Trophic niche overlap in two syntopic colubrid snakes (*Hierophis viridiflavus* and *Zamenis longissimus*) with contrasted lifestyles

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Abstract. In many organisms, including snakes, trophic niche partitioning is an important mechanism promoting species coexistence. In ectotherms, feeding strategies are also influenced by lifestyle and thermoregulatory requirements: active foragers tend to maintain high body temperatures, expend more energy, and thus necessitate higher energy income. We studied diet composition and trophic niche overlap in two south European snakes (*Hierophis viridiflavus* and *Zamenis longissimus*) in the northern part of their range. The two species exhibit contrasted thermal adaptations, one being highly mobile and thermophilic (*H. viridiflavus*) and the other being elusive with low thermal needs (*Z. longissimus*). We analyzed feeding rate (proportion of snakes with indication of a recent meal) and examined more than 300 food items (fecal pellets and stomach contents) in 147 *Z. longissimus* and 167 *H. viridiflavus*. There was noticeable overlap in diet (overlap of *Z. longissimus* on *H. viridiflavus* = 0.62; overlap of *H. viridiflavus* on *Z. longissimus* = 0.80), but the similarity analyses showed some divergence in diet composition. Dietary spectrum was wider in *H. viridiflavus*, which fed on various mammals, birds, reptiles, and arthropods whereas *Z. longissimus* was more specialized on mammals and birds. The more generalist nature of *H. viridiflavus* was consistent with its higher energy requirements. In contrast to our expectation, feeding rate was apparently higher in *Z. longissimus* than in *H. viridiflavus*, but this could be an artifact of a longer transit time in *Z. longissimus*, given its lower mean body temperature. These results allow a better understanding of the ability to coexist in snakes belonging to temperate climate colubrid communities.

Keywords: dietary habits, energetics, *Hierophis viridiflavus*, snake, trophic niche, *Zamenis longissimus*.

Introduction

Among predators, snakes represent a homogeneous group as they almost all forage on live animals and generally feed on very large prey relative to their own size (Cundall and Greene, 2000; Vincent et al., 2006; but see Shine et al., 2004). Most are gape-limited predators ingesting their prey whole (Mushinsky, 1987; Cundall and Greene, 2000; Greene, 2001). Nevertheless, snakes exhibit marked variation in their degree of dietary specialization (Tanaka and Ota, 2002; Luiselli, 2006a): from highly specialized species that feed on a single prey type (e.g. Luiselli, 2003) to generalist species that opportunistically feed on prey in relation to their availability (e.g. Rodriguez-Robles, 2002; Brischoux, Bonnet and Shine, 2008; Halstead, Mushinsky and McCoy, 2008). Within snake communities, dietary niche partitioning may be a mechanism limiting potential competition (Toft, 1985; Luiselli, 2006a).

Differences in dietary resource use between syntopic snake species are often associated with divergence in multiple phenotypic traits such as lifestyle, morphology, behaviour, and physiology (Mori and Vincent, 2008). It is noteworthy that differing food habits are not necessarily driven by interspecific competition. Dietary differences can also reflect contrasted eco-physiological strategies that drive energy requirements (Secor and Nagy, 1994). In a recent review, Luiselli (2006a) showed that the degree of food partitioning in sympatric snakes varied among geographic areas, and

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that this variation could be explained partly by the level of trophic competition. Luiselli (2006a) proposed to distinguish "cold Europe" from "Mediterranean Europe" snake communities, because these communities differ in the number of sympatric species potentially competing for food. The rationale for such distinction was that sympatric terrestrial snakes in southern Europe, where potential competition is high, feed upon the most abundant prey species and minimize trophic competition by selecting prey of different sizes, rather than prey from different species. Other studies, however, revealed marked divergences in dietary preference among Mediterranean snakes (Rugiero, Capizzi and Luiselli, 2002; Capizzi et al., 2008). The lack of a clear pattern in the degree of dietary overlap within snake communities may be caused by interpopulation variation in environmental factors such as habitat structure or prey availability (e.g. Rodriguez-Robles, 2002; Tanaka and Ota, 2002).

We studied dietary composition of two syntopic south European snakes (European whipsnake *Hierophis viridiflavus* and Aesculapian snake *Zamenis longissimus*) in the northern part of their ranges. These two species are appropriate models to examine the link between lifestyle and dietary habits because they are of similar size, but illustrate two distinct ecological orientations in snakes ("racer" *versus* "ratsnake"; see materials and methods for details on terminology). *H. viridiflavus* is a very active snake that selects higher body temperatures and exhibits higher energetic requirements than the elusive *Z. longissimus* (Lelièvre et al., 2010a, 2011). We expected that the difference in energy requirements should translate into dietary differences. Specifically, we expected that *H. viridiflavus* should be an opportunistic forager exhibiting a wider spectrum of prey, and a higher feeding rate, compared to *Z. longissimus*. Because both species largely dominate the snake community at our study site (jointly representing over 80% of captures), we assessed diet

overlap to evaluate the possibility of interspecific competition along this niche axis.

Materials and methods

Hierophis viridiflavus and *Zamenis longissimus* are south European oviparous colubrids. *H. viridiflavus* is a typical racer according to its morphological (slender body, long tail, large eyes), behavioural (fast, diurnal, terrestrial), and ecological (high levels of activity and exposure) characteristics (Naulleau, 1984; Luiselli, 2006b). *Z. longissimus* shows strong morphological and behavioural similarities (constricting abilities, semi-arboreal, highly secretive) to ratsnakes (Naulleau, 1984; Burbrink and Lawson, 2007). These two species differ in their range of preferred body temperature (T_{set}): *H. viridiflavus* is thermophilic (T_{set} 27.5-31°C) whereas *Z. longissimus* prefers cooler temperature (T_{set} 21.5-25.5°C; Lelièvre et al., 2010a). We conducted our study at the Centre d'Études Biologiques de Chizé in Western France (46°07′ N; 00°25′ O). The study site is a 2600-ha biological reserve managed by the Office National des Forêts, dominated by deciduous trees (*Fagus*, *Quercus*, *Carpinus*, *Acer*), regeneration areas characterized by scrubby species (*Rubus*, *Clematis*), and grasslands. Climatic conditions are temperate oceanic with annual precipitation between 800 and 1000 mm, annual mean temperature of 12°C, and annual sunlight of 2000 h.

Snakes were captured during the activity season (April to October) between 1984 and 2009 under concrete boards (120×80 cm) disposed throughout the study site (Bonnet and Naulleau, 1996; Bonnet, Naulleau and Shine, 1999). Concrete boards are located in edge habitats and are used by snakes for thermoregulation. Each snake captured was measured for snout-vent length (SVL, to the nearest ±0.5 cm) and body mass (BM, to the nearest ±1 g), and individually marked by ventral scale clipping. Individuals were divided in 3 age classes: neonates (SVL < 40 cm and BM < 15 g), juveniles (40 < SVL < 80 cm and 15 < BM < 100 g), and adults (SVL > 80 cm and BM > 100 g). Each snake was ventrally palpated to detect the presence of prey in the digestive tract. Prey in the stomach and/or abundant faeces with undigested remains (scales, feathers, etc.) indicate a recent meal (<1 week; Bonnet et al., 2011), therefore the proportion of snakes with a prey in the stomach was used as an index of feeding rate. Food items were collected if voluntary regurgitation or defecation occurred in the capture bag. Almost 50% of prey items were identified to the lowest taxon possible and the remaining 50% were only classified at the prey category level (mammal, bird, reptile, or arthropod). We identified prey from faecal pellets using tooth shape or hair for mammals (Debrot et al., 1982; Erome and Aulagnier, 1982), using feather for birds, scales for reptiles, and exoskeleton for arthropods. Because only regurgitation allows counting the number of prey items from the same species (in faeces only the number of different prey types could be assessed), we could not estimate the number of prey items accurately. Thus, we used the frequency of occurrence of each prey type in our analyses.

To assess the similarity in diet composition between groups (species, sex, and age class), we used the ANOSIM procedure. ANOSIM is a non-parametric test designed to evaluate spatial differences and temporal changes in the assemblages of species (Clarke, 1993; Chapman and Underwood, 1999). ANOSIM is based on the comparison of intra- and inter-group distances calculated as average ranked values of the abundances and the types of organisms among samples. The ANOSIM statistic R is based on the difference of mean ranks between groups (r_B) and within groups (r_W) (N stands for the sample size):

$$R = (r_B - r_W)/(N(N-1)/4)$$

R-values range between -1 and 1, and a P-value is provided to assist in decision making: two sampled units are considered similar when R is equal to 0 and are considered totally different when R is equal to 1. ANOSIM were performed using the Vegan library (Oksanen et al., 2010) in R 2.10.1 (R Development Core Team, 2007).

To quantify the diet overlap between species, we calculated the index of MacArthur and Levins (1967; in Krebs, 1999), as:

$$M_{jk} = \frac{\sum_{i}^{n} P_{ij} P_{ik}}{\sum P_{ij}^{2}}$$

where M_{jk} is the overlap of species j on species k; P_{ij} is the proportion of prey i (in number of species or in biomass) consumed by species j, and P_{ik} is the proportion of prey i consumed by species k. M_{kj} is calculated in the same way for species k. Because our sample sizes were too small to allow the splitting by group and still maintain power and large enough sample sizes to allow confidence in the estimated frequencies, especially for neonates and juveniles, the indices were calculated for the whole dataset with pooled sexes and age classes.

To avoid pseudoreplication, data from recaptured individuals were not used in the analyses: we only considered prey items collected from the first capture of each individual snake (total of 147 Z. longissimus and 167 H. viridiflavus).

Results

The proportion of snakes captured with prey in the stomach varied markedly between years: 15 to 55% (mean ± SD = 29.4 ± 12.5) in Z. longissimus and 9 to 41% (mean ± SD = 24.5 ± 10.9) in H. viridiflavus (fig. 1). The proportion of individuals with prey in the stomach differed between species ($\chi^2 = 167.88$; $df = 12$; $P < 0.001$). In most years, Z. longissimus was observed more often with prey in the stomach, suggesting a higher feeding rate, compared

to H. viridiflavus. Over the study period, for both species, the proportion of snakes captured while digesting ($F_{1,11} = 15.94$; $P = 0.002$ and $F_{1,11} = 6.60$; $P < 0.001$ for Z. longissimus and H. viridiflavus respectively) and the total number of captures increased ($F_{1,11} = 8.46$; $P = 0.01$ and $F_{1,11} = 31.06$; $P < 0.001$ for Z. longissimus and H. viridiflavus respectively).

We analyzed food items from 147 Z. longissimus and 167 H. viridiflavus. ANOSIM were restricted to well-identified prey corresponding to 12 taxa described at various taxonomic levels (table 1; $n = 100$ items for Z. longissimus and $n = 111$ for H. viridiflavus). Within each species, adult males and females did not differ in diet composition ($R = 0.002$, $P = 0.375$ for Z. longissimus, $n = 50$ males and 28 females; $R = 0.003$, $P = 0.373$ for H. viridiflavus, $n = 60$ males and 19 females). Dissimilarities were observed between age classes in Z. longissimus ($R = 0.044$, $P = 0.036$, $n = 78$ adults, 14 juveniles, and 3 neonates), but not in H. viridiflavus ($R = -0.009$, $P = 0.608$, $n = 79$ adults, 19 juveniles, and 12 neonates). Neonates of both species mainly foraged on lizards (Podarcis muralis), but a strong ontogenetic shift occurred in Z. longissimus. While juvenile and adult H. viridiflavus frequently fed on reptiles, adult Z. longissimus specialized on mammals and birds (fig. 2). Thus, adults of both species showed a significant difference in diet composition ($R = 0.017$, $P = 0.045$, $n = 78$ Z. longissimus and 79 H. viridiflavus). H. viridiflavus exhibited a wider prey spectrum than Z. longissimus (table 1; fig. 2). Despite the observed dissimilarity, both species showed a strong overlap in diet. The indices of MacArthur and Levins were high (overlap of Z. longissimus on H. viridiflavus = 0.62; overlap of H. viridiflavus on Z. longissimus = 0.80). Indeed, in both species most of the diet is comprised of small mammals (90.6% in Z. longissimus vs. 70.5% in H. viridiflavus). Mammalian taxa were found in similar proportions in both species (Spearman correlation; $R^2 = 0.92$; $P < 0.05$; fig. 3).
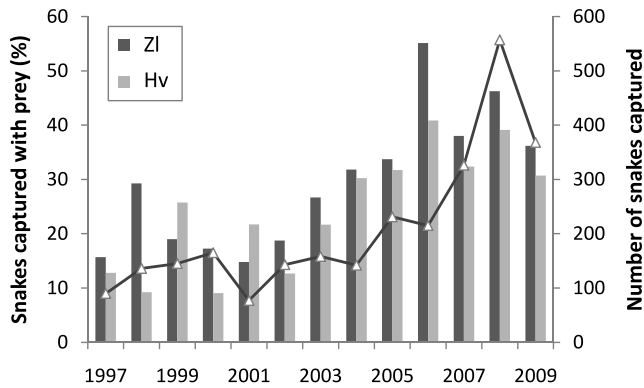
Figure 1. Changes in the proportion of Aesculapian snakes *Zamenis longissimus* (Zl) and European whipsnakes *Hierophis viridiflavus* (Hv) captured with a prey in the stomach, and in the total number of captures over the study period (1997 to 2009).

Table 1. Prey eaten by adult Aesculapian snakes *Zamenis longissimus* (Zl; $n = 113$) and European whipsnakes *Hierophis viridiflavus* (Hv; $n = 123$) in Chizé biological reserve in Western France. Items were collected between 1984 and 2009. Note that the number of collected items is higher than the number of snakes sampled for both species because of the occurrence of multiple prey species in faecal pellets.

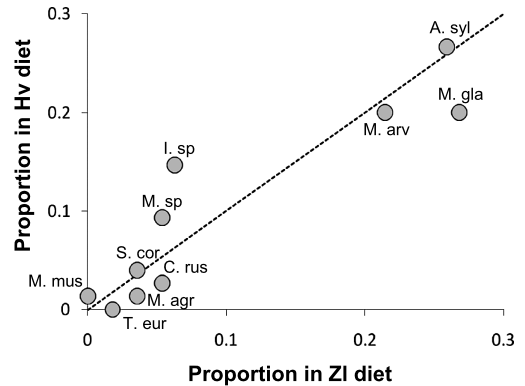| Prey	Frequency of occurrence *(n)*		Taxa used in ANOSIM analyses
	Zl	Hv	
Arthropoda			
Orthoptera indet.	–	0.03 *(5)*	×
Reptilia			
Podarcis muralis	–	0.07 *(12)*	×
Lacerta bilineata	–	0.02 *(4)*	×
Lacertidae indet.	–	<0.01 *(1)*	
Zamenis longissimus	–	0.02 *(4)*	
Vipera aspis	–	<0.01 *(1)*	×
Hierophis viridiflavus	–	<0.01 *(1)*	
Serpentes indet.	–	0.03 *(5)*	
Aves			
Passeriformes (ad)	0.01 *(2)*	–	×
Passeriformes (nestlings)	0.06 *(8)*	0.07 *(12)*	
Mammalia			
Myodes glareolus	0.15 *(20)*	0.07 *(11)*	×
Apodemus sylvaticus	0.14 *(24)*	0.09 *(14)*	×
Microtus arvalis	0.10 *(14)*	0.07 *(10)*	×
Microtus agrestis	0.03 *(4)*	<0.01 *(1)*	×
Mus musculus	–	<0.01 *(1)*	×
Microtus sp.	0.03 *(4)*	0.02 *(4)*	
Rodentia indet.	0.15 *(21)*	0.11 *(19)*	
Mammalia indet.	0.19 *(26)*	0.30 *(50)*	
Crocidura russula	0.02 *(3)*	0.01 *(2)*	
Sorex coronatus	0.03 *(4)*	0.01 *(2)*	×
Talpa europea	<0.01 *(1)*	–	×
Insectivora indet.	0.06 *(8)*	0.04 *(6)*	
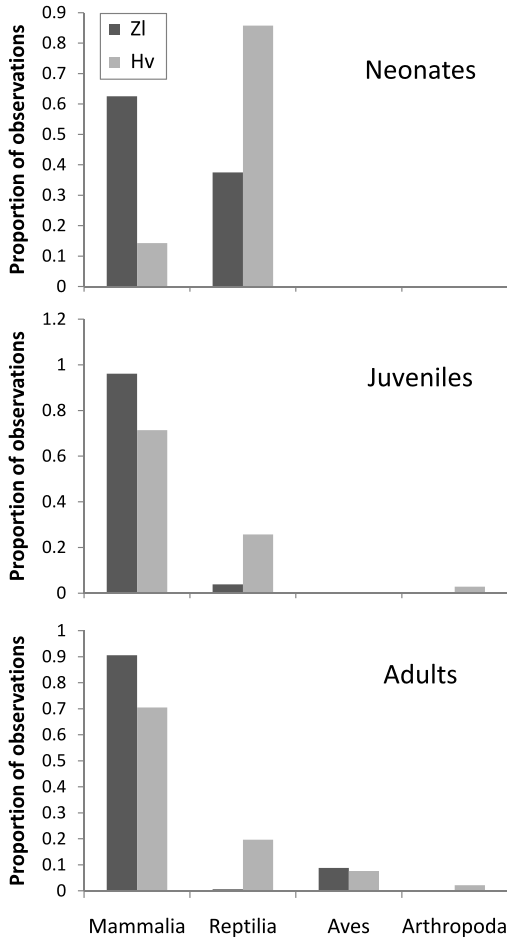
Figure 2. Proportion of prey eaten by Aesculapian snakes *Zamenis longissimus* (Zl) and European whipsnakes *Hierophis viridiflavus* (Hv) for the three age classes. Neonates are defined as SVL < 40 cm and BM < 15 g, juveniles as 40 < SVL < 80 cm and 15 < BM < 100 g, and adults as SVL > 80 cm and BM > 100 g.

Figure 3. Proportion of the various mammalian taxa in the diet of Aesculapian snakes *Zamenis longissimus* (Zl) and European whipsnakes *Hierophis viridiflavus* (Hv). The dashed line represents equal proportions between the species. M. gla: *Myodes glareolus*; A. syl: *Apodemus sylvaticus*; M. arv: *Microtus arvalis*; M. agr: *Microtus agrestis*; M. mus: *Mus musculus*; M. sp: *Microtus* sp.; C. rus: *Crocidura russula*; S. cor: *Sorex coronatus*; T. eur: *Talpa europea*; I. sp: Insectivora indet.

Discussion

In South European snake communities, *Z. longissimus* and *H. viridiflavus* often occur in syntopy. These two species strongly differ in thermal adaptations (Lelièvre et al., 2010a) and thus provide a good opportunity to investigate the relationship between thermal strategy and dietary strategy.

We documented a significant increase in the proportion of snakes captured with prey in the stomach, and in the total number of snake captures over the study period. The factors underly-ing these temporal increases in snakes captures and in the proportion of snakes digesting remain unclear. The number of concrete boards in the study area considerably increased starting in 1997; perhaps the snakes became accustomed to such novel thermoregulatory opportunities and then used the boards more intensively for digestion. Alternatively, an elevation of prey abundance or changes in climatic conditions may be responsible (Lourdais et al., 2002), but in the absence of long-term monitoring of prey availability we cannot further speculate.

The higher proportion of *Z. longissimus* with a prey in the stomach was counterintuitive. Instead, we expected that lower energy requirements should be associated with lower food intake in this species. It is possible that the proportion of snakes found with a prey in the stomach did not reflect accurately actual feeding rates, thereby flawing the comparison between the species. Indeed, digestion duration is shorter in *H. viridiflavus* owing to its higher body temperature in the field. In a previous study (Lelièvre et al., 2010a), we found that transit duration at the preferred body temperature of each species was 2.75 ± 1.26 days in *Z. longissimus* vs. $1.50 \pm$

0.55 days in *H. viridiflavus*. Consequently, prey should remain detectable for almost twice as long in *Z. longissimus*. In addition, *Z. longissimus* seems to specialize on larger prey (voles, passerine birds), thereby requiring longer periods to digest. Importantly, because snakes were captured under boards, our sample was biased towards individuals involved into thermally demanding processes such as digestion, and such bias may differ between the two snake species: the most secretive species, *Z. longissimus*, may well shelter more often under boards during digestion than the active *H. viridiflavus* (Lelièvre et al., 2010b, 2011). Although further investigation is required to clarify these issues, our results revealed interesting complications to interpret a simple feeding rate index.

Dietary analyses revealed differential use of resource in the two snake species. The most marked contrast concerned reptilian prey. *H. viridiflavus* consumed all lizard and snake species available, including *Z. longissimus*, and even displayed cannibalistic behaviour (Schmidlin, Bonnet and Tege, 1996). Mammalian taxa were found in similar proportions in both species, probably reflecting their availability and similar attractiveness to snakes. As mammals are large prey, especially for juvenile snakes, we surmise that neonates and juveniles probably consume shrews, which are the smallest prey species, and also young rodents. Unfortunately, we could not identify prey species but only prey groups for neonates, and young mammals are difficult to detect in faeces as they have no hair or teeth, and are thus entirely digested. Interestingly, *Talpa europea* was only found in *Z. longissimus*. Large prey species seem generally consumed by *Z. longissimus* (see Capizzi et al., 2008 for mention of *Rattus* sp. and *Talpa europea* in *Z. longissimus* diet), but avoided by *H. viridiflavus*. Differences in head size do not explain such pattern, as adult *H. viridiflavus* have larger jaws than adult *Z. longissimus* (30-39 mm vs. 25-34 mm; unpublished data). Alternatively, this pattern could arise because *Z. longissimus*

has better constricting abilities and is thus capable of capturing larger prey.

Overall, we found that *H. viridiflavus* and *Z. longissimus* in the Biological Reserve of Chizé forage mainly on small rodents (e.g., voles) and exhibit strong overlap in their trophic niches. *H. viridiflavus* is an active and voracious snake that can be locally abundant (Filippi and Luiselli, 2006). Our study confirmed that it is sometimes ophiophagous (see also Vanni and Lanza, 1977). Hence, both direct and indirect competition may potentially occur between these two snake species. As expected *H. viridiflavus* showed a wider prey spectrum. Indeed, *H. viridiflavus* expends almost twice as much energy as *Z. longissimus* due to its elevated thermal preference (Lelièvre et al., 2010a), and this snake may maximize feeding rate by foraging opportunistically on a wide range of prey. Moreover, locomotor performance and habitat use depend on thermoregulation in terrestrial ectotherms (Huey, 1982; Stevenson, Peterson and Tsuji, 1985; Blouin-Demers and Weatherhead, 2002). *H. viridiflavus* moves faster than *Z. longissimus* (Lelièvre et al., 2010a) and selects more open habitats (Rugiero, Capizzi and Luiselli, 2002; Scali, Mangiacotti and Bonardi, 2008; Lelièvre et al., 2011), which probably increases encounter probability with heliothermic lizards, and thus explain the relative abundance of this prey type in its diet. Previous studies on dietary habits conducted in Italy on the two snake species we examined here provided conflicting results. Some studies did not reveal a difference in diet composition (Capizzi et al., 1995; Capizzi and Luiselli, 1996) while others showed a similar pattern to the one we observed (Rugiero, Capizzi and Luiselli, 2002; Capizzi et al., 2008). Other studies of sympatric and parapatric populations are required to further evaluate potential competitive interaction, and assess the influence of prey availability on diet variation in snake communities (Aubret et al., 2006).

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