

Dietary patterns of two sympatric Mediterranean snakes (*Hierophis viridiflavus* and *Zamenis longissimus*) along a gradient of habitat alteration

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The food habits of two species of colubrid snakes (*Hierophis viridiflavus* and *Zamenis longissimus*) were studied in three areas in Mediterranean central Italy representing a gradient of natural habitat alteration from a natural mixed oak forest towards an entirely deforested, urban–agricultural habitat. Two diet descriptors were used: 1) total number of prey items eaten by each species in each study area, and 2) number of individual snakes containing a given prey type. Only adults were studied. There was no significant body size difference within species or among sites, and the diets of males and females were similar in both species. Our results revealed that habitat alteration drives some directional changes in the diet composition of these snakes: food niche breadth decreased in the two species from the least to the most altered study area, thus suggesting higher dietary generalism of snakes in natural areas. Food niche overlap values were similar interspecifically and intraspecifically, but tended to increase interspecifically with habitat alteration.

Key words: food habits, Italy, niche breadth, niche overlap, Reptilia, vegetation gradient

INTRODUCTION

Thousands of years of human intervention have drastically modified the natural environment and, as a consequence, populations and communities of animals have been reshaped (Eltringham, 1984; Bellamy et al., 1996; Blondel & Lebreton, 1996). In particular, a subset of species has been able to establish viable populations in and around human settlements (Bolger et al., 1997; Battisti, 2004; Lockwood et al., 2007). Adaptation to progressive habitat alteration would be accomplished with progressive behavioural and ecological modifications (Boulinier et al., 1998; Kluza et al., 2000; Lockwood et al., 2007), and thus it is intrinsically interesting to evaluate the modifications in ecological and behavioural characteristics of the few species that are able to live in urban and suburban areas. In this case it may be useful to use a comparative approach, studying the ecology of the various species along gradients of habitat alteration (e.g. Andren, 1994; Battisti, 2004; Lockwood et al., 2007).

The Mediterranean landscape has been shaped by human intervention in the natural forested habitat for 2000 years, and currently is generally characterized by a patchy mosaic of forest fragments and maquis interspersed within a very wide matrix of agricultural and urban zones (Battisti et al., 2000; Battisti, 2004). Snakes are usually found in the natural habitat fragments, but they may also occur in very altered habitats (e.g. Bologna et al., 2003). Although there are several studies on a wide variety of aspects of the population ecology of Mediterranean snakes (e.g. Capizzi & Luiselli, 1996a; Gomille, 2002), including negative or positive responses to habitat

fragmentation (e.g. Luiselli & Capizzi, 1997; Segura et al., 2007), to our knowledge there is no study concerning the comparative analysis of the ecological characteristics of single snake species along a gradient of natural habitat alteration or fragmentation. For instance, there are many studies revealing interpopulation variability in snake diets (e.g. review in Luiselli, 2006a), but none was specifically devoted to studying dietary variations related to habitat alteration. Studies of this type would be very important for a better understanding of the ecology of snakes, and to improve conservation plans for endangered snake species.

In this paper we use some previously published datasets (Capizzi & Luiselli, 1996a; Rugiero et al., 2002; Rugiero & Luiselli, 2004) to compare the food habits of two Mediterranean colubrid snake species along a gradient of natural habitat alteration. We compare the dietary patterns of the European whip snake *Hierophis* (= *Coluber*) *viridiflavus* and of the Aesculapian snake *Zamenis longissimus* (= *Elaphe longissima*) along a gradient from a large Mediterranean forest towards an entirely deforested, urban–agricultural habitat.

Our aims in this paper are 1) to identify the main dietary patterns occurring along this gradient, and 2) to establish whether dietary generalism and the potential for interspecific competition for food tend to vary with habitat alteration, as suggested by other studies in entirely different climatic scenarios (e.g. see Luiselli, 2006b).

MATERIALS AND METHODS

This paper is based on a comparative re-analysis of already published diet data that were collected at three

Table 1. Means and dispersion measures for body lengths (SVL) of *Hierophis viridiflavus* and *Zamenis longissimus* at the study sites.

Species	Study areas		
	RICH Mean \pm SD cm (n)	MEDIUM Mean \pm SD cm (n)	POOR Mean \pm SD cm (n)
<i>H. viridiflavus</i>			
Males	83.8 \pm 11.1 (254)	80.8 \pm 14.2 (122)	87.5 \pm 12.7 (18)
Females	74.3 \pm 9.1 (233)	76.1 \pm 12.7 (102)	79.3 \pm 7.6 (13)
<i>Z. longissimus</i>			
Males	95.8 \pm 15.2 (149)	98.3 \pm 13.9 (53)	102.6 \pm 8.7 (8)
Females	73.8 \pm 14.4 (140)	76.6 \pm 14.8 (46)	93.1 \pm 2.4 (6)

study areas in Mediterranean central Italy during long-term field research (e.g. Capizzi & Luiselli, 1996a; Rugiero et al., 2002; Rugiero & Luiselli, 2004). Because details of study areas and data collection have already been presented in the original sources, here we present only some concise and essential information concerning the study areas and the methodologies used to collect the food items from free-living snakes.

Study areas

Three distinct study areas, representing a clear gradient of forest habitat alteration, were used for this study: Macchia della Manziana (RICH) was the natural study area, Marcigliana (MEDIUM) the medium-conserved study area, and Tor Bella Monaca (POOR) the very altered study area. Data for RICH were given in Rugiero et al. (2002), for MEDIUM in Capizzi & Luiselli (1996) and for POOR in Rugiero & Luiselli (2004). All these areas are situated in the province of Rome, central Italy, and are characterized by a Mediterranean-temperate bioclimate. All areas sampled were about 50 ha.

RICH is a hilly (300–350 m a.s.l.), old-growth oak forest dominated by *Quercus cerris*, *Q. frainetto*, *Q. ilex*, *Acer campestre* and *Tilia* sp., with populations of *Carpinus betulus* and *C. orientalis* in cooler parts. This forest is the last remnant of the once huge “Sylva Mantiana” (= forest of Manziana in Latin), that during the age of the Roman Empire (approximately 2000 years ago) covered the whole region of the Sabatini, Ceriti and Tolfa mountains. Thus, this is one of the few remnants of natural Mediterranean forest still found in central Italy (Spada, 1977). Ninety per cent of the study area was covered with woods and it was entirely surrounded by woodlands and agro-forest landscape.

MEDIUM is a partially deforested area situated outside Rome at about 70–130 m a.s.l., and characterized by a patchy mosaic of oak woodlands (dominant species being *Q. cerris*, *Q. robur*, *Ulmus minor*, *A. campestre* and *Fraxinus ornus*), grassy fields and cultivation. Thirty per cent of the study area was covered with woods and bushy corridors connecting wood patches, and 75% of its perimeter was surrounded by agro-forest landscape, and the other 25% by urban landscape.

POOR is a deforested area situated in the peripheral southern side of the Rome metropolis at about 20–70 m a.s.l., between two busy roads (via Prenestina and via Casilina). This area was dominated by grassy fields used for grazing and cultivation. None of the study area was

covered with woods; 25% of its perimeter was surrounded by agro-forest landscape, and 75% by urban landscape.

Field methods

Identical field methods were applied in the three study areas, although field effort varied, being higher at the RICH and MEDIUM sites than at the POOR site (see Capizzi & Luiselli, 1996; Rugiero et al., 2002; Rugiero & Luiselli, 2004 for details). Snakes encountered in the field were individually marked by ventral scale clipping, measured for snout–vent length (SVL) and sexed, and then processed for food items. Food items were obtained by forcing the captured animals to regurgitate by abdominal palpation and by collection of faecal pellets through massage of the posterior part of the abdomen, and were identified to the lowest taxonomic level possible. This method is safe for snakes. To avoid data pseudoreplication, data were recorded only once from each individual, and we never counted prey items from stomach and faeces from the same individual. Details of the methods used to process snakes and analyse items in the laboratory are given in the original sources. Only adult snakes (i.e. longer than 75 cm SVL in *H. viridiflavus* and 85 cm SVL in *Z. longissimus*) were considered for this study. Ontogenetic dietary shifts are known for both species (Rugiero & Luiselli, 1995; Rugiero et al., 2002), but our juvenile samples were too small for sound comparative analyses among populations. Adults were recognized by their dorsal colour patterns, which are clearly divergent from juvenile and subadult patterns in both species (Bruno & Maugeri, 1990).

Data analysis

Since we were able to collect a large sample size only at two study sites (RICH and MEDIUM), we performed statistical analysis of data only for snakes captured in these areas. Data collected at POOR were compared only from a qualitative point of view in order to support our main conclusions with additional information. For analysis of snake dietary spectrums, we considered two diet descriptors: 1) total number of prey items (TNP) eaten by each species in each study area, and 2) number of snake individuals containing a given prey type (TSP). However, as in both species and in all study areas TSP was highly correlated with TNP (for *H. viridiflavus*: $P < 0.001$; for *Z. longissimus*: $P < 0.01$; Pearson's correlation coefficient), we considered the responses of TSP to habitat alteration

Table 2. Summary of the diet data (number of prey items) collected for the two study species from the three categories of habitat gradient, and relative food niche breadth for each population calculated by Simpson's (1949) index. n = number of prey items; RICH = Macchia della Manziana (natural area); MEDIUM = Marcigliana (fairly good area); POOR = Tor Bella Monaca (very altered area).

Prey type	<i>Hierophis viridiflavus</i>			<i>Zamenis longissimus</i>		
	RICH ($n=165$)	MEDIUM ($n=115$)	POOR ($n=15$)	RICH ($n=108$)	MEDIUM ($n=68$)	POOR ($n=6$)
AMPHIBIA						
<i>Rana italica</i>	0.6					
REPTILIA						
<i>Lacerta bilineata</i>	18.2	4.3	33.3	8.3	7.4	
<i>Podarcis sicula</i>	4.2	14.8	20		11.8	
<i>Podarcis muralis</i>	23	29.6	13.3	12	23.5	
<i>Anguis fragilis</i>	0.6					
<i>Chalcides chalcides</i>	0.6					
<i>Zamenis longissimus</i>	0.6					
MAMMALIA						
<i>Apodemus</i> sp.	6.1	27		33.3	27.9	
<i>Mus domesticus</i>		0.9				
<i>Rattus norvegicus</i>			6.7		2.9	83.3
<i>Rattus rattus</i>				4.6	2.9	
<i>Clethrionomys glareolus</i>	20	7		18.5	13.2	
Muridae (undetermined)	4.2		26.7			
<i>Crocidura</i> sp.	1.8	9.6		1	10.3	
<i>Talpa</i> sp.						16.7
Insectivora (undetermined)	0.6			1		
AVES						
<i>Parus caeruleus</i>				2.8		
<i>Sylvia atricapilla</i>				1		
<i>Serinus serinus</i>				1.8		
<i>Carduelis chloris</i>				3.7		
Passerine indet.	10.3	7		12		
INVERTEBRATES						
Orthoptera	1.2					
Food niche breadth	8.695	4.926		5.576	5.494	

nearly identical to those for TNP, and in order to save space we did not present detailed results for TSP. In all study areas, and in both species, data from males and females were pooled after we verified that there was no statistically significant difference (χ^2 test) in the diet composition of the two sexes (see the original sources for more details).

Food niche breadth (B) was measured using Simpson's (1949) diversity index. Food niche overlap between populations was quantified using Pianka's (1986) symmetric equation with values ranging from 0 (no overlap) to 1 (total overlap).

Differences among populations in terms of frequency of consumption of the various prey types were evaluated by χ^2 tests, with a Monte Carlo procedure using 30,000 random permutations (Gotelli & Graves, 1996). All data were checked for normality and homoscedasticity prior to applying any parametric test, and normalized if necessary. Pearson's correlation coefficient was used for correlation of two variables that were normally distributed. Means are presented \pm 1 S.D. In all cases, alpha was set at 5% and the statistical tests were two-tailed. STATISTICA (ver-

sion 8.1) software was used for all tests. Monte Carlo permutations were done with Ecosim software (version 700; Gotelli & Entsminger, 2004).

RESULTS

Snake body sizes

Adult body size (SVL) of the snakes containing food in the guts was on average higher in *Z. longissimus* than in *H. viridiflavus* (Table 1). However, there were no significant intraspecific SVL differences among populations in either sex (one-way ANOVA; at least $P=0.251$ for *H. viridiflavus* and $P=0.086$ for *Z. longissimus*). Thus, for the following analyses prey type composition was compared directly among populations without taking into account the average body size of each population sampled.

Total number of prey items

Overall, a total of 295 prey items were recorded from *H. viridiflavus* and 182 from *Z. longissimus* (Table 2). Lizards were the main prey for *H. viridiflavus* and rodents for *Z. longissimus*. Taxonomic diet compositions of the four

Table 3. Food niche overlap among populations of the two snake species studied. HV = *Hierophis viridiflavus*; ZL = *Zamenis longissimus*

	HV (RICH)	HV (MEDIUM)	ZL (RICH)
HV (MEDIUM)	0.709	–	
ZL (RICH)	0.687	0.779	–
ZL (MEDIUM)	0.726	0.959	0.837

populations were significantly different from one other (in all cases, at least $P < 0.05$, χ^2 test). For *H. viridiflavus* the most noteworthy pattern was the greater variety of prey species found in RICH than in MEDIUM; for *Z. longissimus* the most noteworthy interpopulation difference was the presence of several passerine birds in the diet at RICH (Table 2). The few data available from POOR suggested that *Rattus norvegicus* was the main prey species for *Z. longissimus* at this site. In both snake species, food niche breadth values were higher at RICH than at MEDIUM, but the difference was much higher for *H. viridiflavus* than *Z. longissimus* (Table 2). However, the few data available from POOR for *Z. longissimus* suggested that food niche breadth should be very narrow in this altered site ($B = 1.385$).

Overlap values calculated among populations showed relatively high similarities in pairwise comparisons, and especially between *Z. longissimus* and *H. viridiflavus* at MEDIUM (Table 3). Mean overlap values between populations were similar intra-specifically (0.777 ± 0.09) and inter-specifically (0.788 ± 0.12 ; raw data in Table 3).

DISCUSSION

Before discussing our results, we will briefly consider a few shortcomings of this study. We collected data from only a single study area in each habitat alteration category, and the lack of replicates limits the significance of our conclusions. However, because of intrinsic methodological/logistic constraints in snake research (Seigel, 1993), the great majority of snake literature is based on unsatisfactorily replicated studies (e.g. Luiselli et al., 2007). We obtained high numbers of prey items for both species in two study areas, so that at least the comparisons between RICH and MEDIUM are certainly sound. Unfortunately, the rarity of snakes prevented us from collecting a large sample size in the highly altered area (POOR), and thus we used data from this latter site for qualitative considerations, while acknowledging the need for further data before making firm statements.

These shortcomings aside, our study has revealed some intriguing patterns of diet divergence within and between species in relation to habitat alteration. To begin with, the food niche breadth increased substantially from MEDIUM to RICH in *H. viridiflavus*, with the same trend also seen in *Z. longissimus*. The few data available for both species at POOR seem to indicate a very narrow niche breadth, thus suggesting that food niche breadth may really increase from altered to natural sites in these snakes. For instance, *H. viridiflavus* fed on invertebrates

and frogs in RICH, while *Z. longissimus* also expanded its diet in RICH, foraging frequently on birds. This pattern may be intuitively linked to the higher number and variety of available prey types in the unaltered sites. It is fairly well documented that several snake species may show high interpopulation differences in prey spectra (e.g. Fukada, 1992; Kadowaki, 1992, 1996; Tanaka & Ota, 2002), and also at a microgeographic scale (King, 1993; for a meta-analysis of interpopulation snake diet variations see Luiselli, 2006a). However, whether these dietary shifts are correlated with habitat alteration is poorly known. In the rainforests of southern Nigeria, two species of large terrestrial vipers (genus *Bitis*) shift their diet composition in relation to habitat alteration and, because of the progressive decrease in prey-type diversity with increasing deforestation, tend to have more similar dietary spectra in altered than in natural forest patches (Luiselli, 2006b). Thus, in these tropical vipers the potential for interspecific competition for food tends to increase with habitat alteration (Luiselli, 2006b). The same pattern was clearly mirrored in our study, with the interspecific overlap increasing from 0.687 at RICH to 0.959 at MEDIUM.

Looking at the data in more detail, it is evident that the prey types that were consumed more or less frequently along the habitat alteration gradient were lizards (increasing with habitat alteration) and birds (decreasing with habitat alteration) in *H. viridiflavus*, and insectivores (increasing with habitat alteration) and birds (decreasing with habitat alteration) in *Z. longissimus*. These patterns did not depend on predator size differences among populations. We suggest that the relative abundance of these prey groups may change along the habitat alteration gradient, being more or less present in snake diets depending on their relative availability in the field. There are two independent lines of evidence supporting this suggestion. Firstly, previous studies from one of our areas (MEDIUM) comparing snake diets with trapping data for their prey types (Capizzi et al., 1995; Capizzi & Luiselli, 1996a,b) revealed that all terrestrial snakes (i.e. *Vipera aspis*, *Elaphe quatuorlineata*, *H. viridiflavus* and *Z. longissimus*) consumed their prey in relation to its relative availability in the field (Capizzi et al., 1995). Secondly, the Norway rat (*Rattus norvegicus*), a large and aggressive rodent that can seriously damage snakes when attacked (Luiselli et al., unpublished data), is never eaten by snakes in RICH and only occasionally in MEDIUM (only by *Z. longissimus*), but in POOR appeared to be the predominant prey of *Z. longissimus* (83.3% of the food items). These rodents are rarely found in forested areas but are usually abundant in urban and suburban sites (Capizzi & Santini, 2007). In contrast, wood mice (*Apodemus sylvaticus* and *Apodemus flavicollis*), which are typically linked to wooded areas (Capizzi & Luiselli, 1996b; Capizzi & Santini, 2007), did not occur in our samples of snake diets at POOR but were common prey in RICH and MEDIUM. Thus, it seems plausible that, despite being potentially dangerous, Norway rats are so common in and around human settlements that they represent a crucial food source for the rare snake populations that may survive in these areas. We can hypothesize that rats should be a crucial food source for many populations

of snakes inhabiting suburban areas (e.g. Luiselli et al., 2002), and therefore the study of the intersection between the inter-annual cycles of these rodents and of their urban snake predators may provide interesting fields for further research. In particular, it would be interesting to study in detail the dietary habits of juveniles in suburban snake populations. Indeed, neonate snakes would have difficulty feeding on even neonate *Rattus norvegicus*, and so the resilience of the system may be compromised in the long term. It is possible that this may be one of the main factors responsible for the very low density of snakes in Mediterranean suburban habitats.

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