all sequences were trimmed to remove primers, allowing for an error rate of up to 15%, using 'cutadapt' ver. 2022.2.0 (Martin 2011). Any of the reads that did not contain the expected forward primer sequence in the expected position were discarded at this stage. Additional quality control filtering was performed in 'dada2' ver. 2022.2.0, including further trimming reads to a fixed length of 180 bp (both forward and reverse reads), discarding reads with quality scores that predicted over 4 total errors in the read, discarding any reads where the individual position quality score dropped below 2, discarding read pairs that did not contain an identical overlap region of at least 12 base pairs in the forward and reverse reads, de-noising reads, and discarding any chimeric sequences (based on a minimum 2-fold difference in parent–child total abundance) (Callahan et al. 2016). Dada2 also classified the reads into amplicon sequence variants (ASV, groups of identical sequences), and enumerated the abundance of each ASV in each snake individual. ASVs represented by fewer than 0.1% reads were excluded from further analysis, given that highly abundant sequences are more likely to represent ecologically meaningful observations, and the lowest abundance ASVs are most likely to contain sequencing errors or to reflect trace contaminants (Tercel and Cuff 2022).

Taxonomy was assigned to each ASV using the vsearch algorithm to compare the sequences against the barcode of life database (BOLD dereplicated) (Ratnasingham and Hebert 2007, Rognes et al. 2016). Taxonomy for mammalian and reptile ASVs of particular abundance or interest were confirmed or further refined using manual BLASTN searches against the NCBI 'nt' database (Altschul et al. 1990) using 97.9% identity as lower threshold for taxon identification. Particular attention was paid to snake ASVs, as the abundance of *C. austriaca* DNA in samples of their gut contents means there is a higher risk of potential misidentification of closely related and genetically similar organisms. A maximum likelihood phylogenetic tree was constructed in MEGA4 (Tamura et al. 2007) including all reptile ASVs and references sequences from genebank for the extent reptiles of Norway (Supporting information).

Results

Visual analysis of faecal samples from the inner Oslo fiord area

The material from the eight localities around the inner Oslo fiord at the northern limit of the distribution of *C. austriaca* in Norway consisted of 75 faeces samples from 61 *C. austriaca*, containing remains of *A. fragilis*, shrews *Sorex* sp., *Z. vivipara*, rodents, unidentified mammal nestlings, and unidentified passerine nestling (Fig. 2A, Supporting information). *Anguis fragilis* was the main prey item, found in 31 of the faeces samples, from all eight localities, and *Sorex* sp. was the second most eaten prey detected in seven of the eight localities in 20 faeces samples. Rodents were found in six of the samples from five localities, and additional unidentified mammal nestlings were detected in four samples. The remains of passerine bird nestling were found once. *Zootoca vivipara* needs attention, as this prey was found only at Locality 1, hence the visual presentation in Fig. 2A may be misinterpreted. Here at Locality 1, 11 of the 20 individual *C. austriaca* had remains of *Z. vivipara* in their faeces. Eight of the nine juveniles had eaten *Z. vivipara*, as well as one subadult and two adults. Two juveniles were found in other locations, and they had only *A. fragilis* in their faeces. *Zootoca vivipara* was not detected in any faeces from the other seven localities. There were no visual remains from snakes (ophiophagy) in the faeces material.

Metabarcoding and visual inspection of 17 smooth snake stomach samples

The majority of the stomach contents from the 17 *C. austriaca* from Agder in southern Norway were significantly digested, making it impossible to visually identify all prey species. However, no attempt was made to use a microscope for further analysis. Morphologically identifiable remains of *A. fragilis* were observed in the stomach and gut contents of snakes SL01 and SL19 (adults), as well as SL26 (juvenile).

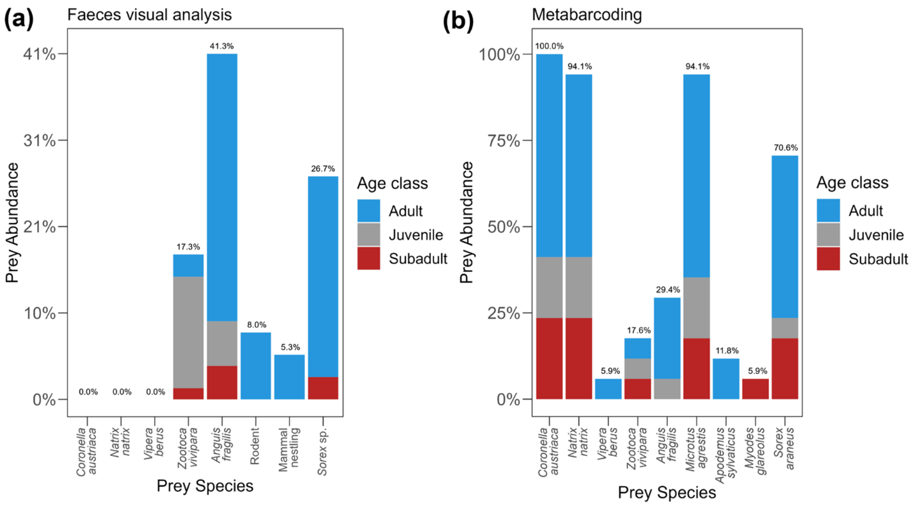

Figure 2. Primary prey species, included host species (*Coronella austriaca*), detected in *C. austriaca* by (A) visual analysis of 75 faeces samples located around inner Oslo fiord and (B) metabarcoding of 17 stomach content samples from southern Norway. The percentage of each prey species detected, displayed above the bars, is calculated by dividing the number of individuals with positive detection by the total number of individuals.

Two field voles *Microtus agrestis* were detected in the stomach of SL24 (adult), indicating recent ingestion. Fur from small mammals was observed in SL19 (adult).

DNA of *C. austriaca* was detected in 100% (17 out of 17) of the samples with a high number of reads in most of the samples (Fig. 2B, Supporting information). Notably, sample SL24 had very few reads from *C. austriaca*, but a substantial amount of DNA from *M. agrestis* (99.4% of the reads). Additionally, two samples (SL01 and SL19, both adults) had exceptionally high levels of *C. austriaca* DNA (664.662 reads, 83.7% and 537.630 reads, 60.3%, respectively). Furthermore, three other samples (SL13, SL15, and SL23) contained significant amounts of *C. austriaca* DNA (over 200.000 reads, ranging between 52% and 95.7%) (Fig. 2B, Supporting information).

Among the reptile prey, grass snake *Natrix natrix* DNA was present in 16 out of the 17 samples (Fig. 2B). However, high read abundance was only found in subadult individual SL09 (14.986 reads). It is also worth mentioning that the adult sample SL15 had 585 reads from *N. natrix*, while the subadult sample SL25 had 206 reads and the juvenile sample SL26 juvenile had 125 reads. The remaining stomach samples contained only 0–40 reads of *N. natrix. Natrix natrix* sequences identified were 100% identical to reference sequences of *N. natrix*, while only 85% similar to sequences of *C. austriaca*, confirming the accuracy of this taxonomic classification (Supporting information). Other reptiles were less commonly observed in the samples. *Anguis fragilis* reads were detected in small to medium numbers (18–4863 reads) in five samples. During dissection, remains of *A. fragilis* were observed in three of these samples (from one juvenile and two adult *C. austriaca*). *Zootoca vivipara* was detected in three out of the 17 samples. The subadult sample SL29 had 10.570 reads while the adult sample SL24 and juvenile sample SL28 had only 134 and 8 reads, respectively. *Vipera berus* DNA was detected in one individual (SL25 subadult) with a low number of reads (40).

Microtus agrestis and the common shrew *Sorex araneus* were the two most common prey species with respect to their appearance in number of samples and number of reads, as well as percentage of total reads in each stomach sample (Fig. 2B and Supporting information). *Microtus agrestis* was detected in all but one sample (SL02 subadult), ranging from 9 reads (0.001%) to 1.889.747 reads (99.4%) in the various samples. *Sorex araneus* was recorded in 12 samples, but in six of these samples the number of reads was low, with under 100 reads. Wood mouse *Apodemus sylvaticus* and bank vole *Myodes glareols* (formerly *Clethrionomys glareolus*) were detected in small numbers of reads (17–82) in three samples (adult samples SL05 and SL08, subadult SL09, respectively).

Apart from the primary prey species, we found a diversity of arthropods, mainly Insecta and Arachnida, as well as Crustaceans, Millipeds, and Collembola. Other phyla identified were Annelida, Nematoda, Gastropoda, Rotifera, Hydrozoa, Porifera, Tardigrada, and 13 classes of fungi. These may have been unintentionally ingested directly or have been secondary prey of the vertebrates consumed (Supporting information).

Discussion

Mammalian diet

Compared to traditional methods, metabarcoding provided a more detailed picture of the prey consumed. This allowed us to identify species from stomach and gut content that was highly digested and unidentifiable morphologically. In the few cases where snakes had identifiable prey remains in their gut contents, the sequencing and morphology results were consistent. The three snakes containing visually identified remains of *A. fragilis* also yielded *A. fragilis* sequences, while the two snake samples containing fur produced sequences from fur-bearing mammals. We were able to achieve a higher resolution of taxa and species by combining search results from the Barcode of Life database (BOLD) with searches against the NCBI nucleotide database. For example, *A. sylvaticus* and *M. glareolus* were detected in the diet this way. The sequencing of the 17 stomachs gave three to four prey species, while visual inspection of faeces gave mainly one prey species. Future sequencing of this faecal material will tell us if the number of prey species is underestimated in visual analysis.

Microtus agrestis was the most common prey item in our metabarcoding of the 17 stomach samples both by frequency (94%) and by number of reads (Supporting information). Both the juvenile and subadult snakes were found to contain DNA from *M. agrestis*. Goddard (1984), Reading and Jofré (2013), and Brown et al. (2014) found an ontogenetic shift from reptile prey in young *C. austriaca* to more mammal prey in adult *C. austriaca* in England. Brown et al. (2014), using PCR analysis, found that predation on mammals was completely absent among juveniles and subadults, which is in contrast to our molecular studies. Norway has the largest *C. austriaca* in the world and also our newborn *C. austriaca* are larger (Dalessi et al. 2020, Sørensen 2023). This may explain why the juvenile *C. austriaca* in Norway also eat mammalian prey, if body size and gape capacity is the crucial factor for diet choice. Molecular analysis did not tell us the age of the prey, but the juvenile *C. austriaca* (mean total length 20.5 cm) may digest newborn mammal nestlings. Only six (8%) adult *C. austriaca* had eaten rodents in the faecal study, in addition to four unidentified mammal nestlings (5%) from the same localities. The study of faeces from locations in the Oslo fiord area therefore aligns with results from England, where young *C. austriaca* were found to consume only reptiles. This highlights the importance of conducting multiple dietary studies to obtain a broad understanding of the prey items of *C. austriaca* in each country. The presence of rodents in *C. austriaca* diet is not unusual and has also been reported in Spain (Galán 1988), Poland (Najbar 2001), Belarus (Drobenkov 1995), Italy (Rugiero et al. 1995, Luiselli et al. 1996), Switzerland (Monney et al. 1995), France (Fretey 1975), England (Spellerberg and Phelps 1977, Goddard 1984, Reading and Jofré 2013, 2020, Brown et al. 2014, Jofré and Reading 2020), and Sweden (Andrén and Nilson 1976), though often in small amounts and mainly predated on by adult *C. austriaca*. *Sorex araneus* was the second most frequent and abundant prey item both in our molecular study (71%) and in our visual study of 75 faeces (27%). However, the faecal analysis only allowed identification to the level of *Sorex* spp. Three out of the four subadults and one out of the three juveniles of the 17 sequenced stomach samples had consumed *S. araneus*. Similarly, two out of the six subadults in the faeces material study also had evidence of this mammal prey. These findings highlight the significance of *S. araneus* as prey for young *C. austriaca* in Norway. Shrews are not commonly found in *C. austriaca* diet in other parts of Europe. However, there are reports of their consumption in England (Spellerberg and Phelps 1977, Goddard 1984, Gleed-Owen 2005, Reading and Jofré 2013, 2020, Brown et al. 2014), Poland (Najbar 2001), and Belarus (Drobenkov 2014). Zuffi (2011) estimated the energetic value (Kcal) of various prey groups for the western whip snake *Hierophis viridiflavus* and found that mammals had a higher energetic value and were eaten more often in a population in the colder continental climate versus a more reptile-based diet in a warmer Mediterranean climate. Zuffi et al. (2010) found that large snake species in Europe had a more diverse and energy-rich diet than smaller snakes. They also found a direct positive relationship between snake body mass or body length and meal energetics. Since *C. austriaca* individuals in Norway are the largest in the world of this species (Dalessi et al. 2020, Sørensen 2023), this may explain the higher consumption of small mammals observed in Norway in all age groups compared to more southern latitudes where *C. austriaca* size is smaller. In Norway, *C. austriaca* would benefit from an increased presence of mammalian prey with respect to central and southern Europe due to its advantageous adaptation to a colder climate. Furthermore, the limited occurrence of legged lizards – a potential alternative reptilian prey – in many *C. austriaca* habitats in Norway may contribute to the higher frequency of predation on small mammals.

Reptile diet

A reptile diet was less common than a mammal diet in all age classes of *C. austriaca* in our molecular study from southern Norway, but not in the faecal visual study from the Oslo fiord locations where *A. fragilis* was the most common prey (41%) and appeared in 31 of the 75 faeces. *Anguis fragilis* were only found in five of the 17 sequenced stomachs (29%), and we would expect *A. fragilis* DNA in more stomach samples if this reptile was a very important prey item for Norwegian *C. austriaca*. However, this may be explained by the abundance of *A. fragilis* and other prey species in the Agder county in southern Norway. Future metabarcoding analysis of a higher number of faeces and stomachs combined with studies on prey availability may shed light on this.

In the faecal material from the Oslo fiord, *Z. vivipara* existed in only one of the eight locations where this reptile species was highly predated, especially by the juvenile *C. austriaca*. Figure 2A may give a misleading picture of the importance of *Z. vivipara* as prey. Without the knowledge that *Z. vivipara* only exists together with *C. austriaca* in one of eight localities, the figure tells us that *Z. vivipara* was detected in 17% of the faeces, which is a relatively high percentage. In reality, this prey was predated by many *C. austriaca*, but only in one locality. However, this tells us that *Z. vivipara* has a high potential as prey for *C. austriaca* in Norway, and that potential future increase in distribution and abundance of this prey species would be of benefit to our snake predator. Our results from Locality 1 with predation on *Z. vivipara* supports the studies from England where juvenile

C. austriaca mainly predated on young *Z. vivipara*. While lizards are generally considered a common prey item for the smooth snake, we only identified DNA sequences from three of the legged lizards in the 17 samples analysed in our study. These results indicates that the presence of lizards in this area is low and that the smooth snakes have consumed alternative prey that may have a beneficial energy content as well. *COI* gene sequences registered in the NCBI Gen Bank show some variation in the region of one of the universal PCR primers used in our study, so the sparse occurrence of *Z. vivipara* DNA in our samples may reflect sub-optimal PCR results. However, observations in our study areas report very low or no presence of lizards.

The use of alternative prey items when legged lizards were scarce or absent has been noted previously. In their study in Latvia, Čeirāns and Nikolajeva (2017) observed that when *Z. vivipara* was absent, *C. austriaca* consumed other prey species, including *A. fragilis*, as well as small mammals and shrews. These findings provide a more optimistic perspective for the future of *C. austriaca* in Norway, as juvenile snakes are not limited to feeding on only one or two reptile species found within the country.

Ophiophagy

Ophiophagy is documented in *C. austriaca* from a wide range of its distributional range (England, France, Spain, the Netherlands, Italy, Romania, Belarus, Poland, Sweden, and Norway). However, reports are anecdotal, and diet studies generally show low numbers of ophidian prey. Some observations also represent animals in captivity. Grass snake species *N. natrix* and *N. helvetica* are the most often reported ophidian prey species (Fretey 1987, Luiselli et al. 1996, Beebee and Griffiths 2000, Najbar 2001, Reading and Jofré 2013, 2020, Strugariu et al. 2014, Johansen 2024), followed by *V. berus* (Saint-Girons 1955, Andrén and Nilson 1976, Luiselli et al. 1996, Beebee and Griffiths 2000, Groen 2018, Johansen 2024). Other *Vipera* species and an *H. viridiflavus* are also recorded as prey species (Rugiero et al. 1995, Pardavila et al. 2012, Di Nicola 2020, Escalante 2023).

In our study, DNA sequences from *N. natrix* were found in 16 out of 17 stomach samples. However, no snake scales were detected in the 75 faecal samples, which might indicate that eventually snake remains have been completely digested. Future metabarcoding of these dried faecal samples or newly collected faeces from the same localities around the inner Oslo fiord may shed light on the degree of ophiophagy in these areas. The number of reads of *N. natrix* was low in eight of the samples. In contrast, the other eight samples had a high number of *N. natrix* reads, suggesting that these *C. austriaca* had consumed *N. natrix*. The subadult SL09 sample had the highest number of *N. natrix* reads (14.986 reads and 44%) and also gave 54% reads of *M. agrestis*, indicating that these prey species had been consumed by this individual. *Natrix natrix* and *C. austriaca* in Norway often share the same locations for activities such as shedding, egg-laying, gravidity, and birth (Beate Strøm Johansen, unpubl.), which makes predation by *C. austriaca* on *N. natrix* plausible. Najbar (2001) suggests that adult *C. austriaca* in Poland seek out the egg-laying sites of *N. natrix* in the autumn to feed on the newly hatched juvenile *N. natrix*, as was documented in Norway in 2023 (Johansen 2024) and again in 2024 (Johansen, unpubl.). Also in England, *N. helvetica* and *C. austriaca* are found to share the same areas, while *V. berus* seemed to avoid those areas (Phelps 1978).

DNA from *V. berus* was detected in one sample with a low number of reads (40). The low number of reads may be explained by a somewhat long period since the *V. berus* was consumed, thus a degraded prey DNA. Andrén and Nilson (1976) in Sweden reported that captive *C. austriaca* will consume *V. berus*. They suggested that *V. berus* might be a more significant prey species for *C. austriaca* than previously believed. According to the NCC Report (1983) referenced in Beebee and Griffiths (2000), approximately 6% of the *C. austriaca* diet in the UK consists of immature and juvenile *V. berus*. A predation attempt on a large *V. berus* was documented by photograph in Norway in 2023 (Johansen 2024). Future metabarcoding of faeces or stomach content from C. *austriaca*, as well as citizen science photographs of snakes, may shed light on the frequency of snakes in the diet.

Cannibalism

There are several reports of cannibalism by *C. austriaca* (Saint-Girons 1955, Galán 1988, Drobenkov 1995, 2014, Luiselli et al. 1996, Amat 1998, Uysal et al. 2019, Jofré and Reading 2020, Kolanek and Bury 2020, Rowland et al. 2021, Zdunek et al. 2023). In our molecular study, DNA from *C. austriaca* was detected in all samples, as predicted, since cells from the host may be isolated with the cell material of the stomach and gut contents. However, the high numbers of *C. austriaca* DNA reads in two to four samples may support the hypothesis of cannibalism in these host individuals. We did not perform further analysis to confirm whether this DNA came from separate prey individuals or the host. Future work may benefit from applying marker genes with higher variability, to disentangle potential conspecific predator and prey DNA. Host DNA was identified in only 69.1% of the stomach samples of *H. viridiflavus* (Mondino et al. 2022). This is a much larger snake species than *C. austriaca*, which means that stomach contents may have been removed without touching the stomach walls to the same degree as when we removed the stomach contents. *Coronella austriaca* shows variation in diet across its distributional range (Völkl and Käsewieter 2003). While dietary differences likely reflect prey availability, they may also have a genetic factor. Scandinavian *C. austriaca* genetically belong to the central European clade of *C. austriaca* (Jablonski et al. 2019). However, a high incidence of shrews in the Norwegian faeces material only compares to diets reported from British *C. austriaca* (Goddard 1984), belonging genetically to the western clade (Jablonski et al. 2019). We regard *C. austriaca* as an opportunistic feeder. Reptiles always dominate the lists of prey animals (Völk and Kāsewieter 2003). Our metabarcoding analysis indicated a high incidence of ophiophagy. While ophiophagy is rarely reported, a higher incidence in Norway may reflect the lack of Lacertid lizards in most Norwegian locations, and the large size of Norwegian *C. austriaca* opens a wider spectrum of prey possibilities of snakes as prey animals.

Main difference between visual faeces analysis and metabarcoding

In contrast to our molecular study, the visual examination of 75 faecal samples from the inner Oslo fiord area revealed that *A. fragilis* was the most common prey item, and that the juveniles had exclusively consumed reptile prey. The second most common prey item was shrew, and this is in accordance with the molecular analysis. However, the main difference between the molecular study from the southern range of *C. austriaca* in Norway and the visual faecal study from the northern range around the inner Oslo fiord is the frequency of rodents consumed. It is uncertain if this suggests a disparity in the abundance of *M. agrestis* in various regions of Norway. However, further investigation of this topic should be conducted in the future. The nature of *C. austriaca* habitats, and prey species found within them, may vary significantly between different parts of Norway. *Microtus agrestis* are often found in humid grass biotopes, but *C. austriaca* are often found in dry and rocky habitats around the inner Oslo fiord. The absence of *M. agrestis* in the Oslo fiord faeces samples may actually reflect drier habitats that are unsuitable for this prey species. The visual analysis of the faecal material was unable to determine the species of shrews or small rodents. This highlights the efficiency of the metabarcoding, which provides more accurate results down to the species level. Future studies should focus on metabarcoding the same number of samples from *C. austriaca* faeces and stomachs from the northern and southern areas of *C. austriaca* range in Norway to reveal if there are differences, or if the differences we now observe are results of a very different sample size (17 sequenced stomachs contra 75 faeces). Some individuals had few reads in total or few reads from certain prey items. The Supporting information contains information about the status of the 17 dead *C. austriaca* which may explain this: for example if they had been dead for several days and prey DNA in stomach and gut might have been degraded. Also, snakes may live with empty stomachs for long time before getting another meal, explaining the few reads. One faeces contained feathers from bird nestling, adding to the knowledge of the wide dietary choice of *C. austriaca.* This snake species may climb bush and trees to predate on the bird eggs in nests (Johansen and Flaatten 2021), and bird nestlings are also found in *C. austriaca* diet in the UK (NCC Report 1983).

Conclusions

We found that molecular analysis using universal primers in PCR with subsequent Next Generation Sequencing (NGS) was a robust method for diet analysis on *C. austriaca* stomach content. Prey species observed during dissection correspond to the DNA analyses, confirming the reliability of the method. DNA sequencing identified several prey species that the traditional dissecting did not detect, demonstrating that molecular analysis makes identification of species possible in cases where traditional methods are unable to. Although the sample size analysed here is limited, this study represents a significant contribution by providing an initial glimpse into the diet of *C. austriaca* in Norway, utilizing high-sensitivity molecular tools. Our results indicate that *C. austriaca* in the studied areas primarily preys on species such as *M. agrestis*, *S. araneus*, *N. natrix*, and *A. fragilis*. We also observed less common prey species including *Z. vivipara*, *V. berus*, *A. sylvaticus*, and *M. glareolus*. This indicates that *C. austriaca* exhibits a variety of dietary prey species, likely influenced by their availability in the environment, and the adaptability of smooth snakes in adjusting their prey selection based on what is locally abundant. Our findings revealed that all the juveniles and subadults had DNA sequences from *M. agrestis,* a mammalian prey item. Since mammalian prey typically provide higher energy intake than reptilian prey, this may be an adaptation to the colder climate and higher latitudes of Norway. Additionally, the relatively large size of Norwegian *C. austriaca* may also suggest that such a dietary preference has evolved as an adaptation to the colder climate.

Our study identified a high degree of ophiophagy, or snake predation, on *N. natrix* and one *V. berus* among the 17 *C. austriaca* stomach samples we analysed using metabarcoding. This finding suggests a relatively high prevalence of snake predation in these ecosystems. Further research on predator–prey relationships and ecological dynamics involving snakes is necessary to gain a more comprehensive understanding of these interactions in Norway and beyond. Visual examination of 75 faeces did not detect any snakes in the diet. However, future DNA sequencing of these samples will potentially reveal if snakes are present but completely digested, not leaving visible traces. This faecal collection was from the inner Oslo fiord in dry habitats, and rodents were only a minor part of the diet, while *A. fragilis* and shrews made up the main prey animals.

Our study underscores the adaptability of *C. austriaca* in Norway to feed on a diverse array of available prey species. We observed that large body size of the species offers opportunities to predate on high-energy mammalian prey in all snake age classes, which may represent a key adaptation to colder climates, and also predation on other snakes may have been enabled by the large size of *C. austriaca* in Norway. Future climate change may make unpredictable scenarios for both *C. austriaca* and their prey. Wild boars *Sus scrofa* have increased their numbers and distributional range in Norway (VKM Norwegian Science Committe for Food and Environment 2018), where mild winters enhance their ability to establish themselves. They are known to have negative impact on snake populations when their numbers are high (Filippi and Luiselli 2002, Graitson et al. 2018). *Sus scrofa* will represent a strong dietary competitor as well as a significant predator species to Norwegian *C. austriaca.* Also, *C. russula* is an invasive species in Norway and may outcompete the native *Sorex* species. The effects on this for *C. austriaca* is unclear as *C. russula* is also a prey species for *C. austriaca* (Galán 1988). Sand lizard *Lacerta agilis* is newly introduced in Norway, and its range may increase which would be to the benefit of *C. austriaca* since *L. agilis* is a known prey of *C. austriaca* (NCC Report 1983, Najbar 2001). Future research should focus on the long-term implications of climate-driven changes in prey communities and competitive pressures on the diet and population dynamics of *C. austriaca*.

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.0000000f5 (Phan et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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