

Variation in the diet of the Lataste's viper *Vipera latastei* in the Iberian Peninsula: seasonal, sexual and size-related effects

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Abstract—Several life-history traits may increase vulnerability of species to extinction. Among snakes, ambush predation and dietary specialisation are factors that increase this vulnerability. European viper species, genus *Vipera*, display such traits and are categorised as endangered in several parts of its range. For their conservation management, a deeper knowledge of their ecology and habitat use is highly relevant. One of the species with less ecological data is the Lataste's viper *Vipera latastei*, a species which lives in the Iberian Peninsula and northwestern Africa. Here, we describe its diet based on the analysis of gut content of 435 museum specimens plus nine bibliographic data from the entire Iberian range. The species showed seasonal and ontogenetic shift in diet but no sexual variations. Feeding activity (percentage of vipers with prey) was low in accordance with its ambush predation tactics, being lower in spring than in summer and autumn. Prey spectrum included two main (reptiles and small mammals), and three sporadic, types of prey (arthropods, amphibians and birds). The consumption of reptiles and mammals was seasonal; the former decreased in occurrence from spring to autumn, whereas the latter showed an opposite pattern. There was an ontogenetic shift in the diet: juveniles fed mainly on reptiles and arthropods, whereas adult vipers progressively substitute this prey with insectivores, and the largest vipers primarily foraged on rodents and birds. Our results suggest that the seasonal variation in prey type was related to prey availability, whereas the ontogenetic shift was linked to gape limitation. The apparently wide prey spectrum of *V. latastei* must therefore be examined, taking into account that there are seasonal and ontogenetic dietary variations as well as geographic differences, the latter probably driven by climatic contrasts into the Iberian Peninsula. This new data of the endangered Iberian *V. latastei* can aid the effective conservation management of this species.

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INTRODUCTION

The Lataste's viper, *Vipera latastei* (fig. 1), is among the most threatened snake species in the Iberian Peninsula: its IUCN category is Near Threatened in Spain and Vulnerable in Portugal (Pleguezuelos and Santos, 2002; Oliveira et al., 2005). Apart from habitat destruction, life-history traits of this European viper are probably contributing to its vulnerability to extinction (Santos et al., 2006a). Previous studies suggest that *V. latastei* is an ambush predator relying on sit-and-wait foraging strategy for capturing prey and that both juvenile and adult vipers are dietary specialists (Bea and Braña, 1988; Brito, 2004). Numerous studies have shown that both sit-and-wait and dietary specialisation increase the proneness of snake species to become extinct (Filippi and Luiselli, 2000; Webb et al., 2002; Reed and Shine, 2002). Because of this, increasing the knowledge of this species' life-history traits is an important concern for conservation management.

The current available knowledge of the dietary habits of *V. latastei* is based on small samples (N = 75 specimens, 40 prey items; Bea and Braña, 1988), or focused on a small geographic area in a peripheral region of its distribution range (Brito, 2004). In the present study, we describe the diet composition of *V. latastei*, analysing



Figure 1. Male *Vipera latastei* (298 mm snout-vent length) from the Garraf Natural Park, NE Iberian Peninsula.

sample data of 444 specimens (435 museum vouchers plus nine bibliographic data) and covering the entire range of the species in the Iberian Peninsula. Specific aims are to determine sexual and seasonal differences, as well as ontogenetic shifts in this viper's diet.

MATERIALS AND METHODS

Study animals

We examined the gut content of 435 preserved specimens of *Vipera latastei* from the following collections: Museu Bocage, Lisbon University (MBL, one specimen), Museu de História Natural, Porto University (MHN, three specimens), Departamento de Biología Animal y Ecología, Granada University (DBAG, 43 specimens), Departament de Biologia Animal, Barcelona University (DBAUB, 15 specimens), Museo Nacional de Ciencias Naturales, Madrid (MNCN, 206 specimens), Museu de Ciències Naturals of Barcelona (MCNB, six specimens), Estación Biológica de Doñana, Seville (EBD, 45 specimens), Instituto Pirenaico de Ecología, Jaca (IPE, four specimens), and Monestir de Montserrat (MMO, two specimens), and the private collection of J.C. Brito (JCB, 110 specimens). Published data were included when sex and size of vipers were known (Valverde, 1967, $n = 9$). Sex was determined by direct observation of gonads, and individuals were considered sexually mature when the snout-vent length (SVL) exceeded 240 mm for males and 260 mm for females (Pleguezuelos et al., in press). We checked vipers only from the Iberian Peninsula because specimens from the remaining distribution area of the species (north-western Africa) were almost absent in museums. Partial sample sizes were not coincident always with total sample size because of: i) some museum vouchers did not have the date of collection, preventing them from being included in the seasonal analysis; ii) sex was not determined for some adult specimens, hence, adult diet was not precisely the total of male and female diets; iii) three preserved vipers showed dilated stomachs which indicated the presence of a recent feed although prey had been removed.

Determination of prey

Stomach content was checked by a mid-ventral incision, and prey was determined to species level where possible. In the intestine, usually only undigested parts of prey were found; exoskeletons of arthropods, body and tail scales from reptiles, hair from mammals, and feathers from birds. Reptile scales found in the intestine were determined by comparison with specimens of the collection at the University of Granada. For mammals, hair was determined by comparison to specimens of the collection at the University of Granada and using specialised guides (Debrot, 1982; Teerink, 1991). Hair from micro-mammals and scales from lizards have low morphological variation in species of the same genus. For this reason, determination

at specific level through gut remains was not possible for pairs of species which show sympatric distributions in the Iberian Peninsula (i.e., *Microtus* and *Sorex* species; Palomo and Gisbert, 2002). Hence, genus was used as the unit for statistical analysis in reptile and mammal prey, although determination to species level was possible in several cases.

Snout-vent length (SVL) of vipers was measured by a cord extended along the mid-dorsal line of the body. As SVL of vipers ranged from 150 to 550 mm, all specimens were grouped into four 100 mm SVL categories, the smallest one being equivalent to the immature category (150-250 mm SVL). The ontogenetic shift in the diet of *V. latastei* was analysed by means of variation in these body size categories in the occurrence of each prey type.

Statistical analysis

We performed a logistic regression analysis to assess which factors influence the presence of prey in the digestive content of vipers. For each viper, we considered the size-class category (see above), date of collection (season), and sex. The logistic regression models (Hosmer and Lemeshow, 1989) determine how several predictors influence the probability of a binomial distribution variable (in this study, presence or absence of prey items). The effectiveness of the model (Peng et al., 2002) was assessed globally by a χ^2 test (i.e., if there is association between the predictors and the dependent variable for $P > 0.20$). The significance of the regression coefficients of predictors (β s) was evaluated individually by Wald χ^2 tests. We performed a stepwise logistic regression, removing predictors of Wald χ^2 scores with $P > 0.05$. The effectiveness of the final model was assessed by a Hosmer-Lemeshow test (i.e., the adjustment of data to the final model was poor when $P < 0.05$, Peng et al., 2002). Logistic regressions were made with the SPSS software.

RESULTS

Feeding activity

Almost half of the sample (46% of vipers, $n = 204$ specimens) had prey in the digestive tract, most of them having a single prey (90.7%). There were seasonal differences in feeding activity: specimens collected in summer (57% of 184 specimens) and autumn (52% of 107 specimens) had prey more frequently than specimens collected in spring (25% of 109 specimens) and pairwise comparisons also showed significant differences (spring-summer: $\chi^2 = 27.92$, $P < 0.001$; spring-autumn $\chi^2 = 17.34$, $P < 0.001$). A similar pattern was observed when adult and immature vipers were separately examined, feeding activity in both groups being higher in summer and autumn than in spring. No sexual differences were detected in the percentage of vipers with prey ($\chi^2 = 1.60$, $P = 0.21$). By seasons, feeding activity for both sexes was similar in spring (males 22.8%, $n = 57$ and

females 29.4%, $n = 34$; $\chi^2 = 0.49$, $P = 0.48$) and summer (males 60.0%, $n = 55$ and females 54.6%, $n = 77$; $\chi^2 = 0.39$, $P = 0.53$). In autumn, the percentage of vipers with prey differed between sexes (males 45.2%, $n = 62$ and females 65.4%, $n = 26$), with statistical differences being nearly significant ($\chi^2 = 3.00$, $P = 0.08$), hence suggesting higher feeding activity for females in this season.

The stepwise logistic regression model identified the variable 'season' as the only predictor explaining the feeding activity of vipers. Globally, the association between the predictor and the dependent variable was good ($\chi^2 = 36.37$, d.f. = 2, $P < 0.0001$) and resulted in 62.3% of correct predictions of presence/absence of prey items. The effectiveness of the final model was excellent (Hosmer-Lemeshow $\chi^2 = 0.0$, d.f. = 1, $P = 1.0$). As the predictor was a categorical variable, results of the logistic regression indicated a low odds ratio for the 'spring' category (B coefficient = -1.259 , Wald $\chi^2 = 18.339$, $P < 0.0001$, odds ratio = 0.284) and opposite results for the 'summer' category (B coefficient = 0.244, Wald $\chi^2 = 0.996$, $P = 0.318$, odds ratio = 1.276). These results indicated a low probability of finding prey items in vipers collected in spring and a high probability of finding them in summer.

Dietary composition

A total of 222 prey items corresponding to five major taxa were determined. Mammals and reptiles were the main prey consumed (57.2% and 32.9% of occurrence, respectively), whereas birds (5.0%), arthropods (3.6%) and amphibians (1.4%) were consumed in lower proportions (table 1). No sexual differences were detected in the occurrence of each prey type ($\chi^2 = 2.83$, d.f. = 4, $P = 0.59$; table 1). On the contrary, diet composition of adult vipers varied by season ($\chi^2 = 16.00$, d.f. = 8, $P = 0.04$), the main difference being an increase of mammals in the autumn diet compared to spring, and opposite patterns in the occurrence of reptiles (fig. 2).

Arthropods (mainly centipedes of the genus *Scolopendra*) were predated both by adult and immature vipers (table 1). Six genera of lizards were detected in the diet of *V. latastei*, with the genus *Podarcis* being the most represented (table 1). The Iberian wall lizard *P. hispanica* was the most common reptile in the diet, probably because of its wide range in the Iberian Peninsula, although the other three Iberian *Podarcis* species (i.e., *P. carbonelli*, *P. bocagei* and *P. muralis*) were also consumed. Birds were consumed only by adult vipers (table 1). Seven genera of small mammals were detected in the diet of *V. latastei*: four rodents (*Arvicola*, *Apodemus*, *Microtus*, *Mus*) and three insectivores (*Crocidura*, *Sorex*, *Suncus*). However, only three of them were common in the diet (table 1): the insectivore *Crocidura russula*, and the rodent *Apodemus sylvaticus*, both of which are widely distributed across the Iberian Peninsula, and rodents of the genus *Microtus*, which were represented by six species with partially sympatric distribution in the Iberian Peninsula (Palomo and Gisbert, 2002).

Table 1.

Occurrence (and number of items) of the different prey types in the diet of adults and immature *Vipera latastei* in the Iberian Peninsula. Only genus is quoted when more than one species of the same genus could be preyed upon. Diet of adult males (n = 89) plus adult females (n = 81) did not coincide with the total adult diet (n = 179) as eight museum vouchers with identified prey (one of them with two prey) were not able to be sexed.

	Adult ♂♂		Adult ♀♀		Adults		Immature	
	n	%	n	%	n	%	n	%
Arthropods	1	1.1	2	2.5	3	1.7	5	11.6
Amphibians	2	2.2	1	1.2	3	1.7	0	0.0
Reptiles								
<i>Blanus cinereus</i>	1	1.1	0	0.0	1	0.6	0	0.0
<i>Chalcides</i> sp.	0	0.0	1	1.2	1	0.6	0	0.0
<i>Acanthodactylus erythrurus</i>	1	1.1	0	0.0	2	1.1	0	0.0
<i>Psammmodromus algirus</i>	2	2.2	2	2.5	5	2.8	7	16.3
<i>Lacerta lepida</i>	3	3.4	0	0.0	3	1.7	1	2.3
<i>Podarcis</i> sp.	12	13.5	13	16.0	25	14.0	28	65.1
Total reptiles	19	21.3	16	19.8	37	20.7	36	83.7
Birds								
<i>Erithacus rubecula</i>	0	0.0	1	1.2	1	0.6	0	0.0
<i>Oenanthe oenanthe</i>	0	0.0	0	0.0	1	0.6	0	0.0
<i>Phalloscopus bonelli</i>	0	0.0	1	1.2	1	0.6	0	0.0
Unidentified birds	3	3.4	5	6.2	8	4.5	0	0.0
Total birds	3	3.4	7	8.6	11	6.1	0	0.0
Mammals								
Insectivores								
<i>Crocidura russula</i>	15	16.9	11	13.6	27	15.1	0	0.0
<i>Sorex</i> sp.	0	0.0	5	6.2	5	2.8	1	2.3
<i>Suncus etruscus</i>	2	2.2	0	0.0	2	1.1	0	0.0
Soricidae not identified	1	1.1	1	1.2	2	1.1	1	2.3
Rodents								
<i>Apodemus sylvaticus</i>	13	14.6	14	17.3	28	15.6	0	0.0
<i>Arvicola sapidus</i>	1	1.1	0	0.0	1	0.6	0	0.0
<i>Microtus</i> sp.	22	24.7	16	19.8	42	23.5	0	0.0
<i>Mus</i> sp.	6	6.7	2	2.5	8	4.5	0	0.0
Unidentified rodents	1	1.1	2	2.5	3	1.7	0	0.0
Unidentified mammals	3	3.4	4	4.9	7	3.9	0	0.0
Total mammals	64	71.9	55	67.9	125	69.8	2	4.7
Total	89		81		179		43	

Ontogenetic shift in the diet

Vipera latastei showed ontogenetic shift in the type of prey consumed (table 2): immature vipers fed mainly on reptiles (83.7% of 43 prey) whereas adult vipers foraged primarily on mammals (69.8% of 179 prey) ($\chi^2 = 68.7$, d.f. = 2, P =

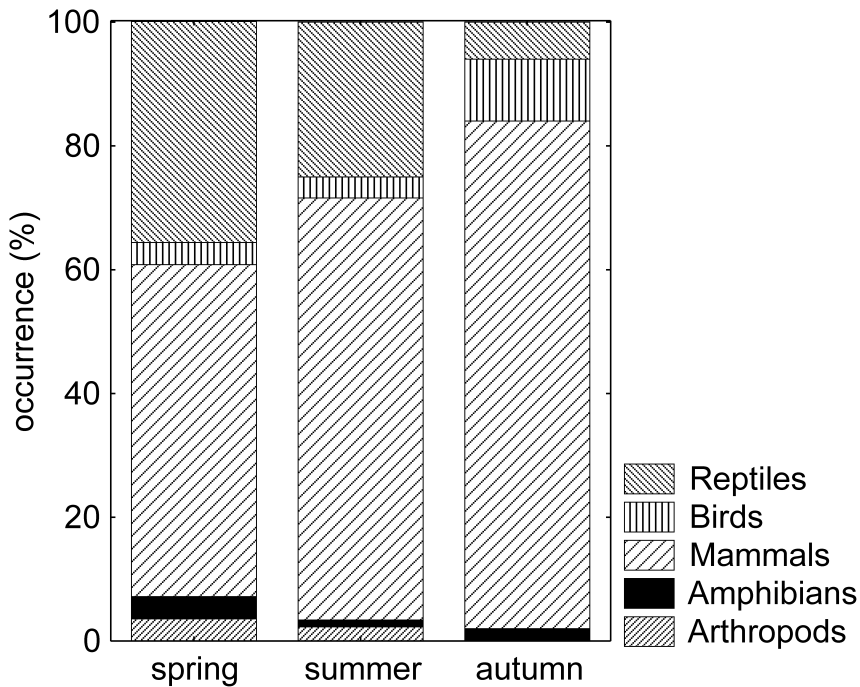


Figure 2. Seasonal variation in the diet of adult *Vipera latastei* in the Iberian Peninsula (males and females pooled by the lack of sexual differences) in relation to the five main prey types consumed.

0.00001). We detected a gradual change in the occurrence of the main prey types rather than an abrupt prey substitution (fig. 3). Reptiles were the main prey of the smallest snakes, whereas birds and rodents were consumed only by vipers larger than 250 mm SVL. Insectivores were consumed by all viper size categories, but the largest occurrence was at an intermediate viper size (fig. 3).

DISCUSSION

The reduced percentage of vipers with prey suggests a rather low feeding frequency in *V. latastei*, a similar pattern to other European vipers (Luiselli and Agrimi, 1991; Luiselli and Anibaldi, 1991; Agrimi and Luiselli, 1992; Saviozzi and Zuffi, 1997). This result agrees with Saint Girons (1979) who reported that the European male vipers fed only on three to five large prey per year. In part, this finding reflects the short effective feeding period of *V. latastei*. Under semi-natural conditions, Parellada (pers. obs.) observed that male *V. latastei* fed during only 3 months of the year (i.e., June-August), whereas females extended their feeding activity from April-May to October, with annual variations according to their reproductive status, i.e., higher feeding frequency in non-reproductive years. Saint Girons (1980a, 1981) reported that vipers did not feed until they shed in late spring. Under natural and semi-natural conditions, *V. latastei* shed in June (Brito, 2003; Parellada, pers.

Table 2.

Variation in the diet of *Vipera latastei* in the Iberian Peninsula according to four size-related categories. Snout-vent length (SVL) in mm.

	Viper size categories							
	<250 mm		251-350 mm		351-450 mm		>450 mm	
	n	%	n	%	n	%	n	%
Arthropods	5	11.9	1	2.2	2	2.7	0	0.0
Amphibians	0	0.0	1	2.2	1	1.4	1	2.3
Reptiles								
<i>Blanus cinereus</i>	0	0.0	0	0.0	1	1.4	0	0.0
<i>Chalcides</i> sp.	0	0.0	1	2.2	0	0.0	0	0.0
<i>Acanthodactylus erythrurus</i>	0	0.0	0	0.0	1	1.4	0	0.0
<i>Psammodromus algirus</i>	6	14.3	1	2.2	3	4.1	1	2.3
<i>Lacerta lepida</i>	0	0.0	2	4.4	1	1.4	1	2.3
<i>Podarcis</i> sp.	29	69.0	13	28.9	10	13.7	1	2.3
Total reptiles	35	83.3	17	37.8	16	21.9	3	7.0
Birds	0	0.0	1	2.2	3	4.1	6	14.0
Mammals								
Insectivores								
<i>Crocidura russula</i>	1	2.4	5	11.1	16	21.9	5	11.6
<i>Sorex</i> sp.	1	2.4	1	2.2	3	4.1	1	2.3
<i>Suncus etruscus</i>	0	0.0	1	2.2	1	1.4	0	0.0
Rodents								
<i>Apodemus sylvaticus</i>	0	0.0	6	13.3	11	15.1	10	23.3
<i>Arvicola</i>	0	0.0	0	0.0	0	0.0	1	2.3
<i>Microtus</i> sp.	0	0.0	8	17.8	18	24.7	14	32.6
<i>Mus</i> sp.	0	0.0	4	8.9	2	2.7	2	4.7
Total mammals	2	4.8	25	55.6	51	69.9	33	76.7
Total	41		45		73		43	
% of vipers with prey		47.8		55.4		45.9		44.5

obs.). These observations match well with the low percentage of snakes found with prey in spring (see logistic regression results), which has been previously reported for *V. latastei* in northern Portugal (Brito, 2004). In this rainy area, foraging activity is concentrated in summer due to the low autumnal temperatures (Brito, 2004). However, we did not observe this pattern when pooling data from all of the Iberian Peninsula. In fact, we found no differences in the percentage of vipers with prey between summer and autumn, suggesting that, in most areas of the Iberian Peninsula, autumn temperatures are favourable for foraging and digestion in vipers (Naulleau, 1982).

Sexual differences in feeding frequency (higher rates in females) appeared in autumn. This pattern was detected by Brito (2004) for northern Portugal, and has

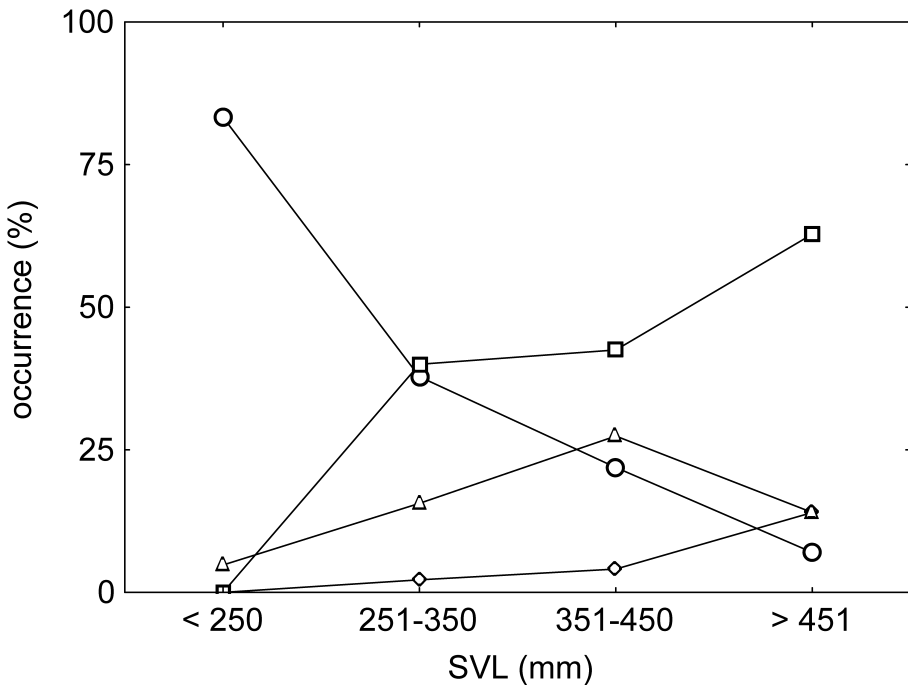


Figure 3. Size-related variation in the occurrence of the main prey taxa in the diet of *Vipera latastei* in the Iberian Peninsula (Circle: reptiles, Rhomb: birds, Triangle: insectivore mammals, Square: rodent mammals).

been observed in captive *V. latastei* under semi-natural conditions (Parellada, pers. obs.). In *V. aspis*, Zuffi et al. (1999) reported that females fed after reproduction to regain fat reserves quickly and hence to be potentially reproductive in the subsequent year. However, this autumnal activity was related to favourable climatic conditions, and northern populations of *V. aspis* did not feed in autumn and consequently delayed reproduction (to a biannual frequency) until attaining a minimum fat-body mass (Bonnet and Naulleau, 1996; Saint Girons, 1996). Thus, feeding activity in female vipers is influenced by their reproductive status and probably driven by the need for females to regain fat reserves up to a threshold value for reproduction (Naulleau and Bonnet, 1996). Females of some *Vipera* species also fed during vitellogenesis (*V. aspis*, Lourdais et al., 2003; *V. latastei*, Pleguezuelos et al., 2007). This observation suggests a complex scenario to explain when a female viper needs to feed, and the role of long-term and short-term reserves to fuel reproduction (Lourdais et al., 2003).

The diet of *V. latastei* includes a high number of different prey types. This finding is in part due to the ontogenetic dietary differences experimented by this viper. In addition, there were seasonal differences in the diet of adult vipers: mammal occurrence increased from spring to autumn whereas reptile occurrence decreased. Seasonal differences in diet of snake species are usually related to

variation in prey availability (e.g., Santos et al., 2000, 2006b), and this is the most plausible explanation for *V. latastei*. In the Iberian Peninsula, lizards are less available in autumn, when reproduction has finished and for most species only juveniles are active (Carretero, 1993; Carretero et al., 2006). In the same way, amphibians were consumed in the rainiest Iberian region where they might be more available, although, not having undigested parts, amphibians could be potentially underrepresented since bones were also digested in the gut. Among birds, some prey species eat (*Erithacus rubecula*, *Oenanthe oenanthe*) or nest (*O. oenanthe*, *Philloscopus bonelli*) on the ground, hence facilitating predation by a ground ambush predator. A single observation exists of a *Mustela nivalis* preyed upon by an adult viper (López-Jurado and Ruiz-Caballero, 1981).

The Lataste's viper showed size-related shifts in the main prey consumed similar to that observed in other European vipers (Saint Girons, 1980b; Bea et al., 1992): immature individuals consumed arthropods and lizards, and, progressively, vipers substituted these prey types with insectivores and rodents when they grew. In fact, the dietary ontogenetic shift of *V. latastei* (fig. 3) suggests that this species can forage on at least ten different main prey types during its lifespan. Although this finding could be an artefact of some geographic differences in the Iberian Peninsula, the ontogenetic pattern obtained in our study when all Iberian vipers were pooled did not differ from that reported for *V. latastei* from Geres (Brito, 2004) or for other European vipers (Saint Girons, 1980b, 1983; Bea et al., 1992). The ontogenetic dietary shift must be driven by gape limitations of small individuals, as occurred in other snake species (Shine, 1991; Shine and Thomas, 2005): large vipers fed on large and wide prey (i.e., mammals and birds) whereas small vipers on small and thin prey (i.e., centipedes and lizards). Among small mammals as prey, insectivores were consumed by all viper size categories, although medium-sized adults (351-450 mm SVL) achieved the maximum consumption of these small mammals (fig. 3) due to their relative small size (*Suncus etruscus* is considered one of the smallest mammals in the world). Rodents are larger and wider than insectivores, and they were only consumed by snakes larger than 250 mm SVL, with occurrence greatest for the largest snakes (fig. 3). We suspect that relative differences in the feeding of insectivores and rodents among viper size categories are related to the size and/or shape of these prey types (see also Bea et al., 1992).

The ontogenic shifts detected in *V. latastei* (i.e., larger vipers fed on larger, wider and heavier prey than small vipers) should in part be driven by the larger snakes' requirement for more food to respond to the competing demands of growth, maintenance and reproduction (Madsen and Shine, 2002). *Vipera latastei* did not ontogenetically increase the number of prey eaten per year, i.e., there were no size-related difference in the percentage of vipers with prey (table 2). Consequently, more food could be obtained by foraging on larger prey and eliminating small prey from the diet. Why large vipers ignore small prey is probably controlled by multiple factors, some of them related to local relations between predators and prey (Shine,

1991; Webb and Shine, 1993; Shine and Thomas, 2005) and, ultimately, by the optimisation of foraging on profitable prey (Schoener, 1971; Arnold, 1993).

The present distribution of *V. latastei* in the Iberian Peninsula is mainly restricted to mountain chains as the species has become extinct in lowlands and valleys through human activities (Santos et al., 2006a). Its dietary specialisation, both at juvenile and adult stages, as well as other life-history traits, increases the vulnerability of the species and its proneness to local extinction. For this reason, conservation management of *V. latastei* must include habitat structure as well as demographic data of prey in localities where this Iberian viper is still present.

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REFERENCES

- Agrimi, U. & Luiselli, L. (1992) Feeding strategies of the viper *Vipera ursinii ursinii* (Reptilia: Viperidae) in the Apennines. *Herpetol. J.*, 2, 37-42.
- Arnold, S.J. (1993) Foraging theory and prey-size-predator-size relations in snakes. In: R.A. Seigel & J.T. Collins (Eds.), *Snakes. Ecology and Behavior*, pp. 87-116. McGraw-Hill.
- Bea, A. & Braña, F. (1988) Nota sobre la alimentación de *Vipera latastei*, Boscá, 1878 (Reptilia, Viperidae). *Munibe*, 40, 121-124.
- Bea, A., Braña, F., Barón, J.P. & Saint Girons, H. (1992) Régimes et cycles alimentaires des vipères européennes (Reptilia, Viperidae). *Ann. Biol.*, 31, 25-44.
- Bonnet, X. & Naulleau, G. (1996) Catchability in snakes: consequences for estimates of breeding frequency. *Can. J. Zool.*, 74, 233-239.
- Brito, J.C. (2003) Seasonal and daily activity patterns of *Vipera latastei* in northern Portugal. *Amphib.-Reptilia*, 24, 497-508.
- Brito, J.C. (2004) Feeding ecology of *Vipera latastei* in northern Portugal: ontogenetic shifts, prey size and seasonal differences. *Herpetol. J.*, 14, 13-19.
- Carretero, M.A. (1993) *Ecología de los lacértidos en arenales costeros del noreste ibérico*. Ph.D. Thesis, Universidad de Barcelona, Barcelona, Spain.
- Carretero, M.A., Ribeiro, R., Barbosa, D., Sá-Sousa, P. & Harris, D.J. (2006) Spermatogenesis in two Iberian *Podarcis* lizards: Relationships with male traits. *Anim. Biol.*, 56, 1-12.
- Debrot, S. (1982) *Atlas des Poils de Mammifères d'Europe*. Institut de Zoologie, Université de Neuchâtel, Neuchâtel, Suisse.
- Filippi, E. & Luiselli, L.M. (2000) Status of the Italian snake fauna and assessment of conservation threats. *Biol. Conserv.*, 93, 219-225.

- Hosmer, D.R. & Lemeshow, S. (1989) *Applied Logistic Regression*. John Wiley & Sons, Wiley Series in Probability and Mathematical Statistics, Canada.
- López-Jurado, L.F. & Ruiz-Caballero, M. (1981) Predación de *Vipera latastei* sobre *Mustela nivalis*. *Doñana, Acta Verteb.*, 8, 298-299.
- Lourdais, O., Bonnet, X., Shine, R. & Taylor, E. (2003) When does a reproducing female viper “decide” on her litter size? *J. Zool. Lond.*, 259, 123-129.
- Luiselli, L.M. & Agrimi, U. (1991) Composition and variation of the diet of *Vipera aspis francisciredi* in relation to age and reproductive stage. *Amphib.-Reptilia*, 12, 137-144.
- Luiselli, L.M. & Anibaldi, C. (1991) The diet of the adder (*Vipera berus*) in two alpine environments. *Amphib.-Reptilia*, 12, 214-217.
- Madsen, T. & Shine, R. (2002) Short and chubby or long and slim? Food intake, growth and body condition in free-ranging pythons. *Aust. Ecol.*, 27, 672-680.
- Naulleau, G. (1982) Action de la température sur la digestion chez les vipères espagnoles du genre *Vipera*. *Publ. Cent. Pir. Biol. Exp.*, 13, 89-94.
- Naulleau, G. & Bonnet, X. (1996) Body condition threshold for breeding in a viviparous snake. *Oecologia*, 107, 301-306.
- Oliveira, M.E. (Coord.), Brito, J.C., Dellinger, T., Ferrand de Almeida, N., Loureiro, A., Martins, H.R., Pargana, J., Paulo, O.S., Rito, P. & Teixeira, J. (2005) Répteis. In: M.J. Cabral, J. Almeida, P.R. Almeida, T. Dellinger, N. Ferrand de Almeida, M.E. Oliveira, J. Palmeirim, A.I. Queiroz, L. Rogado & M. Santos-Reis (Eds.), *Livro Vermelho dos Vertebrados de Portugal*, pp. 121-142. Instituto da Conservação da Naturaza, Lisboa.
- Palomo, L.J. & Gisbert, J. (Eds.) (2002) *Atlas de los Mamíferos terrestres de España*. Dirección General de Conservación de la Naturaleza-SECEM-SECEMU, Madrid, Spain.
- Peng, C.Y., Lee, K.L. & Ingersoll, G.M. (2002) An introduction to logistic regression analysis and reporting. *J. Educ. Res.*, 96, 3-15.
- Pleguezuelos, J.M. & Santos, X. (2002) *Vipera latastei*. In: J.M. Pleguezuelos, R. Márquez & M. Lizana (Eds.), *Atlas y Libro Rojo de los Anfibios y Reptiles de España*, pp. 298-300. Dirección General de Conservación de la Naturaleza & Asociación Herpetológica Española, Madrid.
- Pleguezuelos, J.M., Santos, X., Brito, J.C., Parellada, X., Llorente, G.A. & Fahd, S. (2007) Reproductive ecology of *Vipera latastei*, in the Iberian Peninsula: Implications for the conservation of a Mediterranean viper. *Zoology*, 110, 9-19.
- Reed, R.N. & Shine, R. (2002) Lying in wait for extinction: ecological correlates of conservation status among Australian elapid snakes. *Conserv. Biol.*, 16, 451-461.
- Saint Girons, H. (1979) Les cycles alimentaires des Vipères européennes dans des conditions semi-naturelles. *Ann. Biol. Anim., Biochim. Biophys.*, 19, 125-134.
- Saint Girons, H. (1980a) Le cycle des mues chez les vipères européennes. *Bull. Soc. Zool. Fr.*, 105, 551-559.
- Saint Girons, H. (1980b) Modifications sélectives du régime des vipères (Reptilia: Viperidae) lors de la croissance. *Amphib.-Reptilia*, 1, 127-136.
- Saint Girons, H. (1981) Cycle annuel et survie de quelques vipères d'Europe. Influence des températures exceptionnellement élevées de l'année 1976. *Vie Milieu*, 31, 59-64.
- Saint Girons, H. (1983) Régime et rations alimentaires des serpents. *Bull. Soc. Zool. Fr.*, 108, 431-437.
- Saint Girons, H. (1996) Structure et évolution d'une petite population de *Vipera aspis* (L.) dans une région de bocage de l'ouest de la France. *Rev. Ecol. Terre Vie*, 51, 223-241.
- Santos, X., González-Solís, J. & Llorente, G.A. (2000) Variation in the diet of the viperine snake *Natrix maura* in relation to prey availability. *Ecography*, 23, 185-192.
- Santos, X., Brito, J.C., Sillero, N., Pleguezuelos, J.M., Llorente, G.A., Fahd, S. & Parellada, X. (2006a) Inferring conservation status with ecological modelling techniques and GIS: an application with *Vipera latastei* in the Iberian Peninsula. *Biol. Conserv.*, 130, 416-425

- Santos, X., Vilardebó, E., Casals, F., Llorente, G.A., Vinyoles, D. & de Sosota, A. (2006b) Wide food availability favors intraspecific trophic segregation in predators: the case of a water snake in a Mediterranean river. *Anim. Biol.*, 56, 299-309.
- Saviozzi, P. & Zuffi, M.A.L. (1997) An integrated approach to the study of the diet of *Vipera aspis*. *Herpetol. Rev.*, 28, 23.
- Schoener, T.W. (1971) Theory of feeding strategies. *Annu. Rev. Ecol. Syst.*, 2, 369-404.
- Shine, R. (1991) Why do larger snakes eat larger prey items? *Funct. Ecol.*, 5, 493-502.
- Shine, R. & Thomas, J. (2005) Do lizards and snakes differ in their ability to take large prey? A study of relative prey mass and feeding tactics in lizards. *Oecologia*, 144, 492-498.
- Teerink, B.J. (1991) *Hair of West-European Mammals*. Cambridge University Press, Cambridge.
- Valverde, J.A. (1967) *Estructura de Una Comunidad Mediterránea de Vertebrados Terrestres*. Monografías de Ciencias Modernas 1, CSIC, Madrid.
- Webb, J.K. & Shine, R. (1993) Pre-size selection, gape limitation and predator vulnerability in Australian blindsnakes (Typhlopidae). *Anim. Behav.*, 45, 1117-1126.
- Webb, J.K., Brook, B.W. & Shine, R. (2002) What makes a species vulnerable to extinction? Comparative life-history traits of two sympatric snakes. *Ecol. Res.*, 17, 59-67.
- Zuffi, M.A.L., Guidici, F. & Ioalè, P. (1999) Frequency and effort of reproduction in female *Vipera aspis* from a southern population. *Acta Oecol.*, 20, 633-638.