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The prey spectrum of terrestrial snakes in the Tolfa Mountains (Latium, Central Italy). A synthesis from earlier analyses

Das Beutespektrum terrestrischer Schlangen in den Tolfa Bergen (Latium, Mittelitalien). Eine Synthese aus früheren Untersuchungen

LUCA LUISELLI & FRANCESCO M. ANGELICI

KURZFASSUNG

Daten zur Nahrungszusammensetzung sechs terrestrischer Schlangenarten (*Vipera aspis francisciredi, Hierophis viridiflavus viridiflavus, Elaphe longissima longissima, Elaphe quatuorlineata quatuorlineata, Coronella austriaca austriaca, Coronella girondica*) aus einem hügeligen Gebiet Mittelitaliens (Tolfa Berge, 150 m bis 450 m ü. NN, etwa 60 km nördlich von Rom) wurden mit multivariaten statistischen Verfahren untersucht. Die Hauptkomponentenanalyse (PCA) erklärt die größten Ernährungsunterschiede zwischen den Schlangenarten durch Unterschiede in der Häufigkeit des Erbeutens von Mauereidechse (*Podarcis muralis*) und Waldmaus (*Apodemus sylvaticus*), die gleichzeitig jeweils die häufigste Eidechsen- bzw. Nagerart im Gebiet darstellen. Ein Dendrogramm auf Grundlage der Ähnlichkeit in der Ernährung bestätigt die Ergebnisse der PCA: Es gruppiert *V. aspis* Jungtiere, *C. austriaca* und *C. girondica* einerseits, die beiden *Elaphe* Arten andererseits, und stellt adulte *V. aspis* in einigen Abstand dazu. So könnten phylogenetisch einander nahestehende Taxa (z. B. die beiden *Coronella* bzw. *Elaphe* Arten) wegen ihrer ähnlichen Ernährungsgewohnheiten, Körpergröße und Lebensweise Nahrungskonkurrenten darstellen. Ihre parapatrische Verbreitung im Gebiet der Tolfa Berge könnte mit der Verringerung einer solchen Nahrungskonkurrenz in Zusammenhang stehen.

ABSTRACT

Data on prey composition of six species of terrestrial snakes (*Vipera aspis francisciredi, Hierophis viridiflavus viridiflavus, Elaphe longissima longissima, Elaphe quatuorlineata quatuorlineata, Coronella austriaca austriaca, Coronella girondica*) from a hilly area of Central Italy (Tolfa Mountains, elevations between 150 m and 450 m a.s.l., approximately 60 km north of Rome) is analyzed by means of multivariate statistics. Principal Component Analysis (PCA) revealed that most of the dietary differences between snake species are explained by the different frequency of predation upon the Wall Lizard (*Podarcis muralis*) and the Wood Mouse (*Apodemus sylvaticus*), that are the most abundant lizard and rodent species, respectively, in the study area. A dendrogram based on dietary similarities confirmed the conclusions of PCA: It clustered *V. aspis* juveniles, *C. austriaca* and *C. girondica* at one hand, the two *Elaphe* species at the other, and placed *V. aspis* adults in some distance. It seems that phylogenetically closely related taxa (i.e., the two *Coronella* and the two *Elaphe* species) could be strong food competitors because of similarities in diet, body size, and habits. Thus, their parapatric ecological distribution in the Tolfa Mountains could be essential to minimize competition.

KEY WORDS

Colubridae, Viperidae; *Vipera aspis francisciredi, Hierophis viridiflavus viridiflavus, Elaphe longissima longissima, Elaphe quatuorlineata quatuorlineata, Coronella austriaca austriaca, Coronella girondica;* feeding ecology; Mediterranean area, Central Italy

INTRODUCTION

In recent years, a strong development in the field research on snake dietary habits has produced considerable progress in understanding these organisms' foraging tactics. It was found that snake activities and reproductive performances are much dependent on fluctuations in prey availability (ANDREN 1982; ANDREN & NILSON 1983) so that the interplay between feeding and reproductive ecology is extremely complex and could be responsible for conspicuous allometry in the reproductive output of females (e. g., LUISELLI & al. 1996). Furthermore, snakes could be involved in re-

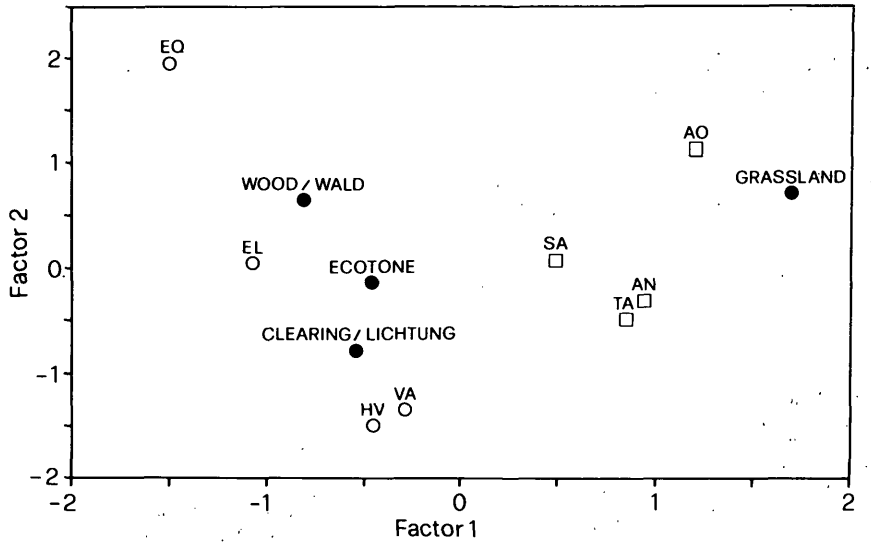

Fig. 1: Loadings of the first two factors extracted from a PCA representing the habitat types of sympatric predators (owls and snakes) for conducting their predatory activity (agroforested area of Central Italy, for details see CAPIZZI & LUISELLI 1996a). The owls are associated with grasslands, whereas the snakes are associated with ecotones and forested areas. EQ - *Elaphe quatuorlineata;* EL - *Elaphe. longissima;* HV - *Hierophis viridiflavus;* AO - *Asio otus;* SA - *Strix aluco;* VA - *Vipera aspis;* AN - *Athene noctua*; TA - *Tyto alba.*

Abb.1: Ladungen der ersten beiden Faktoren einer Hauptkomponentenanalyse (PCA) zur Darstellung der von sympatrischen Prädatoren (Eulen und Schlangen) zum Beutemachen genutzten Habitattypen in einem agroforstlich genutzten Gebiet Mittelitaliens (Einzelheiten siehe CAPIZZI & LUISELLI 1996a). Die Eulen sind Bewohner des Graslandes, die Schlangen bewaldeter Gebiete und der Ökotone. EQ - *Elaphe quatuorlineata;* EL - *E. longissima;* HV - *Hierophis viridiflavus;* AO - *Asio otus;* SA - *Strix aluco;* VA - *Vipera aspis;* AN - *Athene noctua*; TA - *Tyto alba.*

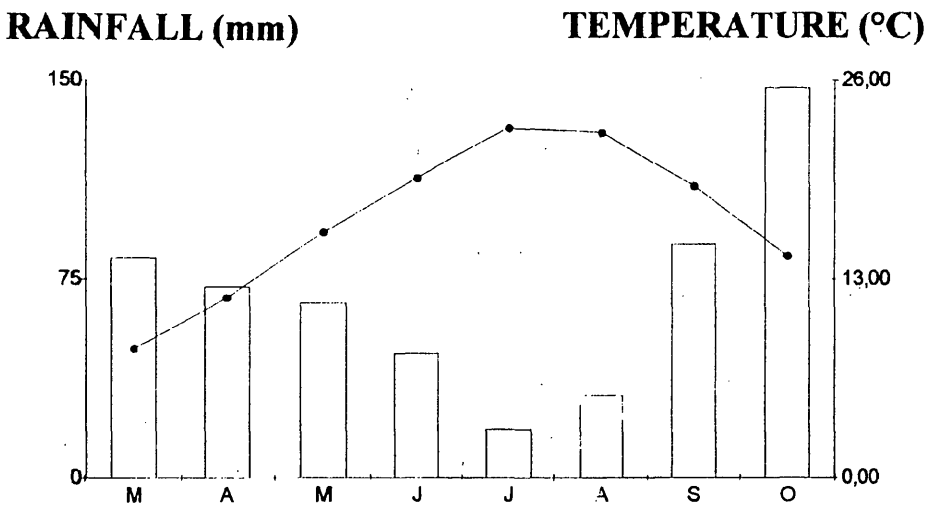

Fig. 2: Mean air temperature (°C, dots) and rainfall (mm, columns) in the Tolfa Mountains given for the months March through October. Source: Metereological Centre of Civitavecchia (Rome).

Abb. 2: Mittlere Lufttemperatur (°C, Punkte) und Regenmenge (mm, Säulen) in den Tolfa Bergen für die Monate März bis Oktober. Quelle: Meteorologisches Zentrum von Civitavecchia (Rom).

markable 'migrations' to match 'seasonal migrations' of their natural prey (MADSEN & SHINE 1996a, 1996b).

Thus, emerging evidence suggests that the dietary tactics of snakes are much more complicated than expected a few years ago, and that comparison of alimentary data of sympatric species could be of valuable help in understanding snake foraging ecology.

Since 1985, we have studied in detail the feeding habits of Mediterranean snakes in two different territories of Central Italy:

(1) in an agro-forested landscape subject to coppice management ('La Marcigliana' hunting reserve near the village of Settebagni, about 15 km northeast of Rome, 20 m to 120 m elevation); and

(2) in the bushy pastures of the Tolfa Mountains, about 60 km northwest of Rome (150 m to 450 m elevation).

In area (1) we studied:

(i) alimentary relationships between four species of terrestrial snakes (*Vipera aspis, Hierophis viridiflavus, Elaphe longissima, E. quatuorlineata*) along with the availability of their primary prey (lizards and small mammals), and

(ii) the trophic interactions between these snakes and four sympatric owl species (*Tyto alba, Athene noctua, Asio otus, Strix aluco*).

We demonstrated that:

(i) all sympatric snakes had similar prey spectra (CAPIZZI & al. 1995);

(ii) all snakes were opportunist predators in feeding on the most abundant prey in their environment (CAPIZZI & al. 1995);

(iii) all snake species searched for prey primarily in mature forest and bushy ecotone, while owls did this mainly in grassy semicultivated fields (fig. 1; cf. CAPIZZI & LUISELLI 1995, 1996a);

(iv) the potential for food competition was higher between snakes and owls (i. e. between guilds of predators phylogenetically closely related and morphologically congruent) than among snakes and owls (i. e. among phylogeneticcally and morphologically distant predators (cf. CAPIZZI & LUISELLI 1996a).

Conversely, our long-term research in the Tolfa Mountains focussed more on autoecological aspects of individual snake populations than on functioning of snake assemblages. As a consequence, several studies on single species have appeared in the recent years, but none of them was centered on the trophic relationships between the various sympatric (or contiguously allopatric) species.

It is the aim of this paper to collate data previously published on food habits of individual snake species in the Tolfa Mountains and to discuss them in the light of interspecific relationships between these species.

MATERIALS AND METHODS

General considerations

This paper is entirely based on published long-term research data which were obtained by ourselves and our associates (see "Acknowledgments"). Table 1 summarizes the food items collected from six terrestrial snake species and the literature source from which this information has been taken: Asp Viper - *V. aspis francisciredi* LAURENTI, 1768, Smooth Snake - *Coronella austriaca austriaca* LAURENTI, 1768, Southern Smooth Snake - *C. girondica* (DAUDIN, 1803), Western Whip Snake - *Hierophis viridiflavus viridiflavus* (LACÉPÈDE, 1789), Aesculapian Snake - *Elaphe longissima longissima* (Laurenti, 1768), Four-lined Snake - *E. quatuorlineata quatuorlineata* (LACÉPÈDE, 1789). Two more aquatic species were excluded from the analysis: The European Grass Snake (*Natrix natrix*), primarily batrachophagous, and the Dice Snake (*N. tessellata*), primarily ichthyophagous (LUISELLI & RUGIERO 1991; FILIPPI 1995; FILIPPI & al. 1996). For *H. viridiflavus* we used data collected in a study area situated about 30 km SE the territory of Tolfa Mountains (cf. RUGIERO & LUISELLI 1995), but characterized by the same climatic and environmental characteristics. This was necessary because no study has ever been published on the diet of *H. viridiflavus* in the

Table 1: Food items examined in six species of terrestrial snakes in the territory of the Tolfa Mountains, Latium, Central Italy; bibliographic source included. R - rodents, L - lizards, B - birds, A - arthropods.

Tab. 1: Die untersuchten Nahrungsobjekte bei sechs Arten terrestrischer Schlangen im Gebiet der Tolfa Berge, Latium, Mittelitalien, mit Angabe der Literaturquelle. R -Nager, L -Eidechsen, B -Vögel, A - Arthropoden.

Species Art	Ingesta examined Untersuchte Ingesta	Primary prey Hauptnahrung	Reference Literatur
Vipera aspis francisciredi, adult	97	R	LUISELLI & AGRIMI 1991
Vipera aspis francisciredi, juvenile	26	L	LUISELLI & AGRIMI 1991
Hierophis viridiflavus	52	R L	RUGIERO & LUISELLI 1995
Elaphe longissima	34	R L	LUISELLI & RUGIERO 1993
Elaphe quatuorlineata	65	R B	CAPIZZI & LUISELLI 1996b
Coronella austriaca	44	L	RUGIERO & al. 1995
Coronella girondica	32	L A	AGRIMI & LUISELLI 1994
Total/Gesamt	350		

territory under study. Our unpublished observations confirmed that the diet of Western Whip Snake populations of Tolfa is indeed very similar to that of those from the area where RUGIERO & LUISELLI (1995) carried out their study.

Study area

All data given here were collected in the territory of the Tolfa Mountains (elevations between 150 m and 450 m a.s.l.), This hilly region is situated approximately 60 km north of Rome. The climate is characterized by cold winter (without snow covering), rainy spring and autumn, and dry and hot summer (hypomesaxeric subregion of type B according to TOMASELLI & al. 1973). Averages of rainfall and air temperatures of the study area are given in figure 2.

Field data were collected in six spots nearly identical in terms of climate and vegetation characteristics. These spots are: Oriolo Romano, La Matrice (Manziana), Macchia della Manziana, Rio Fiume Valley, Canale Monterano, Sassoni di Furbara.

The vegetation consists of riverine woods (*Ulmus campestris*, but also *Salix* sp., *Populus* sp.), wide areas covered by bushy pastures (*Spartium junceum, Cytisus scoparius, Prunus spinosa, Rubus ulmifolius, Crataegus monogyna*) and mesophilous forests (*Quercus cerris, Qu. pubescens, Ostrya carpinifolia*) (SPADA 1977).

Methods

Detailed information on the procedures employed to obtain food items from living snakes is given elsewhere (e. g., LUISELLI & AGRIMI 1991; LUISELLI & RUGIERO 1993; FILIPPI 1995). For this 'synthetic' paper the main procedures shall be summarized as follows.

Sampling was carried out primarily between 07.00 and 15.30, and occasionally in the late afternoon. Snakes were captured by hand during standardized routes across the study areas. Snakes were sexed by examination of external tail morphology, weighed, and measured for total length. For future identification, each snake was scale-clipped and paint-marked dorsally. Stomach contents and faecal pellets were obtained by gentle palpation of the snake's abdomen until regurgitation or defecation occurred. Examination of faecal pellets included identification of hairs by light microscopic analysis of surface and cross-section.

Cluster analysis on the taxonomical dietary composition of the various snake populations was done with the Simple Linkage method, standardized to 100%. Principal Component Analysis (PCA) was performed on the proportional shares of the various prey types in the snake diets. Thus, cases were snake populations and factors were the various prey types. Both Cluster and PCA analyses were computed with a SAS (version 6.0) microcomputer package.

RESULTS

Our previous papers, based on a total of 350 ingesta analyzed, indicate that most of the terrestrial snake species of the Tolfa mountains are primarily mammalophagous, except two small species (*C. austriaca, C. girondica*), the juveniles of *V. aspis* and of larger snakes (e. g., *H. viridiflavus*) which all are primarily lacertophagous (table 1). However, PCA permitted to explore the similarities and differences between diets of these sympatric snakes in more detail: The loadings of the first two factors are given in table 2. Factor 1 (proportion of *Podarcis muralis* eaten; eigenvalue = 3.70961) explaines 52.99% of total variance, whereas factor 2 (proportion of *Apodemus sylvaticus* eaten; eigenvalue = 1.47212) explaines 21.03% of total variance (cummulative explained variance: 74.02%). Thus, most of the differences between snake species are explained by different frequencies of predation upon the Wall Lizard (*Podarcis muralis*) and the Wood Mouse (*Apodemus sylvaticus*), that represent the most abundant lizard and rodent species, respectively, in the area (RUGIERO & LUISELLI 1995; CAPIZZI & al., unpublished data). The plot of loadings from this PCA (fig. 3) indicates that three groups of snakes can be distinguished on the basis of their diet:

(1) a group constituted by *E. quatuorlineata* and adult *V. aspis*,

(2) a group represented solely by *E. longissima*, and

(3) a group formed by *H. viridiflavus*, *C. austriaca*, *C. girondica*, and *V. aspis* juveniles.

A dendrogram based on dietary similarities (fig. 4) confirms the conclusions of PCA in clustering *V. aspis* juve-

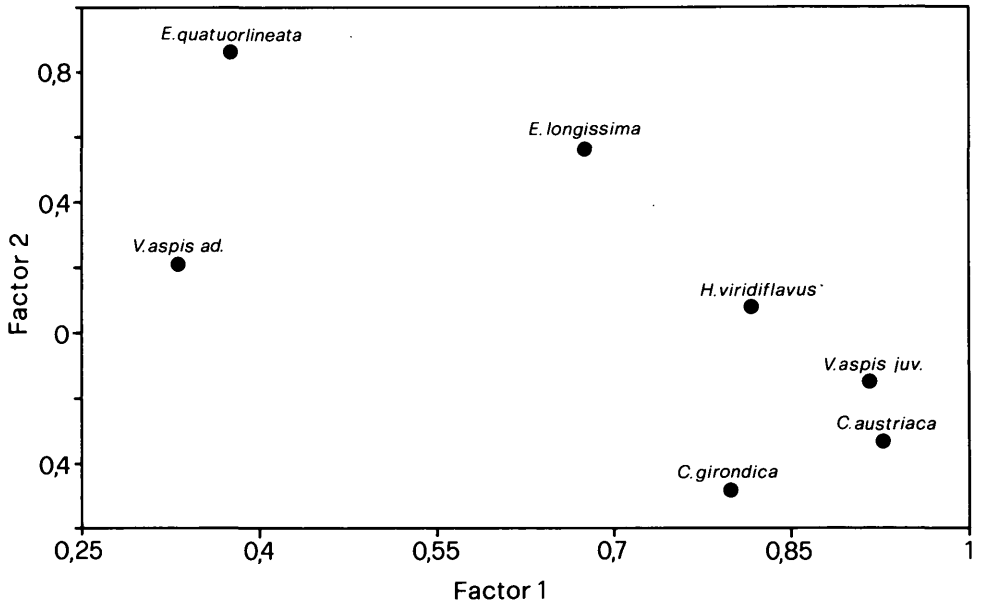

Fig. 3: PCA on the proportional shares of the various prey types in the diets of the snake species studied. Plot of the loadings of the first two factors. For statistical details, see text.

Abb. 3: Die Aufladungen der ersten beiden Faktoren aus der Hauptkomponentenanalyse über das anteilige Vorkommen verschiedener Beutetierarten in der Nahrung der untersuchten Schlangenarten.

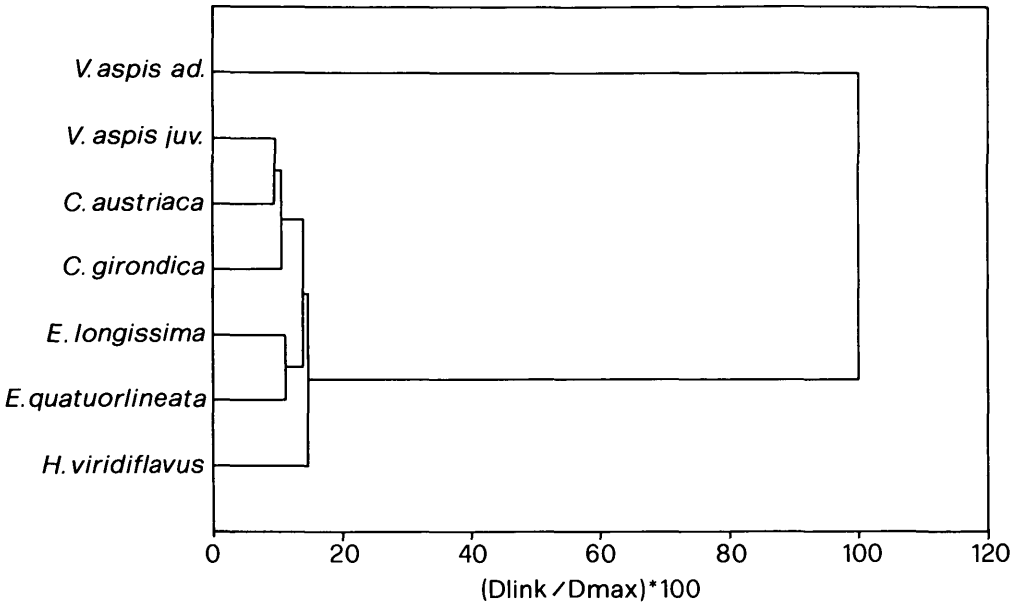

Fig. 4: The snake species analyzed in the Tolfa Mountains, clustered (simple linkage method, standardized to 100%), by their dietary similarity.

Abb. 4: Clusteranalyse (simple linkage Methode, standardisiert auf 100%) der aus den Tolfa Bergen untersuchten Schlangenarten nach der Ähnlichkeit ihrer Nahrungszusammensetzung.

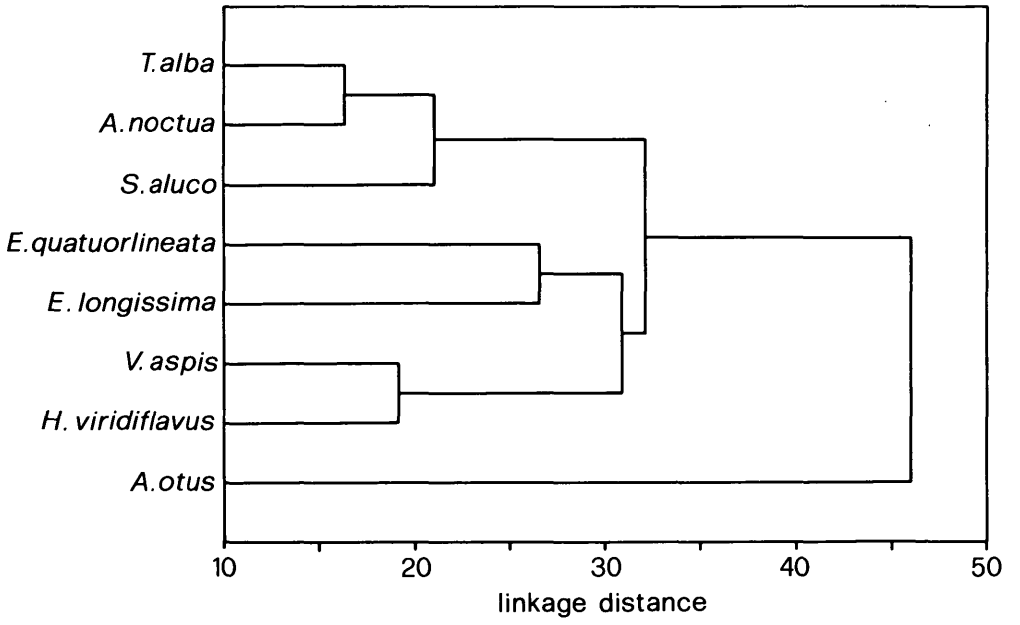

Fig. 5: Four species of snakes and four species of owls in an agroforested area of Central Italy, clustered (simple linkage method) by dietary similarity (for more details, see CAPIZZI & LUISELLI 1996a).

Abb. 5: Vier Schlangen- und vier Eulenarten aus einem agroforstlich genutzten Gebiet Mittelitaliens, gruppiert (Clusteranalyse, simple linkage Methode) nach der Ähnlichkeit ihrer Nahrungszusammensetzung (Einzelheiten siehe CAPIZZI & LUISELLI 1996a).

Table 2: Loadings of factor 1 (proportion of *Podarcis muralis* eaten) and factor 2 (proportion of *Apodemus sylvaticus* eaten) extracted from PCA on the taxonomical dietary composition of snakes of the Tolfa Mountains.

Tab. 2: Ladungen von Faktor 1 (Nahrungsanteil *Podarcis muralis*) und Faktor 2 (Nahrungsanteil *Apodemus sylvaticus*) aus einer Hauptkomponentenanalyse zur taxonomischen Nahrungszusammensetzung bei Schlangen aus den Tolfa Bergen.

Taxon	Factor 1	Factor 2
Vipera aspis, adult	0.331176	0.208213
Vipera aspis, juvenile	0.915685	-0.152037
Hierophis viridiflavus	0.816506	0.078138
Elaphe longissima	0.675304	0.560868
Elaphe quatuorlineata	0.375739	0.860057
Coronella austriaca	0.926847	-0.333078
Coronella girondica	0.799002	-0.484083
Eigenvalues	3.70961	1.47212
Explained variance (%)	52.99	21.03
log determinant of correlation matrix		-3.055

niles, *C. austriaca* and *C. girondica* at one hand, the two *Elaphe* species at the other, and placing *V. aspis* adults in some distance. This distant position of the latter is mainly explained (i) by the higher taxonomical diversity of the small mammals eaten by adult Asps than by any other snake studied, and (ii) by the fact that vipers frequently feed upon shrews (LUISELLI & AGRIMI 1991), that are a very unusual prey to the other snakes.

E. longissima and *E. quatuorlineata* are clustered together by the actual analysis. This parallels the observations made in an agro-forested area in the Roman county which was subject to coppice management (CAPIZZI & LUISELLI 1996a), although in this latter territory the diet of *V. aspis* was more similar to that of *H. viridiflavus* than in the Tolfa Mountains (fig. 5).

DISCUSSION

The ecological implications of the alimentary patterns observed are too complex to be resolved on the basis of our present knowledge. However, some considerations seem worth mentioning.

There is much evidence that phylogenetically closely related taxa (on the one hand the two *Coronella* species, and on the other hand the two *Elaphe* species) can be strong food competitors in case of similarities in their diet, body size and habits. It is obvious that this may depend on accidental similarities of the taxa under study, since generalizations are difficult in this case. In fact, there are many examples, either in tropical or temperate regions, showing that phylogenetically closely related syntopic snakes tend to partition the available resources and to be low competitors (e. g., see the case of *N. Natrix* and *N. tessellata* - LUISELLI & RUGIERO 1991). However, it may be possible that, within a given snake guild, the actual resource partitioning derived from a primitive strong interspecific competition (cf. RICKLEFS 1973) and that even the snake guilds of the Tolfa Mountains will tend to partition the resources more clearly in the future. Thus, it is likely that the parapatric distribution of these congeneric species within the territory of the Tolfa mountains (for *Coronella* see CAPULA & al. 1995; for *Elaphe* see MACEDONE 1989; FILIPPI 1995) is essential to minimize competition (sensu RICKLEFS 1973). This parapatric distribution (i. e., habitat partitioning at a very local scale) could be even more important if we consider that the two *Coronella* species are nearly identical also in terms of activity patterns (including both seasonal and daily peaks of activity, see CAPULA & al. 1995), the same being true for the two *Elaphe* species (see FILIPPI 1995). Although species-specific daily activity rhythms may contribute to differentiate diets of sympatric predators (cf. RICKLEFS 1973), different activity times do not really define separate niches (e. g., see JAKSIC 1982). Spatial and temporal segregation do not necessarily reduce exploitation competition if the prey in question is available in various habitats or periods of time. The use of prey by one group may still reduce its availability to a second group, even if they operate at different places or times (JAKSIC 1982).

This study reveals that the lacertophagous snakes *C. austriaca* and *C. girondica* and the juveniles of the genera *Vipera, Elaphe,* and *Hierophis* could be subject to strong interspecific food competition, their diet being based primarily

(or almost exclusively) on the lizard *P. muralis*. Although this lizard is very abundant in the study area, the juvenile snakes are probably food-limited organisms, as they are often rather emaciated, especially during the spring months (LUISELLI & al., unpublished data). In this respect it should be noted that the feeding cycles of juvenile snakes - contrary to those of adults - last throughout their whole period of activity (from March-April to October-November), which means that competition cannot be minimized by time-shifted 'alternate phases of feeding and non-feeding'.

Assuming the presence of strong interspecific food competition in juvenile snakes, are there 'winners' and 'succumbing' species in the studied territory? Despite the long timespan of research and the strong field effort, our data are still not exhaustive to answer this crucial question, but some specifically directed field experiments are now in progress to test it. However, our unpublished data allow to formulate a few preliminary ideas:

(i) Judged from year-by-year fluctuations in the number of snakes observed, no species seems to be clearly declining, their local abundance being rather constant;

(ii) Local distribution of both *Coronella* species is scattered, and each species is relatively common only in places where other snake species (especially *H. viridiflavus* and *V. aspis*) are very rare or not present at all;

(iii) Young vipers (sample size 1985-1996: $n = 163$) appeared in significantly (two-ways ANOVA: $P < 0.0005$) better physical conditions (sensu LUISELLI & al. 1996, once body weight is taken into account) than young *H. viridiflavus* ($n = 238$), *E. longissima* ($n = 57$), and *E. quatuorlineata* ($n = 28$);

(iv) Judged from our unpublished mark-recapture data, young vipers were much more frequently found in the field than juveniles of any other snake species, including *H. viridiflavus*, that is the most abundant species in the territory studied (BRUNO 1977; LUISELLI & RUGIERO 1990).

Thus, taking into account all above considerations, we suggest that, if interspecific competition for food is indeed strong among juvenile snakes,

(i) the two small species (*Coronella*) should be constrained to refuge sites relatively inhospitable to other snakes, and

(ii) the juvenile vipers should be the most successful competitors, possibly due to their ambush foraging tactic and ability to ingest larger prey than young colubrids (POUGH & GROVES 1983). In the field, young vipers are clearly observed more frequently than juveniles of any other snake (taking into account the relative abundances of the various species). This is perhaps another evidence of their status of successful competitors, although one cannot reject the hypothesis that juvenile colubrids may be much more elusive.

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AUTHORS: Dr LUCA LUISELLI, Dipartimento di Biologia Animale e dell'Uomo, Università di Roma 'La Sapienza', via Alfonso Borelli 50, I-00161 Roma (Italia); Dr FRANCESCO M. ANGELICI, Dipartimento di Biologia Animale e dell'Uomo, Università di Roma 'La Sapienza', viale dell'Università 32, I-00152 Roma (Italia).