Ecological Relationships between Sympatric *Vipera aspis* and *Vipera ursinii* in High-Altitude Habitats of Central Italy

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Abstract.—The ecological relationships between two sympatric vipers (*Vipera aspis* and *Vipera ursinii*) were studied at a mountainous area in central Italy (Gran Sasso, Abruzzo), between spring 2004 and autumn 2006. The two species differed significantly in their altitudinal distribution: *V. ursinii* being confined to the higher elevations (above 1650 m elevation), and *V. aspis* being present from the lowest to the highest altitudes (1200–1900 m). We recorded a wide sector of approximately 250 m elevation (between 1650 and 1900 m elevation) where the two species overlapped. In these areas, the two species exhibited significant difference in microhabitat use and diet composition. Male and female *V. aspis* were larger (SVL) than male and female *V. ursinii*. Furthermore, the two species exhibited a significant difference in sexual size dimorphism, with females being larger than males in *V. ursinii*, whereas no such difference in SVL was observed in *V. aspis*. However, we did not observe any difference in SVL of male and female vipers when comparing sympatric and allopatric populations. Overall, the potential for competition between these two species appears to be low because of their clearly different realized ecological niches.

The ecology of European vipers has received considerable interest since the pioneering studies conducted by Saint Girons (1952, 1978, 1980). Some European viperids (notably *Vipera berus*) are currently among the ecologically best known snake species in the world (e.g., Madsen, 1988; Madsen and Stille, 1988; Madsen and Shine, 1992a). However, most studies have focused on the population biology of a single species (e.g., Madsen and Shine, 1992b, c), whereas comparatively few studies have explored the population biology of sympatric populations (for a review, see Luiselli, 2006a). The first study on the ecology of sympatric viper populations was a field study on *Vipera aspis* and *V. berus* in Western France (Saint Girons, 1975). After this pioneer study, only a few detailed studies have been conducted, the most significant being those on sympatric *V. aspis* and *V. berus* populations in the mountains of Switzerland (Monney, 1996) and on sympatric *Vipera seoanei* and *Vipera latastei* populations in the northwestern Iberian peninsula (Brito and Crespo, 2002; Martinez et al., 2006). In general, these studies suggest that sympatric vipers tend to partition the habitat niche axis to minimize competition, whereas their diets and activity patterns are very similar (Luiselli, 2006a).

However, much still needs to be known concerning the ecological relationships of sympatric European viper populations to further test competition/niche partitioning issues and also to explore conservation implications of threatened species/populations. In this paper, we describe the ecological relationships between two viper species, the European Asp (*V. aspis*) and the Meadow Viper (*Vipera ursinii*), in a mountainous area of central Italy. The Meadow Viper is an endangered species which inhabits a few scattered mountain peaks in Western Europe (Bruno, 1985; Bombi et al., 2006).

The aim of the present study is to explore the following key questions: (1) Do the two species co-occur along an altitudinal gradient? The two species are known to inhabit different altitudes in central Italy, with *V. aspis* inhabiting mainly lowlands and moderate altitudes, whereas *V. ursinii* being confined to high altitudes (Bruno, 1985; Mallow et al., 2003). (2) In sympatry, do the two species differ in microhabitat use and prey choice? (3) Does sympatry affect body size? That is, is the body size of a given species different in sympatric compared to allopatric populations?

Materials and Methods

Study Areas.—Data were collected between April 2004 and October 2006 (Di Lena, 2006). Field work was conducted at three sites of the Gran Sasso massif (Abruzzo, central Italy), a mountainous area characterized by cool alpine

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climate and prolonged snow cover during the winter months (from November to May). The three sites were as follows: ''Monte Brancastello,'' from 1650–1950 m elevation, ''Monte San Gregorio di Paganica,'' from 1670–1900 m elevation, and ''Tre Valloni,'' from 1200–2100 m elevation. All sites are situated inside the protected territory of the ''Gran Sasso-Monti della Laga'' National Park. The study sites are characterized by extensive meadow ''prairies,'' both natural and human-made. The prairies are mainly found above 1800 m elevation. The main vegetation consists of grasses such as *Nardus stricta*, *Poa alpina*, *Anthoxanthum odoratum*, *Brachypodium rupestre*, *Brachypodium genuense*, *Sesleria tenuifolia*, *Festuca macrathera*, and sedges such as *Luzula italica*. Locally, extensive areas are covered by dwarf junipers (*Juniperus communis nana*) and bearberries bushes (*Arctostaphylos uva-ursi*).

Protocol.—Snakes were captured by hand, sexed by examining the shape of the cloacal region and external coloration, measured for snout–vent length (SVL, to the nearest 1 mm), and individually marked by ventral scale clipping for future identification. Food items were collected 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 (for the methods employed, see Filippi and Luiselli, 2002; Filippi et al., 2005). All individuals were released at the exact spot of capture immediately after the data recording procedures.

Altitude and microhabitat at each capture site were recorded for all vipers captured. That is: (1) large, >7 m diameter *Juniperus* bushes, including cases where two or more bushes are joined together (LJN); (2) small, <5 m diameter *Juniperus* bushes (SJN); (3) open ground with no stones and bushes, covered with short grass (OPG); (4) stonepiles and stone walls (STP); (5) grassy area with sparse non–juniper bushes (GRS); (6) grassy area with dense non–juniper bushes (GRD); (7) rocky area with trees and non–juniper bushes (ROT); (8) woodland (WOD); (9) tall grass (TAG); (10) piles of cut wood and tree-trunks (PWT).

Sympatry versus allopatry was defined as follows: A snake's location was considered sympatric if it was found in a site of <1000 m distance to a site of the other species. The local distribution of the two species in the study area is very well known because of long-term research (1985–2006) by two of the writers (LL, EF) and staff scientists of the National Park; thus, it is very unlikely that in the present study some cases of sympatry were wrongly attributed to allopatry.

Trophic niche analysis was performed by analyzing the interspecific differences in taxonomic composition of the diet by (1) prey items and (2) individuals containing a given prey type. These two methods, used together, can describe efficiently the diet composition of snake populations (e.g., Rodriguez-Robles and Greene, 1999; Rodriguez-Robles et al., 1999a,b).

Statistical Analyses.—To avoid pseudoreplication, data were recorded only once from each individual. To evaluate whether the two viper species were observed with a similar frequency of occurrence along the altitudinal gradient, the altitudinal distribution was grouped into 50-m intervals, ranging from 1200–1950 m elevation. Then we determined the relative sampling effort per altitude interval by dividing the number of hours spent in the field in each altitude interval by the total number of hours in the field during the entire research period. Using a null hypothesis of equal distribution frequency among altitude intervals, we then generated the expected number of vipers at each altitude interval by multiplying the total number of vipers found during the study by the relative sampling effort for each altitude interval. Finally, observed and expected values were compared by χ^2-test (see below). Data on the altitudinal distribution of the two viper species were analyzed corrected by field effort (i.e., by number of hours spent searching for vipers at each altitude interval). The data matrix assembled was subsequently subjected to 5000 Monte Carlo randomizations using the EcoSim software (Aquired Intelligence Corp., Kesey-Bear; http://www.uvm.edu/biology/Faculty/Gotelli/Gotelli.html), and the resulting simulated indices were compared by χ^2-test according to Gotelli and Graves (1996). The same Monte Carlo procedure for χ^2-test was also used to investigate microhabitat differences between the species. EcoSim uses a randomization test for the independence hypothesis in a two-way contingency table, randomizes the matrix, and calculates a χ^2-deviation statistic for both the observed and simulated data.

Interspecific niche overlap in habitat use and prey species was calculated using the symmetric formulas of Pianka (1973) and Czechanowski (Feinsinger et al., 1981), with values from 0 (no similarity) to 1 (absolute identity). As we did not have a static measure of habitat type and prey availability at the study area, we used the setting of equiprobable resource states available in EcoSim software (Laurent and Kingsbury, 2003). The EcoSim software was used to calculate overlap indices and to generate Monte Carlo simulations (Gotelli and Graves, 1996).

All other statistics were conducted using SPSS (SPSS 11.0 for Windows) and Statistica (Statis-

tica 6.4 for Windows), all tests being two-tailed and alpha set at 0.05. The homogeneity of sample variances was checked by Levene test, and if the variables were nonnormal, they were normalized by log transformation. Parametric tests were applied to normally distributed variables and nonparametric tests to nonnormal variables. Means are presented ± 1 SD.

RESULTS

Altitudinal Distribution.—After pooling the three study sites to increase the sample size, our analyses revealed a significant altitudinal difference in occurrence (Table 1): *V. ursinii* being confined to high altitudes (above 1650 m elevation) and with significant differences among altitude intervals (observed vs. expected $\chi^2_{13} = 91.11$, $P < 0.0001$), and *V. aspis* being captured from the lowest to the highest altitudes without significant differences among altitude intervals ($\chi^2_{13} = 11.17$, $P = 0.596$). The altitudinal distribution difference between species was statistically significant after 5000 Monte Carlo randomizations of the raw data-matrix (simulations χ^2-procedure of EcoSim software; observed index = 45.88, mean of the simulated indices = 27.54, variance = 68.61, $P = 0.034$). However, despite this significant interspecific difference in altitudinal distribution, there was a wide sector of approximately 250 m elevation, between 1650 and 1900 m elevation, where the two species overlapped (Table 1).

Microhabitat Use and Prey Choice.—The microhabitat use patterns of sympatric *V. aspis* and *V. ursinii* are summarized in Figure 1. The main interspecific differences were in the higher use of LJN and OPG by *V. ursinii*, and of STP and WOD by *V. aspis*. (5000 Monte Carlo randomizations of the data-matrix with simulations χ^2-procedure of Ecosim software; observed index = 46.77, mean of the simulated indices = 18.69, variance = 43.57, $P = 0.002$.) Within the sample of *V. ursinii*, the strong prevalence of LJN over SJN is particularly important, because the availability in the field of SJN is more than three times that of LJN (Di Lena, 2006); thus, the differences in viper's use of these microhabitat types were highly significant ($P < 0.0001$ at observed vs. expected χ^2).

A total of 17 prey items from 15 different individuals of *V. aspis* and 41 prey items from 17 *V. ursinii* were collected from sympatric populations. In terms of number of prey items, the diet of *V. aspis* consisted mainly of rodents (over 80% of the total prey items) and that of *V. ursinii* mainly of Orthoptera species (over 90% of the total prey items; Table 2). The two species differed significantly in terms of dietary composition after 5000 Monte Carlo randomizations

TABLE 1. Altitudinal distribution of sympatric *Vipera ursinii* and *Vipera aspis* from three study sites in Gran Sasso, central Italy, showing that *V. ursinii* is confined to high elevations while *V. aspis* is present throughout. Note that this table includes only 84 snake individuals (i.e., 48 *V. ursinii* and 34 *V. aspis*), because we included here only those individuals from sites where in theory the presence of both species was possible. Many other individuals (N = 129) were captured and processed for SVL, but came from allopatric populations of the two species and thus were not included in this table. "Total" is the field effort (hours), "sampling effort" is the relative index of field effort per altitude interval calculated as described in the text.

|	1200<X<1250	1250<X<1300	1300<X<1350	1350<X<1400	1400<X<1450	1450<X<1500	1500<X<1550	1550<X<1600	1600<X<1650	1650<X<1700	1700<X<1750	1750<X<1800	1800<X<1850	1850<X<1900
Total	17.5	25.3	10.6	14.5	14	26	18.6	12.6	15	23.3	25.2	10	26.5	11
Sampling effort	0.0699	0.1012	0.0424	0.0579	0.056	0.104	0.0744	0.0503	0.0599	0.0932	0.1007	0.0399	0.106	0.0439
V. ursinii	0	0	0	0	0	0	0	0	0	7	17	6	12	7
V. ursinii expected	3.35	4.86	2.035	2.78	2.69	4.99	3.57	2.41	2.87	4.47	4.83	1.91	5.09	2.11
V. aspis	2	3	3	2	2	2	3	2	1	4	7	2	0	1
V. aspis expected	2.38	3.44	1.44	1.97	1.9	3.54	2.53	1.71	2.04	3.17	3.42	1.36	3.6	1.49
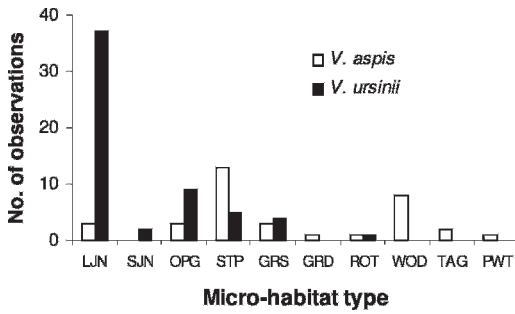
FIG. 1. Microhabitat use of sympatric *Vipera ursinii* and *Vipera aspis* from three study sites of Gran Sasso, central Italy. Symbols: LJN = large *Juniperus* bush, SJN = small *Juniperus* bush, OPG = open ground, STP = stonepile, GRS = grassy area with sparse non-juniper bushes, GRD = grassy area with dense non–juniper bushes, ROT = rocky area with trees and non–juniper bushes, WOD = woodland, TAG = tall grass, PWT = piles of cut wood and tree-trunks. Significant differences at Monte Carlo χ^2-procedure between pairs of bars were found in LJN ($P < 0.0001$), OPG, STP, and WOD (all $P < 0.01$).

of the data-matrix with simulations χ^2-procedure of Ecosim software (observed index = 44.70, mean of the simulated indices = 7.05, variance = 15.18, $P = 0.0002$). The trophic niche overlap between species was 0.0521 by Pianka index, and 0.0976 by Czechanowski index, in both cases showing an extremely low dietary similarity between species. In terms of number of snakes containing a given prey type, the same patterns highlighted above were confirmed: the great majority of *V. ursinii* contained Orthoptera and the great majority of *V. aspis* contained rodents (Table 2). The two species differed significantly after 5000 Monte Carlo randomizations of the data-matrix with simulations χ^2-procedure of Ecosim software (observed index = 21.96, mean of the simulated indices = 6.90, variance = 14.46, $P = 0.004$). The trophic niche overlap, calculated on the percentage of individuals containing a given prey type and not on the total number of prey items, was 0.1274 by Pianka index, and 0.2352 by Czechanowski index, once more confirming very low overlap between species.

Body Sizes.—In total, the snout–vent length (SVL) of 213 vipers were recorded in sympatric (denoted SYM) and allopatric populations (denoted ALL, Table 3). SVL of both male and female *V. aspis* was significantly larger than that of male and female *V. ursinii* (Table 3). Furthermore, the SVL of female *V. ursinii* was significantly larger than that of males (Table 3), whereas no such sexual size dimorphism was evident *in V. aspis* (Table 1). However, we did not detect any difference in SVL (at one-way ANOVAs) in male and female *V. aspis* or *V. ursinii* among the sympatric and allopatric populations (*V. aspis*: $F = 2.48$, $P = 0.991$ for males and $F = 2.67$, $P = 0.998$ for females; *V. ursinii*: $F = 1.97$, $P = 0.889$ for males, $F = 2.14$, $P = 0.778$ for females). SVL and body mass were highly correlated in both sexes of *V. ursinii* (females: $r = 0.97$, $N = 45$, $P < 0.0001$; males: $r = 0.94$, $N = 37$, $P < 0.001$) and *V. aspis* (females: $r = 0.89$, $N = 35$, $P < 0.001$; males: $r = 0.95$, $N = 32$, $P < 0.0001$).

DISCUSSION

Sympatry of *V. ursinii* and *V. aspis* populations have been recorded previously (Bruno, 1985; Luiselli, 2004). Prior to the present study, nothing was known about the altitudinal extent of sympatry, and on the ecological relationships of coexisting *V. aspis* and *V. ursinii*. Our data show that the altitudinal overlap zone of the two species is much larger than previously suspected covering at least 250 m of elevation (Table 1). However, the actual overlap zone may be even larger because suitable habitats for *V. ursinii* extend down to approximately 1400 m

TABLE 2. Diet composition of sympatric *Vipera ursinii* and *Vipera aspis* from three localities of Gran Sasso d'Italia National Park. Symbols: N = numbers of prey items; $\%N$ = percentage of items of a given prey type to the total number of prey items; n = number of snakes containing a given prey type; $\%n$ = percent of snakes containing a given prey type in relation to the total number of snakes with prey.

Prey items	*V. aspis* N (%N)	*V. aspis* n (%n)	*V. ursinii* N (%N)	*V. ursinii* n (%n)
MAMMALIA				
Microtus nivalis	7 (41.2)	6 (40.0)	2 (4.9)	2 (11.8)
Apodemus sylvaticus	7 (41.2)	7 (46.7)	0 (0)	0 (0)
REPTILIA				
Podarcis muralis	3 (17.6)	2 (13.3)	2 (4.9)	2 (11.8)
INSECTA				
Orthoptera indet.	0 (0)	0 (0)	37 (90.2)	13 (76.4)
TOTAL	17 (100.0)	15 (100.0)	41 (100.0)	17 (100.0)

TABLE 3. Summary of the means and dispersion measures for body length (SVL, mean ± SD, cm) of *Vipera aspis* and *Vipera ursinii* in sympatry (defined SYM) and in allopatry (defined ALL). Means are presented for both sexes pooled and separated. Overall, there were statistically significant SVL differences between species, sexes, and between populations SYM and ALL (one-way AVOVA—$F_{7,205}$ = 31.929, $P < 0.0001$). P-values derived for Tukey HSD post-hoc comparisons of paired samples are given in the table, below each compared pairs. Statistical significance in these comparisons is in boldface.

	SVL	N
SEXES POOLED		
V. aspis SYM	58.33 ± 10.46	24
V. ursinii SYM	37.84 ± 6.46	40
P < 0.0001		
V. aspis ALL	58.73 ± 9.18	67
V. ursinii ALL	35.64 ± 14.36	82
P < 0.0001		
SEXES SEPARATED		
V. aspis male SYM	56.96 ± 12.49	14
V. aspis female SYM	60.25 ± 6.90	10
P = 0.996		
V. aspis male ALL	57.03 ± 9.73	35
V. aspis female ALL	60.59 ± 8.29	32
P = 0.999		
V. ursinii male SYM	31.58 ± 5.32	13
V. ursinii female SYM	40.86 ± 4.54	27
P < 0.0001		
V. ursinii male ALL	33.41 ± 20.27	37
V. ursinii female ALL	37.49 ± 6.00	45
P < 0.0001		

altitude in other parts of Gran Sasso National Park.

In general, the results from the present study confirm findings obtained in previous population studies of *V. ursinii* and *V. aspis* (e.g., a substantial difference in diet, habitat choice, SVL, and sexual size dimorphism [Bruno, 1985; Luiselli and Agrimi, 1991; Agrimi and Luiselli, 1992; Capizzi and Luiselli, 1996; Filippi and Luiselli, 2004]). More interesting, we did not detect any effect on SVL between allopatric and sympatric viper populations. Both in experimental and wild populations, interspecific competition for prey may affect traits such as growth rates and body size (Mokany and Shine, 2003; Luiselli, 2006a). Therefore, we suggest that the lack of any effects of sympatry and allopatry on SVL in the present study is most likely caused by the very low overlap in diet recorded among the two species, but the reverse may obviously be true.

Our results demonstrate a profound habitat partitioning of the two vipers; hence, mirrors results obtained in other sympatric viper populations such as *V. aspis* and *V. berus* in France (e.g., Saint Girons, 1975) and in Switzerland (Monney, 1996), and in three species of sympatric vipers in the Italian Alps (i.e., *V. aspis*, *V. berus*, and *Vipera ammodytes*; Lapini, 1983). In the latter studies, the diets of the different sympatric taxa were quite similar (Saint Girons, 1975; Monney, 1996); hence, habitat partitioning has been suggested to reduce interspecific competition for food (Luiselli, 2006a). In contrast to previous studies, the results of the present study reveal a significant difference in diet of the two vipers. These considerable differences in the diets of the vipers (either using prey numbers of percentage or snakes containing a given prey type) cannot be attributed to the fact that the timing of collection of the specimens can greatly influence the prey type found. Indeed, although some prey items were clustered at certain times in the year (for instance, Orthoptera during summertime; see Agrimi and Luiselli, 1992), the foraging period of both species is virtually restricted to late June to mid-September because of the very cold climatic conditions (night temperatures being often below 0°C). Hence, the timing of collection of dietary items was identical for the two species and cannot explain the observed differences between the species. Thus, we conclude that the two species differed in their partitioning of altitude distribution, habitat, and diet, showing an overall low overlap in their realized niches.

Our study presents aspects that were both expected and unexpected on the basis of the literature available on temperate zone snakes, with particular reference to Viperidae species (see Luiselli, 2006a). The expected result is that our two *Vipera* species clearly partitioned the spatial resource (both the elevational gradient and the microhabitat), this fact being in agreement with evidence from other *Vipera* species from Europe (e.g., Saint Girons, 1975; Monney, 1996), as well as from *Crotalus* from North America (e.g., Pough, 1966; Beck, 1995), that is, with the predicted patterns of coexistence of Viperidae (Orlov, 1997; Luiselli, 2006a,b). The unexpected result is that our two species also clearly partitioned the trophic resource, which is uncommon in Viperidae (but see Luiselli and Akani, 2003; Luiselli, 2006c) and especially in European snake communities, where the coexisting species tend to feed on the same prey types, perhaps subtly partitioning the prey size (Luiselli, 2006a). It would be interesting to study other systems similar to that studied here to verify whether the patterns highlighted in this study may be applied to other comparable systems.

LITERATURE CITED

AGRIMI, U., AND L. LUISELLI. 1992. Feeding strategies of the viper *Vipera ursinii ursinii* (Reptilia, Viperidae) in the Appennines. Herpetological Journal 2:37–42.

BECK, D. D. 1995. Ecology and energetics of three sympatric rattlesnake species in the Sonoran Desert. Journal of Herpetology 29:211–223.

BOMBI, P., A. LYET, L. LUISELLI, F. CORSI, M. CHEYLAN, E. FILIPPI, A. K. SKIDMORE, A. G. TOXOPEUS, AND M. A. BOLOGNA. 2006. Modelling the potential western range of the meadow viper, *Vipera ursinii*. *In* M. A. Bologna, M. Capula, G. M. Carpaneto, L. Luiselli, C. Marangoni, and A. Venchi, A. (eds.), Proceedings del 6th Congresso Nazionale della Societas Herpetologica Italica, pp. 141–142. Stilgrafica, Roma.

BRITO, J. C., AND E. G. CRESPO. 2002. Distributional analysis of two vipers (*Vipera latastei* and *V. seoanei*) in a potential area of sympatry in the northwestern Iberian peninsula. *In* G. W. Schuett, M. Höggren, M. E. Douglas, and H. W. Greene (eds.), Biology of the Vipers, pp. 129–138. Eagle Mountain Publishing, Eagle Mountain, UT.

BRUNO, S. 1985. Le vipere d'Italia e d'Europa. Edagricole, Bologna, Italy.

CAPIZZI, D., AND L. LUISELLI. 1996. Feeding relationships and competitive interactions between phylogenetically unrelated predators (owls and snakes). Acta Oecologica 17:265–284.

DI LENA, E. 2006. Studio di un possibile caso di competizione interspecifica tra *Vipera aspis* e *Vipera ursinii* in alcuni siti del Parco Nazionale del Gran Sasso-Monti della Laga, Abruzzo. Unpublished Master Thesis, University of L' Aquila, Italy.

FEINSINGER, P., E. E. SPEARS, AND R. W. POOLE. 1981. A simple measure of niche overlap. Ecology 62:27–32.

FILIPPI, E., AND L. LUISELLI. 2002. *Vipera ursinii ursinii* nel Parco Nazionale del Gran Sasso-Monti della Laga. Unpublished Report, Gran Sasso-Monti della Laga National Park, Assergi (AQ), Italy.

———. 2004. Ecology and conservation of the Meadow viper, *Vipera ursinii*, in three protected mountainous areas in central Italy. Italian Journal of Zoology 71 (suppl. 2): 159–161.

FILIPPI, E., L. RUGIERO, M. CAPULA, D. CAPIZZI, AND L. LUISELLI. 2005. Comparative food habits and body size of five populations of *Elaphe quatuorlineata*: the effects of habitat variation, and the consequences of intersexual body size dimorphism on diet divergence. Copeia 2005:517–525.

GOTELLI, N. J., AND G. R. GRAVES. 1996. Null Models in Ecology. Smithsonian Institution Press, Washington, DC.

LAPINI, L. 1983. Anfibi e rettili (del Friuli Venezia Giulia). Carlo Lorenzini Editore, Udine, Italy.

LAURENT, E. J., AND B. A. KINGSBURY. 2003. Habitat separation among three species of water snakes in Northwestern Kentucky. Journal of Herpetology 37:229–235.

LUISELLI, L. 2004. Meadow viper, *Vipera ursinii*, in Italy: aspects of conservation ecology (Reptilia, Viperidae). Italian Journal of Zoology 71 (suppl. 1): 167–172.

———. 2006a. Resource partitioning and interspecific competition in snakes: the search for general geographical and guild patterns. Oikos 114: 193–211.

———. 2006b. Site occupancy and density of sympatric Gaboon viper (*Bitis gabonica*) and nose-horned viper (*Bitis nasicornis*). Journal of Tropical Ecology 22:555–564.

———. 2006c. Food niche overlap between sympatric potential competitors increases with habitat alteration at different trophic levels in rain-forest reptiles (omnivorous tortoises and carnivorous vipers). Journal of Tropical Ecology 22:695–704.

LUISELLI, L., AND U. AGRIMI. 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., AND G. C. AKANI. 2003. Diet of sympatric Gaboon Vipers (*Bitis gabonica*) and Nose-Horned Vipers (*Bitis nasicornis*) in southern Nigeria. African Journal of Herpetology 52:101–106.

MADSEN, T. 1988. Reproductive success, mortality and sexual size dimorphism in the adder, *Vipera berus*. Holarctic Ecology 11:77–80.

MADSEN, T., AND R. SHINE. 1992a. A rapid sexually-selected shift in mean body sizes in a population of snakes. Evolution 46:1220–1224.

———. 1992b. Sexual competition in brothers may influence offspring sex ration in snakes. Evolution 46:1549–1552.

———. 1992c. Determinants of reproductive success in female adders, *Vipera berus*. Oecologia 92:40–47.

MADSEN, T., AND B. STILLE. 1988. The effect of size dependent mortality on colour morphs in male adders, *Vipera berus*. Oikos 52:73–78.

MALLOW, D., D. LUDWIG, AND G. NILSON. 2003. True vipers: natural history and toxinology of Old World vipers. Krieger Publishing Company, Malabar, FL.

MARTINEZ, F., J. C. BRITO, AND M. LIZANA AVIA. 2006. Intermediate forms and syntopy among vipers (*Vipera aspis* and *V. latastei*) in Northern Iberian Peninsula. Herpetological Bulletin 97:14–18.

MOKANY, A., AND R. SHINE. 2003. Competition between tadpoles and mosquito larvae. Oecologia 135: 615–620..

MONNEY, J. C. 1996. Biologie comparée de *Vipera aspis* L. et de *Vipera berus* L. (Reptilia, Ophidia, Viperidae) dans une station des Prealpes Ber-

noises. Unpubl. Ph.D. diss., University of Neuchatel, Neuchatel, Switzerland.

ORLOV, N. L. 1997. Viperid snakes (Viperidae Bonaparte, 1840) of Tam-Dao mountain ridge (Vinh-Phu and Bac-Thai Provinces, Vietnam). Russian Journal of Herpetology 4:64–74.

PIANKA, E. R. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4:53–74.

POUGH, F. H. 1966. Ecological relationships of rattlesnakes in southeastern Arizona with notes on other species. Copeia 1966:676–683.

RODRIGUEZ-ROBLES, J. A., AND H. W. GREENE. 1999. Food habits of the long-nosed snake (*Rhinocheilus lecontei*), a ''specialist'' predator? Journal of Zoology, London 248:489–499.

RODRIGUEZ-ROBLES, J. A., C. J. BELL, AND H. W. GREENE. 1999a. Gape size and evolution of diet in snakes: feeding ecology of erycine boas. Journal of Zoology, London 248:49–58.

———. 1999b. Food habits of the Glossy Snake, *Arizona elegans*, with comparisons to the diet of the sympatric Long-Nosed Snakes, *Rhinocheilus lecontei*. Journal of Herpetology 33:87–92.

SAINT-GIRONS, H. 1952. Écologie et ethologie des vipères de France. Annales des Sciences Naturelles, Zoologie 14:263–343.

———. 1975. Coexistence de *Vipera aspis* et de *Vipera berus* en Loire-Atlantique: un problème de compétition interspécifique. Revue d' Ecologie (Terre et Vie) 29:590–613.

———. 1978. Thermorégulation comparée des Vipères d' Europe. Revue d' Ecologie (Terre et Vie) 32:417–440.

———. 1980. Le cycle des mues chez les vipères européennes. Bulletin de la Société Zoologique de France 105:551–559.