FEEDING HABITS OF A MEDITERRANEAN COMMUNITY OF SNAKES IN RELATION TO PREY AVAILABILITY

Dario CAPIZZI*, Luca LUISELLI**, Massimo CAPULA**, Lorenzo RUGIERO***

INTRODUCTION

Relationships between snakes and their prey have been studied in detail by several authors (Mushinsky, 1987). Most predictive studies on such issue come from North-American assemblages of species, essentially with aquatic or semi-aquatic habits (for a recent review, see Mushinsky, 1987). Conversely, feeding ecology of most western European snakes is known by essentially detailed lists of the prey items found in snake stomachs and faeces (e.g. see Saint Girons, 1980, 1983 ; Bea & Braña, 1988 ; Braña *et al.,* 1988 ; Monney, 1990 ; Pleguezuelos & Moreno, 1990 ; Luiselli & Agrimi, 1991, Bea *et al.,* 1992 ; Luiselli & Rugiero, 1993).

The kernel conviction generated from the complex of studies of snake community ecology is that these organisms, contrary to most of other vertebrates, do not partition the habitat resource but the available food resource (e.g. see Mushinsky & Hebrard, 1977 ; Luiselli & Rugiero, 1991). However, the occurrence of food partitioning has never been tested in assemblages of terrestrial snakes of Mediterranean habitats, despite such habitats are frequently characterized by (i) remarkable snake species diversity (Corsetti & Capula, 1992) and (ii) high prey species diversity (especially lizards and small mammals) (Canova & Fasola, 1993).

In this paper we test (1) whether the same trophic resource is used by different species in a community of terrestrial sympatric snakes, (2) whether a food partitioning does exist, and (3) whether the snake species feed upon their prey in relation to the relative prey availability in the environment.

MATERIALS AND METHODS

STUDY AREA AND THE SPECIES

Data given here were entirely collected in a locality situated about 15 km north-east of Rome, central Italy (Settebagni, about 20-100 m a.s.l. ; 42° 03' N,

* National Council of Research (CNR), Centre of Evolutionary Genetics, via Lancisi 29, I-00161 Roma (Italy).

** Dipartimento di Biologia Animale e dell'Uomo, Università di Roma « La Sapienza », via Alfonso Borelli 50, I-00161 Roma (Italy).

*** Via Domenico Cimarosa 13, I-00198 Roma (Italy).

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12° 35' E). The area is characterized by an agro-forest landscape. The wooded area (about 100 ha surface) is a coppice forest of *Quercus cerris, Q. robur, Ulmus minor, Acer campestris, Fraxinus ornus* and *Laurus nobilis*. The underbrush is constituted of *Crataegus monogyna, Rosa canina, Prunus spinosa, Euonimus europaeus*. The wooded area is surrounded by semi-cultivated fields with bushy zones with *Rubus ulmifolius, R. idaeus, Spartium iunceum* and some arboreal *Robinia pseudoacacia*. The coppice forest is periodically clear-cut (once every twenty years), but the human influence on the whole area is globally low. The climate is typically Mediterranean, with rainfall concentrated in late autumn and winter, and dry and hot summer.

The study area is inhabited by numerous reptiles, amphibians and small mammals : there are five lizards (*Anguis fragilis, Chalcides chalcides, Lacerta viridis, Podarcis muralis, P. sicula*), one turtle (*Testudo hermanni*), five snakes (*Vipera aspis, Coluber viridiflavus, Elaphe longissima, E. quatuorlineata, Natrix natrix*), two amphibians (*Bufo bufo* and *Rana dalmatina*), six rodents (*Apodemus sylvaticus, A. flavicollis, Mus domesticus, Rattus norvegicus, R. rattus, Clethrionomys glareolus*) and two shrews (*Crocidura leucodon, C. suaveolens*).

SAMPLING METHODS

The research was carried out between spring 1990 and autumn 1994.

Dietary habits of snakes. — For studying dietary habits of free-living snakes, we conducted random routes throughout the study area. Each route lasted from 08 : 30 a.m. to 18 : 30 p.m. When a snake was encountered, it was captured by hand, identified to species, sexed by analysing tail structure, individually marked by scale-clipping, measured for total length (TL, to the nearest ± 0.5 cm) and processed in order to obtain food items. Food items were obtained by forced palpation of the snake abdomen and by faecal pellets (e.g. see Monney, 1990 ; Luiselli & Agrimi, 1991, for the methods employed), and then examined in the laboratory. After identification of food items, they were placed in ethanol and preserved in the private collections of the authors.

The employed methods were not dangerous for the handled specimens. Only adult snakes were used for our investigation. Vipers were considered adults when they exceeded 52 cm total length (Luiselli & Agrimi, 1991), while adults of the other three species (*Coluber viridiflavus, Elaphe longissima* and *E. quatuorlineata*) were easily identified by their dorsal color pattern, as these species show remarkable ontogenetic change (Bruno & Maugeri, 1990).

Density of lizards. — Lizard density was estimated by mark-and-recapture of specimens in an area of 2.4 ha surface where snakes were frequently encountered. This area was a bushy, ecotonal area. Lizards were noosed or captured by hand, identified to species and sex, toe-clipped and painted on the dorsal surface for visual identification without further disturbance. Lizard density was studied in March, 1993. About four weeks were necessary for capturing nearly all the lizards inhabiting this portion of the study area.

Density of small mammals. — The relative density of small mammals was estimated by live-trapping, during the years 1992, 1993 and 1994. We used self-made WEB traps (Le Boulengé & Le Boulengé-Nguyen, 1987), placed in three different grids, each situated in a specific habitat type (i.e. coppice forest, bushy ecotone and clear-cut wooded area). The traps were modified to prevent shrew escapes. We arranged a squared grid of 81 traps (9 × 9) spaced 15 m apart and covered a surface area of 1.5 ha, considering also a little arbitrary boundary strip to approximate the above-cited surface (Flowerdew, 1976). Trapping was carried out twice per year, the former in May and the latter in October, and each trapping session lasted five nights (see Pelz, 1982). Bait employed was oat mixed with mackerel, that proved to be a very effective mixture for capturing either rodents or shrews. Every captured animal was identified to species, weighed, sexed and marked by toe-clipping. Then, the captured specimens were released unharmed in the field. In central Italy *A. sylvaticus* and *A. flavicollis* are morphologically similar (Filippucci *et al.,* 1989). Therefore, we discriminated them by using a discriminant function calculated on the populations of this area (Capizzi, in prep.).

STATISTICAL ANALYSIS

Statistical analyses were performed by SAS computer package (1987). Statistics used are described in Siegel (1956) and Sokal & Rohlf (1969). All tests used are two-tailed, and α was assessed at 5 %. Food niche breadth was measured by Simpson's (1949) diversity measure, while food niche overlap between species was calculated by Pianka's (1973) symmetric equation with values ranging from 0 (no overlap) to 1 (total overlap). The statistical differences among these measures were assessed by non-parametric matrix correlation Mantel test (see Banley, 1985).

RESULTS

DIETARY HABITS OF SNAKES

We handled a total of 448 snakes (including both the captures, n = 129, and the recaptures, n = 319), 143 were *V. aspis* (with 26 captures), 83 were *E. longissima* (with 38 captures), 49 were *E. quatuorlineata* (with 13 captures) and 173 were *C. viridiflavus* (with 52 captures). The grass snake (*N. natrix*) was excluded from this count because of its semi-aquatic habits and primarily batrachophagous diet.

The summary of the dietary data of snakes is given in table I. Small mammals and lacertid lizards were the most important prey for all the snake species.

In *V. aspis* the small mammals constituted 70.3 % of the total diet, the lacertid lizards accounted for 25.7 % of the diet, and the remaining 4 % was represented by terrestrial frogs and nestling birds.

C. viridiflavus fed on lizards more frequently than adult vipers (χ^2, df = 1, $P < 0.05$) ; lacertids accounted for over 49 % of the total diet, small mammals for 44 % and nestling birds for the remaining 6.8 %.

E. longissima preyed upon both small mammals (55.5 % of the total diet) and lacertid lizards (44.5 %). No passerine birds were found in this snake's guts, although it is known as a semi-arboreal species in several areas of its wide geographic range. In this regard, our data completely confirm those obtained from other *E. longissima* populations from central Italy (Luiselli & Rugiero, 1993).

The bulk of prey of *E. quatuorlineata* was constituted by small mammals (74 % of the total diet), while lacertid lizards accounted for only 11.1 % of the taxonomical diet composition ; Passerine birds represented about 15 % of the diet. These latter are cited as primary prey for *E. quatuorlineata* in another central Italy area (Cattaneo, 1979).

TABLE I

Dietary habits of the four snake species at the study area. N represents the total number of food items, and % N represents its relative proportion.

Prey Type	*Vipera aspis*		*Coluber viridiflavus*		*Elaphe longissima*		*Elaphe quatuorlineata*	
Apodemus sp.	33	44.6 %	15	25.4 %	14	25.9 %	8	29.6 %
Mus domesticus	2	2.7 %	1	1.7 %	—		—	
Rattus rattus	—		—		2	3.7 %	3	11.1 %
Rattus norvegicus	—		—		2	3.7 %	2	7.4 %
Clethrionomys glareolus	8	10.8 %	4	6.8 %	6	11.1 %	4	14.8 %
Crocidura sp.	9	12.2 %	6	10.2 %	6	11.1 %	3	11.1 %
Lacerta viridis	—		2	3.4 %	3	5.6 %	—	
Podarcis muralis	17	23.0 %	16	27.1 %	13	24.1 %	3	11.1 %
Podarcis sicula	2	2.7 %	11	18.6 %	8	14.8 %	—	
Passeriformes	1	1.3 %	4	6.8 %	—		4	14.8 %
Rana dalmatina	2	2.7 %	—		—		—	

Quantitative analysis of food niche breadth (see Table II) suggests that *V. aspis* is significantly more specialized in the food choice than all the other sympatric species (in all comparisons : $P < 0.01$, Mantel test), while the width of the food niche breadth of the other three species did not differ significantly ($P > 0.5$, Mantel test).

TABLE II

Values of food niche breadth (measured by Simpson's index), calculated on the precise taxonomical diet composition, for the four snake species inhabiting the study area.

Species	$\Sigma\ Pi^2$	Bs
Vipera aspis	0.275	3.636
Coluber viridiflavus	0.193	5.181
Elaphe longissima	0.177	5.649
Elaphe quatuorlineata	0.174	5.747

Measures of food niche overlap between species (see Table III) demonstrate that the taxonomical composition of the diet is very similar among species : the lowest similarity was found between *C. viridiflavus* and *E. quatuorlineata* (Ojk = 0.694) while the highest similarity was found between *C. viridiflavus* and *E. longissima* (Ojk = 0.967).

AVAILABILITY OF POTENTIAL PREY

Lizards. We captured a total of 61 common wall lizards, *P. muralis* (24 males, 12 females and 25 juveniles), 19 Italian wall lizards, *P. sicula* (7 males, 4 females and 8 juveniles) and 24 green lizards, *L. viridis* (9 males, 6 females and 9 juve-

TABLE III

Values of food niche overlap (calculated on the taxonomical diet composition by means of Pianka's symmetric equation) between species at the study area.

Species	*C. viridiflavus*	*E. longissima*	*E. quatuorlineata*
V. aspis	0.873	0.905	0.863
C. viridiflavus		0.967	0.694
E. longissima			0.789

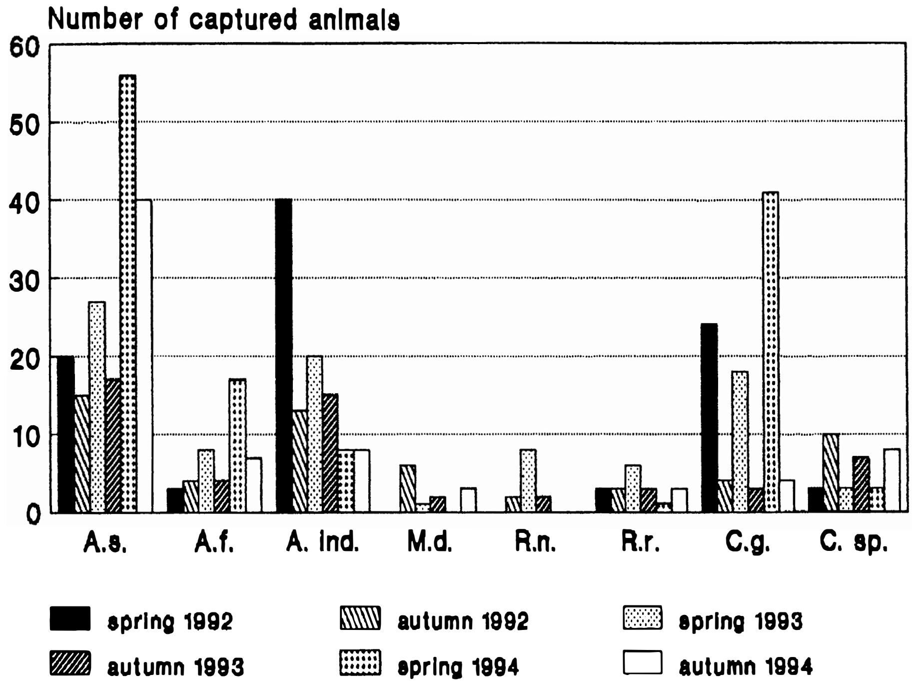

Figure 1. — Number of captured specimens of each small mammal species at the study area. Sampling performed in spring and in autumn are considered separately. The numbers given here are cumulative from three different grids (see methods for further details). A.s. = *Apodemus sylvaticus*, A.f. = *A. flavicollis*, A. ind. = *Apodemus* indetermined, M.d. = *Mus domesticus*, R.n. = *Rattus norvegicus*, R.r. = *R. rattus*, C.g. = *Clethrionomys glareolus*, C. sp. = *Crocidura* species.

niles). The approximate spatial density of these three species was respectively : 25.4 individuals per ha (*P. muralis*), 8.1 individuals per ha (*P. sicula*) and 10 individuals per ha (*L. viridis*). The cumulative lizard density of this area was 43.5 individuals per ha. The observed density is probably underestimated, as it is possible that we failed in capturing at least some juveniles.

Small mammals. The summary of the data collected on this issue is given in figure 1. Pooling together data collected in the three study years (since there were no statistically significant differences between years at ANOVA), we captured a total of 493 small mammals. The two species of *Apodemus* proved to be the commonest in the study area, accounting together for over 65 % of the total sample captured (χ^2 test, $P < 0.001$ in all cases). *C. glareolus* (accounting for over 19 % of the total sample) and *Crocidura* sp. (6.9 %) were also frequently captured, while *Mus* and the two *Rattus* species were captured less frequently (less than 4 % of the total). Significant seasonal fluctuations in the number of captured animals were found only in *C. glareolus,* that was captured much more frequently in spring rather than in autumn (difference between seasons : $\chi^2 = 27.6$, df = 1, $P < 0.00001$). Considering that the frequency of *C. glareolus* in the snake guts did not vary significantly between seasons (χ^2 test with df = 1, $P < 0.1$), we are lead to think that the observed fluctuations of this rodent in our trapping were only apparent and depended on species-specific behavioural traits resulting in a different efficiency of trapping procedure.

The estimated average density per ha of the various small mammal species is given in figure 2. The distribution of the small mammal species in relation to the habitat type is shown in figure 3.

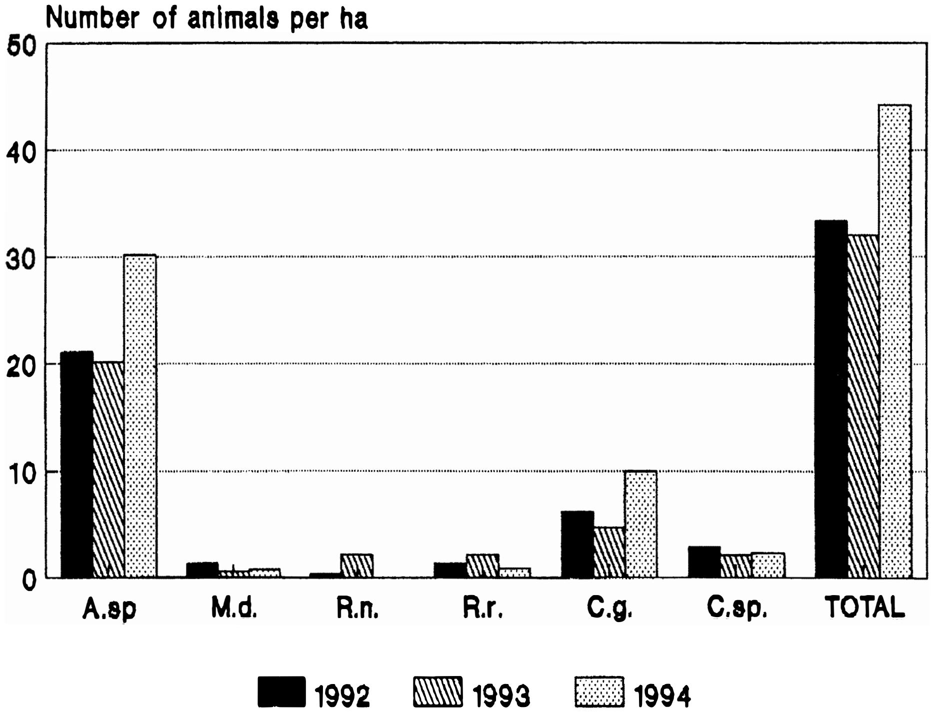

Figure 2. — Estimated average density per ha of each small mammal species at the study area. A.sp. = *Apodemus* species, M.d. = *Mus domesticus,* R.n. = *Rattus norvegicus,* R.r. = *R. rattus,* C.g. = *Clethrionomys glareolus,* C.sp. = *Crocidura* species.

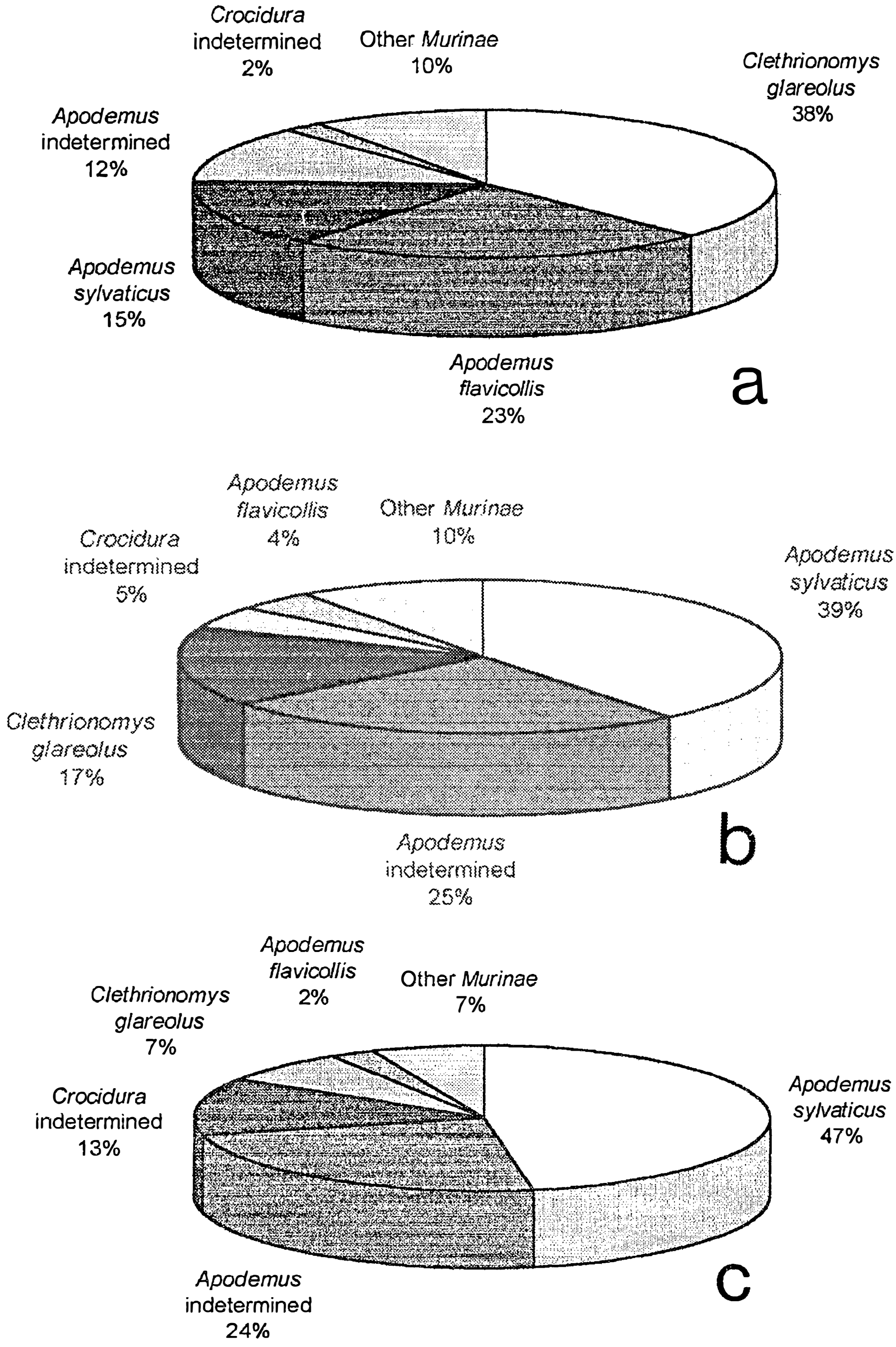

Figure 3. — Composition of small mammal communities in three different habitats : (a) coppice forest, (b) bushy ecotone, (c) clear-cut wooded area.

RELATIONSHIPS BETWEEN SNAKE DIETS AND PREY RESOURCE AVAILABILITY

Small mammal species occurred in the diet of all snake species of the area in relation to their relative availability in the field (Tab. IV). Moreover, there was no statistically significant difference between the regression lines relative to the four studied snake species in either ordinate intercepts or slopes (in all cases, ANCOVA : $P > 0.01$).

TABLE IV

Statistics of the regressions between prey availability (small mammals) in the field and taxonomical dietary composition for all the snake species in the study area. In all cases, df = 1,4.

	V. aspis	*C. viridiflavus*	*E. longissima*	*E. quatuorlineata*
Spearman's r :	0.97	0.94	0.94	0.92
ANOVA F :	77.6	30.4	31.2	21.6
mean square :	0.277	0.216	0.124	0.074
P value :	0.0009	0.005	0.005	0.009

Conversely, although the correlation coefficients of the relationships between lizard availability and proportion of lizard eaten were very high in all cases (Spearman's *r* ranging from 0.7 to 0.99), the reduced number of regression point ($N = 3$) impeded us to obtain statistical significance and to stress firm conclusions about any positive trend between lizard availability and proportion of lizard eaten. These high *r* values permit to suggest, however, that the same positive correlation detected above is present in this latter case also.

DISCUSSION

Adults of the four snake species inhabiting the study area ranged in size from about 60-75 cm (*V. aspis*) to 130-170 cm (*E. quatuorlineata*), the two other species (*E. longissima* and *C. viridiflavus*) being intermediate (about 90-130 cm in total length). In reptilian communities there is both theoretical and empirical evidence showing that (1) competition (e.g. food competition) tends to be reduced when there are relevant size differences between potential competitors (Ricklefs, 1973), and that (2) ecologically similar species tend to partition the available food resource for minimizing competition between populations (Mushinsky & Hebrard, 1977). The data given in the present paper are not very consistent with these general predictions. In fact our snakes clearly did not partition the available food resource, as it is shown by the very high overlap estimates between taxa. Small mammals and lacertid lizards were the bulk of prey of all the species studied, while the other prey types (e.g. nestling birds and frogs) were more occasionally eaten.

This occurrence widely confirmed previous studies on feeding habits of Mediterranean snake species (e.g. see Pozio, 1976 ; Cattaneo, 1979 ; Luiselli & Agrimi, 1991 ; Luiselli & Rugiero, 1993).

On the whole, the trophic spectrum of the studied viper population is closely resembling that of other Mediterranean populations of this species studied earlier (see Luiselli & Agrimi, 1991). Moreover, the occasional occurrence of brown frogs in this viper' diet is a further demonstration that *V. aspis* may feed on this prey type in idoneous wet biotopes, as already demonstrated in alpine populations of the same and of closely related species (Luiselli & Anibaldi, 1991 ; Monney, 1993 ; Luiselli *et al.,* 1995). Interestingly, the food niche breadth of this viper population is slightly wider than that of other populations of the same species (Bs = 3.36 *versus* 2.94) studied in areas where the diversity of the potential prey types (essentially of the small mammal species) was largely higher (Capula & Luiselli, 1990 ; Luiselli & Agrimi, 1991). The value of food niche overlap between *V. aspis* and *E. longissima* given here (see Tab. III) is extremely similar to that calculated between sympatric populations of these species in Tolfa mountains, central Italy (Ojk = 0.912, see Luiselli & Rugiero, 1993). Considering that the diversity of the potential prey resource varied remarkably between these areas, it would be stated as a rather general rule that the diet composition of these species is almost identical in the places where they do occur in sympatry.

We suggest that the lack of food partitioning presented in this study (that does not exclude interspecific competition) depended on three major reasons : (1) the snakes are sympatric (e.g., specimens belonging to different species were frequently found basking on the same spots), (2) the habitat structure is homogeneous, with only two macrohabitats available to both snakes and their prey (the wooded zone and the ecotone bushy strip bordering the forest), and (3) the prey resource availability is sufficient to maintain a relatively diversified community of snakes. In this regard it is interesting to note that the habitat selection of the various snake species of this area is similar, although it usually varies elsewhere, with *V. aspis* being more typical of wet biotopes, *E. longissima* and *C. viridiflavus* rather ubiquitarian and *E. quatuorlineata* strictly bounded to the dry habitats (e.g. see Corsetti and Capula, 1992). Concerning *Elaphe* species, it should be noted that these snakes are also semi-arboreal in several regions of their wide distribution (Naulleau & Bonnet, 1995).

The other primary conclusion of this study is that all snake species proved to be generalist predators. This is clearly evidenced (1) by the highly significant positive relationships between prey availability in the field and prey frequency in the snake guts, and (2) by the presence of nearly all the potential prey of the area (including both lizards and small mammals) in the snake guts. Rats were not found in the guts of *V. aspis* and *C. viridiflavus,* but this probably depended on (1) the smaller body size of the former, and (2) on the fact that the latter does not suffocate the captured prey (as *Elaphe* species usually do), thus being probably unable to eat big and vigorous rodents like rats. On the other hand *M. domesticus,* a small mouse rather rare in the study area, was not found in the guts of either *Elaphe* species, but we are unable to find a reason for this absence.

The extremely similar diet composition of the studied snakes suggests that interspecific competition may be strong not only in the actual situation, but also if the prey resource becomes to decline, and may be also without change in food partitioning.

SUMMARY

Food habits of four sympatric terrestrial snakes (*Vipera aspis, Coluber viridiflavus, Elaphe longissima, Elaphe quatuorlineata*) are studied in a forested area of the « Roman Country », about 15 km northeast of Rome. All species proved to be extremely similar in food choice, preying primarily upon small mammals (rodents and shrews) and lacertid lizards. Adult vipers occasionally preyed on brown frogs, while nestling birds were captured by all species (especially *E. quatuorlineata*) apart *E. longissima.* We estimated the relative density of several potential prey (all the small mammals and three of the lizard species), and found highly positive relationships between prey availability and prey use by snakes. Because of the high overlap between diets of the four snake species in the area, a strong interspecific competition may be predicted if the prey resource tends to decline.

RÉSUMÉ

Les habitudes alimentaires de quatre espèces sympatriques de serpents terrestres (*Vipera aspis, Coluber viridiflavus, Elaphe longissima, Elaphe quatuorlineata*) ont été étudiées dans une zone forestière de la « Campagne romaine », environ 15 km au nord-est de Rome. Toutes les espèces sont apparues extrêmement semblables quant à leurs choix alimentaires, capturant avant tout des petits mammifères (rongeurs et musaraignes) et des lézards (Lacertidés). Les vipères adultes capturent occasionnellement des grenouilles ; à l'exception d'*E. longissima,* toutes les espèces, et en particulier *E. quatuorlineata,* prennent des oisillons. La densité relative de diverses proies potentielles (tous les petits mammifères et trois espèces de lézards) a été estimée et une forte relation positive a été trouvée entre la disponibilité des proies et leur consommation par les serpents. En raison du fort recouvrement des régimes alimentaires des quatre espèces de serpents dans la zone d'étude, une forte compétition interspécifique apparaît prévisible en cas de diminution des proies.

REFERENCES

BANLEY, (1985). — *The statistics of natural selection.* Chapman & Hall, New York.

BEA, A. & BRAÑA, F. (1988). — Nota sobre la alimentacion de *Vipera latastei,* Bosca, 1878 (Reptilia, Viperidae). *Munibe,* 40 : 121-124.

BEA, A., BRAÑA, F., BARON, J.-P. & SAINT GIRONS, H. (1992). — Régimes et cycles alimentaires des vipères Européennes (Reptilia, Viperidae). *Ann. Biol.,* 31 : 25-44.

BRAÑA, F., BEA, A. & SAINT GIRONS, H. (1988). — Composicion de la dieta y cyclos de alimentacion en *Vipera seoanei* Lataste, 1879. *Munibe,* 40 : 19-27.

BRUNO, S. & MAUGERI, S. (1990). — *Serpenti d'Italia e d'Europa.* Editoriale Giorgio Mondadori, Milano.

CANOVA, L. & FASOLA, M. (1993). — Food habits and trophic relationships of small mammals in six habitats of the northern Po plain (Italy). *Mammalia,* 57 : 189-199.

CAPULA, M. & LUISELLI, L. (1990). — Contributo allo studio della microteriofauna di un' area dell'Italia centrale (Monti della Tolfa, Lazio) mediante analisi del contenuto stomacale di *Vipera aspis* (Reptilia, Viperidae). *Hystrix,* 2 : 101-107.

CATTANEO, A. (1979). — Osservazioni sulla nutrizione di *Elaphe quatuorlineata* (Lac.) a Castelporziano (Roma). *Atti Soc. ital. Sci. nat. Mus. civ. Stor. nat. Milano,* 120 : 203-218.

CORSETTI, L. & CAPULA, M. (1992). — The Amphibians and Reptiles of the Lepini Mountains (Latium, central Italy) : checklist and provisional atlas. *Brit. Herp. Soc. Bull.,* 39 : 8-16.

FILIPPUCCI, M.G., SIMSON, S. & NEVO, E. (1989). — Evolutionary biology of the genus *Apodemus* Kaup, 1829 in Israel. Allozymic and biometric analyses with description of a new species : *Apodemus hermonensis* (Rodentia, Muridae). *Boll. Zool.,* 56 : 361-376.

FLOWERDEW J.R. (1976). — Ecological methods. *Mammal Review,* 6 : 123-159.

LE BOULENGÉ, E. & LE BOULENGÉ-NGUYEN, P.Y. (1987). — A cost-efficient live trap for small mammal. *Acta Theriol.,* 32 : 140-144.

LUISELLI, L. & AGRIMI, U. (1991). — Composition and variation of the diet of *Vipera aspis francisciredi* in relation to age and reproductive stage. *Amphibia-Reptilia,* 12 : 137-144.

LUISELLI, L. & ANIBALDI, C. (1991). — The diet of the adder (*Vipera berus*) in two alpine environments. *Amphibia-Reptilia,* 12 : 214-217.

LUISELLI, L., ANIBALDI, C. & CAPULA, M. (1995). — The diet of juvenile adders, *Vipera berus,* in alpine habitat. *Amphibia-Reptilia,* 16 : in press.

LUISELLI, L. & RUGIERO, L. (1991). — Food niche partitioning by water snakes (genus *Natrix*) at a freshwater environment in central Italy. *J. Freshwater Ecol.,* 6 : 439-444.

LUISELLI, L. & RUGIERO, L. (1993). — Food habits of the Aesculapian snake (*Elaphe longissima*) in central Italy : Do arboreal snakes eat more birds than terrestrial ones ? *J. Herpetol.,* 27 : 116-117.

MONNEY, J.-C. (1990). — Régime alimentaire de *Vipera aspis* L. (Ophidia, Viperidae) dans les Préalpes Fribourgeoises (ouest de la Suisse). *Bull. Soc. Herpetol. France,* 53 : 40-49.

MONNEY, J.-C. (1993). — Predation of lizards and frogs by adult vipers, *Vipera aspis,* in the Bernese prealpine region (West Switzerland). *Amphibia-Reptilia,* 14 : 93-95.

MONTGOMERY, W.I. & DOWIE, M. (1993). — The distribution and population regulation of the wood mouse *Apodemus sylvaticus* on field boundaries of pastoral farmland. *J. Appl. Ecol.,* 30 : 783-791.

MUSHINSKY, H.R. (1987). — Foraging ecology. p. 302-334. *In :* Seigel, R.A., Collins, J.T., Novak, S.S. (eds.), *Snakes, ecology and evolutionary biology.* MacMillan Publishing Company, New York.

MUSHINSKY, H.R. & HEBRARD, J.J. (1977). — Food partitioning by five species of water snakes in Louisiana. *Herpetologica,* 33 : 162-166.

NAULLEAU, G. & BONNET, X. (1995). — Reproductive ecology, body fat reserves and foraging mode in females of two contrasted snake species : *Vipera aspis* (terrestrial, viviparous) and *Elaphe longissima* (semi-arboreal, oviparous). *Amphibia-Reptilia,* 16 : 37-46.

PELZ, H.J. (1982). — *Apodemus* (Germany). p. 212-213. *In* : Davis, D.E. (ed.), CRC *Handbook of Census Methods for terrestrial vertebrates.* CRC Press Inc., Boca Raton, Florida.

PIANKA, E.R. (1973). — The structure of lizard communities. *Annu. Rev. Ecol. Syst.,* 4 : 53-74.

PLEGUEZUELOS, J.M. & MORENO, M. (1990). — Alimentacion de *Coluber hippocrepis* en el SE de la peninsula Ibérica. *Amphibia-Reptilia,* 11 : 325-337.

POZIO, E. (1976). — La biologia e il ciclo di vita di *Elaphe quatuorlineata* (Lacépède). *Bull. Soc. Zool. France,* 101 : 741-746.

RICKLEFS, R.E. (1973). — *Ecology.* Chiron Press Inc., Portland.

SAINT GIRONS, H. (1980). — Modifications sélectives du régime des vipères (Reptilia : Viperidae) lors de la croissance. *Amphibia-Reptilia,* 1 : 127-136.

SAINT GIRONS, H. (1983). — Régime et rations alimentaires des Serpents. *Bull. Soc. Zool. Fr.,* 108 : 431-437.

SIEGEL, S. (1956). — *Non-parametric statistics for the behavioural sciences.* McGraw-Hill Book Co., New York.

SIMPSON, G. (1949). — Measurement of diversity. *Nature,* 163 : 688.

SOKAL, R.R. & ROHLF, F.J. (1969). — *Biometry. The principles and practice of statistics in biological research.* W.H. Freeman & Co., New York.