

# Prey availability drives geographic dietary differences of a Mediterranean predator, the Lataste's viper (*Vipera latastei*)

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Species that inhabit regions with highly contrasting environmental conditions often exhibit geographic variation in diet as a consequence of differences in prey availability among populations. The Lataste's viper *Vipera latastei* is an ambush predator that lives in regions of the Iberian Peninsula varying from extremely dry (170 mm annual rainfall) to very rainy (3000 mm). Given this high adaptability, we expect interpopulational differences in its diet. We examined the gut content of 347 preserved adult specimens from the entire Iberian range deposited in museum collections. There were geographic differences in the consumption of the two main prey types, small mammals and reptiles. Logistic regression results indicate that three climatic variables (annual rainfall, average temperature and average radiation) explain the consumption of reptiles or small mammals by adult vipers: vipers preferentially forage on small mammals in wet, cold and cloudy areas, but combine the consumption of reptiles and small mammals in dry, hot and sunny ones. As small mammal species diversity and abundance in the Iberian Peninsula increase with rainfall, our results suggest that the consumption of small mammals versus reptiles is driven by prey availability.

*Key words:* feeding ecology, Iberian Peninsula, Viperidae

## INTRODUCTION

Stephens & Krebs (1986) defined foraging as a sequential repetition of search–encounter decisions. These authors placed their theory in an energy context in which animals tend to maximize gains (energy from the prey) and minimize costs (search, handling and digestion). A myriad of different examples arise from this simple assumption, but an extreme and fascinating foraging habit appears in snakes: they generally feed on voluminous prey which are ingested whole, and digestion extends over a long time period (Greene, 1997). Among snakes, most pythons, boas and vipers feed sporadically, normally eating only a very few prey items over an annual cycle. Species with low feeding frequencies are expected to be selective in the consumption of prey, because nutritional benefits must exceed the costs associated with the feeding action. It could be suggested that these snake species will specialize in a few optimal prey types, thus exhibiting minor interpopulational variation in dietary habits (Luiselli, 2006). However, dietary diversity of a predator is influenced by the diversity of the available prey items (Iwasa et al., 1981), and high interpopulational variation will occur in snakes inhabiting regions associated with biodiversity hotspots (Luiselli, 2006). Therefore, species with wide geographic ranges and/or inhabiting regions with highly contrasting environmental conditions could also show interpopulational variation in diet composition

as a consequence of differences in prey availability among populations.

For these reasons, measuring prey availability helps to understand diet composition and prey selection (Santos et al., 2000, 2006b; Luiselli et al., 2007). Although measuring prey availability is not an easy task, especially in studies of a broad geographic scale or of generalist species with wide dietary habits, prey abundance can be estimated by indirect methods. Several climatic factors are directly correlated with the abundance of several vertebrate groups: for example, rainfall explains small mammal abundance throughout the Iberian Peninsula (Barbosa & Benzal, 1996), and temperature explains abundance and diversity of many reptile taxa (Schall & Pianka, 1978; Soares & Brito, 2007). Climatic variables are easily gathered using GIS tools, and how prey availability affects geographic variation in diet composition can be tested in multivariate analyses using several climatic factors as independent predictors.

European vipers (genus *Vipera*), whose dietary habits have been studied intensively, have been described as opportunistic predators (Bea et al., 1992). The primary prey of most viper species are small mammals (Braña et al., 1988; Bea & Braña, 1988; Luiselli & Agrimi, 1991; Luiselli & Anibaldi, 1991; Agrimi & Luiselli, 1992; Bea et al., 1992; Brito, 2004). Luiselli (2006) found high interpopulational similarity in diet composition within *Vipera* species. However, Bea et al. (1992) reported that diet was more similar in

nearby populations of two different species than in two distant populations of a single species. This suggested that species with a widespread distribution could have high interpopulational diet variation (Luiselli et al., 2001). Among the European vipers, *Vipera latastei* is an excellent model for examining geographic differences in diet. This viper inhabits almost the entire Iberian Peninsula as well as some mountain ranges of northwest Africa (Pleguezuelos & Santos, 2002; Stümpel et al., 2005). Within the Iberian range, it lives in strongly contrasting regions, from very dry (170 mm in Cabo de Gata, south-eastern Iberian Peninsula) to very rainy areas (more than 3000 mm in Gerês, north-western Iberian Peninsula) and from sea level (e.g. Doñana, southern Iberian Peninsula) up to 3000 m (Sierra Nevada, south-eastern Iberian Peninsula). The high diversity of environmental regions inhabited by *V. latastei* (Santos et al., 2006a), its foraging habits (i.e. ambush predator) and its rather eclectic diet (Santos et al., 2007) provide a good opportunity for measuring geographic dietary differences, using climatic variables as an indirect measure of the variation in prey availability.

## MATERIALS AND METHODS

### Viper samples and prey determination

We examined the digestive contents of 347 preserved *Vipera latastei* from the following collections: Museu Bocage, Lisbon University (MBL, 1 specimen), Museu de História Natural, Porto University (MHN, 2 specimens), Departamento de Biología Animal, Granada University (DBAG, 35 specimens), Departament de Biologia Animal, Barcelona University (DBAUB, 14 specimens), Museo Nacional de Ciencias Naturales, Madrid (MNCN, 156 specimens), Museu de Ciències Naturals of Barcelona (MCNB, 5 specimens), Estación Biológica de Doñana, Seville (EBD, 37 specimens), Institut Pirenaic de Ecologia, Jaca (IPE, 4 specimens), Monestir de Montserrat (MMO, 2 specimens) and the private collection of J.C. Brito (JCB, 91 specimens). Additional data from publications were included when sex, size and locality was known ( $n=8$ ; Valverde, 1967). Specimens without clear locality were removed from analyses.

We examined geographic dietary differences only for adult specimens. *Vipera latastei* exhibits a remarkable ontogenetic shift in the diet: immature vipers forage mainly on arthropods and small lizards, whereas adults have a more diverse diet, including lizards, amphibians, small mammals and birds (Bea & Braña, 1988; Brito, 2004; Santos et al., 2007). Consequently, pooling data from adult and immature vipers may obscure the geographic analysis. We checked sexual maturity by direct observation of the gonads, and we considered individuals sexually mature when the snout–vent length (SVL) exceeded 240 mm for males and 260 mm for females (Pleguezuelos et al., 2007).

We checked stomach contents via a mid-ventral incision and identified most prey to species level. In the intestine, only undigested parts of prey were usually found: exoskeleton for arthropods, scales for reptiles, hair

for mammals and feathers for birds. Reptile scales found in the intestine were determined by comparison with specimens in the collection at the University of Granada. For mammals, hair was determined by comparison with specimens in the University of Granada collection and using specialized guides (Debrot, 1982; Teerink, 1991). Groups with more than one species in the study area (i.e. *Microtus*, *Sorex*) were determined to genus level. Only birds found in the stomach were classified, as feathers found in intestine did not allow species determination.

### Statistical analysis

We analysed the geographic differences in the diet of adult *V. latastei* with two complementary statistical techniques.

First, a logistic regression analysis (Hosmer & Lemeshow, 1989) was used to determine how several predictors influence the probability of a binomial distribution. Adult *V. latastei* forages mainly on small mammals and reptiles (69.8% and 20.7% of prey, respectively), birds and amphibians being negligible prey items (6.1% and 1.7% of prey, respectively) (Santos et al., 2007). For this reason, we used the consumption of small mammals and reptiles as a dependent binomial variable. We considered five climatic variables (annual rainfall, annual average temperature, annual average radiation, annual average evapotranspiration and average air humidity in July) as predictors in the logistic analysis. We selected these variables as several authors have reported their influence on the abundance and diversity of reptiles and small mammals on a broad scale (Barbosa & Benzal, 1996; Schall & Pianka, 1978; Soares & Brito, 2007). We scored the five climatic variables in a grid cell of UTM 10 × 10 km from published Iberian Climate Atlases of Portugal and Spain (Font, 1983; CNA, 1983). We calculated values of the five variables in the localities where vipers were recorded, classifying vipers into two groups according to the prey consumed: small mammals and reptiles.

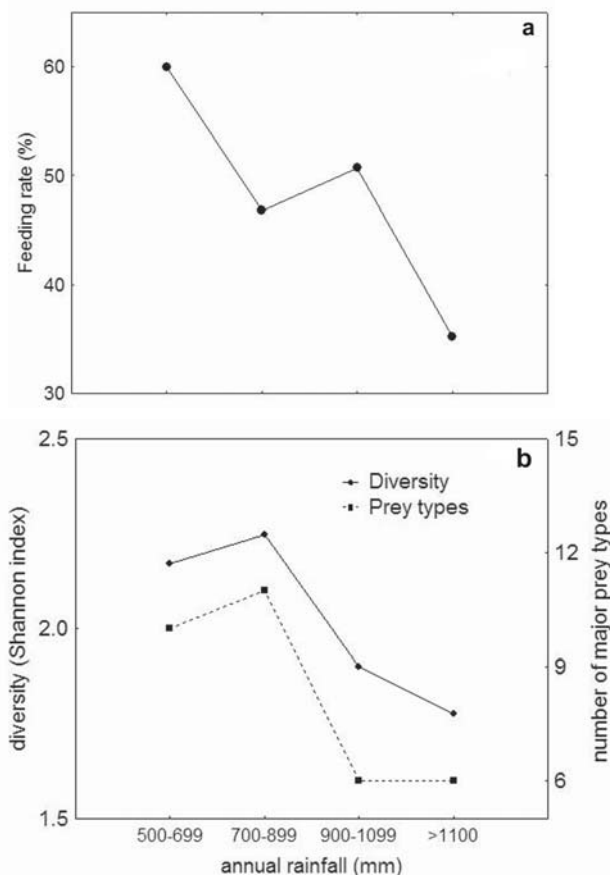
To assess the effectiveness of the logistic regression model (Peng et al., 2002) we first evaluated it overall by a  $\chi^2$  test (i.e. whether the predictors were associated with the dependent variable for  $P>0.20$ ). Afterwards, the significance of the regression coefficients of the predictors ( $\beta$ s) was evaluated individually by the Wald  $\chi^2$  test. We performed a stepwise logistic regression, removing predictors of Wald  $\chi^2$  scores with  $P>0.05$ , and the effectiveness of the final model was assessed by a Hosmer–Lemeshow test. The adjustment of data to the model was considered poor when  $P<0.05$  (Peng et al., 2002). Logistic regressions were done with SPSS software.

Logistic regression has often been used to model species distribution in plants (e.g. Calef et al., 2005) and animals (e.g. Segurado & Araújo, 2004; Venier et al., 2004). In the current study, we used logistic regressions as a mathematical tool to predict which factors affected the consumption of small mammals or reptiles by adult vipers. For the dependent variable (prey type), small mammals were coded as 0 and reptiles as 1. Units and range values of predictors were: annual rainfall (range 393–2557 mm), annual average temperature (range 7–19°C), annual aver-

**Table 1.** Mean and SD of climatic scores of localities with dietary records of small-mammal-eating and reptile-eating adult *Vipera latastei* in the Iberian Peninsula, and results of logistic regression to predict the prey type consumed by vipers based on the three climatic variables selected by the model. Some adult vipers were not sexed: for this reason, totals for males and females do not correspond to the total number of vipers.

| Variables                        | Small-mammal-eating vipers<br>( <i>n</i> = 121;<br>64 males, 55 females) |       | Reptile-eating vipers<br>( <i>n</i> = 35;<br>19 males, 16 females) |       | Logistic regression results |               |          |
|----------------------------------|--|-------|--|-------|-----------------------------|---------------|----------|
|                                  | Mean   | SD    | Mean   | SD    | B coefficient               | Wald $\chi^2$ | <i>P</i> |
| Rainfall (mm)                    | 1068.4   | 713.3 | 848.6  | 507.4 | 0.001                       | 3.6           | 0.057    |
| Temperature (°C)                 | 11.8   | 2.4   | 12.4   | 3.2   | -0.211                      | 4.9           | 0.027    |
| Radiation (Cal/cm <sup>2</sup> ) | 445.1  | 30.3  | 474.3  | 26.4  | 0.063                       | 19.4          | 0.0001   |
| SVL(mm)                          | 398.4  | 90.5  | 341.0  | 80.4  |                             |               |          |

age radiation (range 397–497 Cal/cm<sup>2</sup>), annual average evapotranspiration (range 393–880 mm) and average air humidity in July (range 52–85%). We calculated variance inflation factors (VIF) for explanatory variables, and variables with VIF larger than five were removed from the analysis because it indicates unsatisfactory levels of correlation among variables (Belsley et al., 1980).



**Fig. 1.** Variation in a) feeding rate (measured as the percentage of individuals with gut content) and b) trophic diversity (calculated by Shannon's diversity index) and number of prey types (genus as operative taxonomic unit) consumed by *Vipera latastei* in four areas of the Iberian Peninsula according to rainfall rates. Sample sizes for rainfall areas are given in Table 2.

Second, as small mammals constitute the prey type most consumed by adult vipers and rainfall is the climatic factor that best explains abundance of small mammals throughout the Iberian Peninsula (Barbosa & Benzal, 1996), we conducted a geographic analysis with this single climatic variable. We compared the diet of adult vipers grouped in rainfall classes according to the annual rainfall of localities where specimens were recorded. Adult vipers were grouped into four rainfall classes, each covering 200 mm of precipitation: 1) the driest area, with annual rainfall below 700 mm; 2) rainfall between 700 and 900 mm; 3) rainfall between 900 and 1100 mm; 4) the rainiest area, with rainfall higher than 1100 mm.

Dietary variation among the four rainfall classes was assessed by three diet descriptors: 1) the feeding rate, measured as the percentage of vipers with prey; 2) diet diversity measured by the Shannon diversity index; and 3) number of prey types using the genus level as the taxonomic unit. Most of the vipers used in this study are deposited in museum collections. After a recent meal, vipers are likely to be found basking to aid digestion and therefore are more visible and perhaps more easily captured. We assume then that feeding rate may be overestimated in specimens from museum collections although all the comparisons were made among rainfall classes, i.e. among sub-samples with the same bias.

## RESULTS

### Logistic regression results

The stepwise logistic regression model identified three climatic variables (annual rainfall, average temperature and average radiation) as the best predictors explaining the consumption of reptiles or small mammals by adult vipers (Table 1). VIF scores were lower than two for these three variables and hence none of them were removed from the final model. The other two variables, humidity in July and evapotranspiration, were removed in intermediate steps. Overall, the association between the three predictors and the dependent variable was good ( $\chi^2$  test = 33.7, *df*=3, *P*<0.0001) and resulted in 82.7% of correct predictions of prey type. The effectiveness of the final model was good (Hosmer–Lemeshow  $\chi^2$  test = 11.2, *df*=8, *P*=0.19).

Reptile-eating vipers were smaller than mammal-eating vipers (mammal-eating vipers: SVL=398.4±8.1; reptile-eat-

**Table 2.** Variation in small mammal and reptile items in the diet of adult *Vipera latastei* in four areas of the Iberian Peninsula according to annual rainfall rates. Data include number and percentage of occurrence of all prey items. For each group of vipers, SVL (in mm)  $\pm$  one standard error, SVL of the largest viper and number of males and females are given.

|                                   | Annual rainfall groups |                     |                      |                  |
|-----------------------------------|------------------------|---------------------|----------------------|------------------|
|                                   | <700mm<br>n (%)        | 700–899 mm<br>n (%) | 900–1099 mm<br>n (%) | >1100mm<br>n (%) |
| Arthropods                        |                        | 2 (4.0)             | 1 (2.6)              |                  |
| Amphibians                        |                        |                     | 1 (2.6)              | 2 (6.3)          |
| Reptiles                          |                        |                     |                      |                  |
| <i>Blanus cinereus</i>            |                        | 1 (2.0)             |                      |                  |
| <i>Chalcides</i> sp.              | 1 (1.7)                |                     |                      |                  |
| <i>Psammodromus algirus</i>       | 3 (5.1)                | 2 (4.0)             |                      |                  |
| <i>Lacerta lepida</i>             | 2 (3.4)                | 1 (2.0)             |                      |                  |
| <i>Podarcis</i> sp.               | 10 (17.0)              | 6 (12.0)            | 6 (15.8)             | 3 (9.4)          |
| <i>Acanthodactylus erythrurus</i> | 2 (3.4)                |                     |                      |                  |
| Birds                             | 5 (8.5)                | 3 (6.0)             | 3 (7.9)              |                  |
| Mammals                           |                        |                     |                      |                  |
| Insectivores                      |                        |                     |                      |                  |
| <i>Suncus etruscus</i>            | 1 (1.7)                |                     | 1 (2.6)              |                  |
| <i>Crocidura russula</i>          | 9 (15.3)               | 9 (18.0)            | 4 (10.5)             | 5 (15.6)         |
| <i>Sorex</i> sp.                  |                        | 2 (4.0)             | 1 (2.6)              | 2 (6.3)          |
| Unidentified insectivores         |                        | 2 (4.0)             |                      |                  |
| Rodents                           |                        |                     |                      |                  |
| <i>Microtus</i> sp.               | 13 (22.0)              | 12 (24.0)           | 14 (36.8)            | 3 (9.4)          |
| <i>Mus</i> sp.                    | 4 (6.8)                | 3 (6.0)             |                      | 1 (3.1)          |
| <i>Apodemus sylvaticus</i>        | 8 (13.6)               | 5 (10.0)            | 2 (5.3)              | 13 (40.6)        |
| <i>Arvicola sapidus</i>           |                        | 1 (2.0)             |                      |                  |
| Unidentified rodents              |                        |                     | 3 (7.9)              |                  |
| Unidentified mammals              | 1 (1.7)                | 1 (2.0)             | 2 (5.3)              | 3 (9.4)          |
| Total prey                        | 59                     | 50                  | 38                   | 32               |
| SVL $\pm$ S.E. (mm)               | 377.9 $\pm$ 12.9       | 390.1 $\pm$ 13.4    | 397.2 $\pm$ 13.4     | 396.4 $\pm$ 14.6 |
| SVL of the largest viper          | 640                    | 547                 | 550                  | 560              |
| Males/females                     | 31/23                  | 25/24               | 18/18                | 15/16            |

ing vipers: SVL=341.0 $\pm$ 13.2; Student t-test,  $t=3.47$ ,  $df=160$ ,  $P=0.001$ ).

### Differences among rainfall categories

Significant differences in SVL among the rainfall categories were not found (ANOVA,  $F_{175,3}=0.46$ ,  $P=0.7$ ), and there were no differences in the sex ratio in any group (all  $\chi^2$  tests,  $P>0.05$ ). The feeding rate (frequency of vipers with prey) tended to decrease with increasing rainfall (Fig. 1a), with significant differences among rainfall classes ( $\chi^2=11.76$ ,  $df=3$ ,  $P=0.008$ ). The trophic diversity and the number of prey items decreased with rainfall, although correlations were not significant (trophic diversity: Kendall–Tau correlation  $Z = -1.36$ ,  $P=0.17$ ; number of prey items:  $Z = -1.12$ ,  $P=0.26$ ; Fig. 1b).

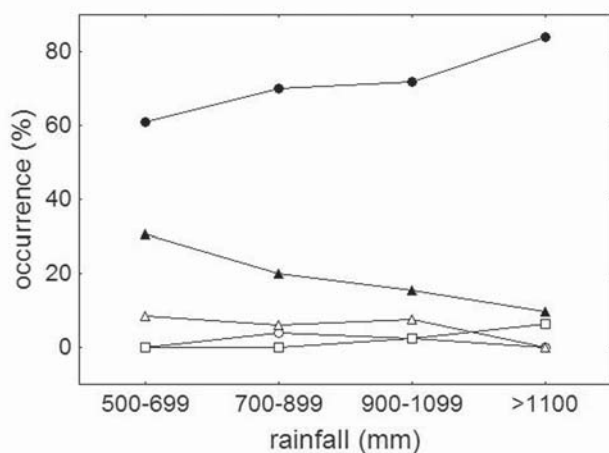
Small mammals were the main prey in the four rainfall classes (Fig. 2). Three of the five prey types showed variation in their occurrence: small mammals and amphibians increased in the diet with rainfall (amphibians: Kendall–Tau correlation  $Z = 1.86$ ,  $P=0.06$ ; small mammals:  $Z = 2.04$ ,  $P=0.04$ ), whereas the proportion of reptiles decreased ( $Z = -2.04$ ,  $P=0.04$ ). Among small mammals, the occurrence of *Apodemus* remained relatively constant in the first three

rainfall groups but increased markedly in the wettest group, whereas *Microtus* proved relatively constant in the first three groups but declined in the wettest one. Furthermore, the occurrence of *Mus* decreased in the rainiest area, while *Sorex* increased. Among reptiles, vipers in the rainiest areas fed only on lizards of the genus *Podarcis*, whereas in the driest areas, adult vipers preyed upon five other lizard genera (Table 2). Although it is known that small mammals are less abundant in spring (Torre et al., 2002), our dietary data were uniformly distributed along the four rainfall classes ( $\chi^2=7.84$ ,  $n=166$ ,  $P=0.25$ ), hence avoiding bias due to more vipers being collected in spring in the dry area.

## DISCUSSION

The logistic regression analysis indicated that the occurrence of small mammals or reptiles in the diet of adult *V. latastei* from the Iberian Peninsula was correlated with three climatic factors: annual rainfall, average temperature and average radiation. The final model showed that adult vipers tend to consume reptiles more frequently in hot, dry and sunny areas than in cold, wet and cloudy ones.





**Fig. 2.** Variation in the occurrence of arthropods (open circles), amphibians (open squares), reptiles (solid triangles), birds (open triangles) and small mammals (solid circles) in the diet of adult *Vipera latastei* in four areas of the Iberian Peninsula according to annual rainfall rates. Sample sizes for the four rainfall areas are given in Table 2.

Although adult vipers eating reptiles were smaller than vipers eating small mammals, we did not find differences in SVL among the four rainfall groups. Thus, there is a trend for increased consumption of small mammals with the size of the viper (Santos et al., 2007), although at similar sizes, adult vipers from dry areas forage on reptiles more frequently than vipers from wet areas.

Several Iberian studies have reported a general increase of richness in small mammals with altitude and latitude (Moreno & Barbosa, 1992; Torre, 2001) and with annual precipitation (Barbosa & Benzal, 1996). If small mammals are more abundant in areas of high precipitation, differences in the occurrence of this prey type in the diet of *V. latastei* according to rainfall categories (Table 2) could be caused by its availability. Hence, the diet composition of this species would be driven by availability of small mammals, with reptiles being substitute prey for adult vipers when small mammals are scarce. This scenario agrees with other snake studies that have reported marked interpopulation diet divergences related to variation in prey abundance (e.g. in mainland and island populations of tiger snakes; Shine, 1987; Fabien et al., 2004), with rainfall being, in some cases, the climatic factor that generates variation in prey availability (Madsen & Shine, 1996, 2000; Shine et al., 1998) and consequently interpopulational or yearly dietary differences.

Low availability of the main prey should favour generalized food habits as opposed to dietary specialization in areas of high availability (Pyke et al., 1977), as occurs in widely distributed snakes (e.g. Daltry et al., 1998; Rodríguez-Robles, 1998; Shine et al., 1998). Our study supports this hypothesis, given that in the driest areas both the number of prey items and the trophic diversity increase (Fig. 1b). Furthermore, the highest feeding rates were found in the driest areas (Fig. 1a), where *V. latastei* adults feed on reptiles at a high frequency (Fig. 2). Rep-

tiles are normally slender-bodied prey, whereas mammals are bulky, indicating that the former provide the vipers with less biomass than the latter. Moreover, reptiles are less energetically profitable prey than mammals (Cummins & Wuycheck, 1971), suggesting that vipers in the driest area increase feeding frequencies to allow similar biomass input compared to mammal-eating vipers in other areas.

The replacement of small mammals by reptiles in the hottest and driest Iberian areas also affects the reptile items preyed on. In the rainiest areas adult vipers prey only on lizards of the genus *Podarcis*, whereas in dry areas, vipers also eat *Podarcis* as well as *Acanthodactylus erythrurus*, *Psammotromus algirus* and immature *Lacerta lepida*. These interpopulation differences do not agree with the geographic distribution of reptiles in the Iberian Peninsula, as there are several reptile genera (*Lacerta*, *Iberolacerta*, *Chalcides*, *Psammotromus* – Pleguezuelos et al., 2002) in wetter areas that are apparently not preyed on by adult vipers. Within the small mammal species, there are also geographic differences in the diet of *V. latastei* (Table 2), which are related to the ecological preferences of some prey species for dry or wet Iberian habitats (e.g. *Mus* in dry areas and shrews of the genus *Sorex* in wet regions; Palomo & Gisbert, 2002). Rodents of the genus *Apodemus* and *Microtus* are the main prey for adult vipers (Table 2), and they are common in all Iberian habitats (Palomo & Gisbert, 2002).

The diet of *V. latastei* reflects variation in prey abundance in different areas according to climatic factors. Hence, our study supports the preliminary results of Bea et al. (1992), who reported that *V. latastei* was a sit-and-wait predator that forages according to prey availability. Bea et al. (1992) extended their conclusions to all the European vipers. With the exception only of *V. ursinii*, probably due to size-related limitations (Agrimi & Luiselli, 1992), *V. latastei* shows the smallest proportion of small mammals in the diet among the European vipers (Saint Girons, 1980, 1983; Bea et al., 1992). The climatic heterogeneity in the area inhabited by *V. latastei*, and its consequent variation in prey availability, could be the cause of geographic dietary differences. In a similar way, *V. berus* has a wide geographic distribution and increases the proportion of amphibians in its diet in some populations (Pielowski, 1962; Pomianowska-Pilipiuk, 1974), as occurred in the rainiest areas inhabited by *V. latastei* (i.e. Gerês; Brito, 2004). In both cases, the increase of amphibians in the diet would be associated with greater abundance of this prey. Luiselli (2006) reported that interpopulation differences in diet composition were higher in snake species inhabiting regions of high diversity of prey sources. Our results support this conclusion, as the Iberian Peninsula is included in a world biodiversity hotspot, the Mediterranean basin (Myers et al., 2000).

*V. latastei* is a sit-and-wait predator with a low feeding rate (males ate only three to five prey per year; X. Parellada, pers. obs.; Santos et al., 2007). The energy cost of this foraging strategy is low, and the long exposure time waiting for prey seems not to increase the risk of the snake being preyed upon itself. As a sit-and-wait preda-

tor, we should expect this viper to be, to some extent, a dietary generalist and to forage according to prey availability. In fact, adult vipers reject lizards under semi-natural conditions (Saint Girons, 1979; Parellada, pers. obs.), probably due to the high availability of rodents. Our study emphasizes the importance of prey availability in the feeding ecology of this predator. Further studies will be useful to establish potential correlates between geographic dietary variation and other life-history traits.

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