FEEDING ECOLOGY OF *VIPERA LATASTEI* IN NORTHERN PORTUGAL: ONTOGENETIC SHIFTS, PREY SIZE AND SEASONAL VARIATIONS

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The dict of Vipera latastei was investigated in northern Portugal from 1998 to 2002. Palpation of stomach contents and forced defaecation from 190 snake specimens resulted in the recovery of 83 identifiable previtems. V. latastei prevs on four species of small mammal (76%), two lizard species (14%), three amphibian species (5%) and arthropods s.l. (5%). Estimates of prey availability demonstrated that the most common prey were also the most frequent prey consumed. No differences between the sexes were detected in terms of the proportion of snakes with prey or diet composition. However, there was an ontogenetic shift in diet composition. Juveniles fed mostly on ecthotermic prey(60%), the majority of subadults fed on insectivorous mammals and lizards (60%), and adults fed mainly on rodents (88%). This ontogenetic shift is mostly due to the morphological constraints imposed on the juveniles, which cannot swallow large prey items. There is a positive correlation between snake size and prey size. V. latastei is selective in terms of both the species and size of prey ingested, with larger snakes being more selective than smaller snakes. Larger snakes have a narrower food niche breadth than smaller snakes, but their diet composition overlaps moderately. There is seasonal variation in the diet composition, with snakes taking amphibians mainly in spring and autumn, lizards in spring, and mammals in summer and autumn. Feeding frequencies indicate that both males and females and subadults and adults - consume prey more frequently during summer.

Key words: dietary habits, food selection, prey availability, snakes, Viperidae

INTRODUCTION

Foraging ecology plays a direct or indirect role in virtually all aspects of snake life-history (Mushinsky, 1987). For instance, obtaining sufficient energy is a crucial factor in reproduction and it may influence the frequency of reproduction (Naulleau & Bonnet, 1996), reproductive output (Gregory & Skebo, 1998) or the maternal condition after reproduction (Shine & Madsen, 1997). Feeding also affects demographic traits of populations, especially rates of growth and survival (Madsen & Shine, 2000).

Although the diet of western European vipers (*Vipera* spp.) is relatively well documented (Bea *et al.*, 1992), data on Lataste's viper (*Vipera latastei*) are scarce and mostly anecdotal (Valverde, 1967; Vericad & Escarre 1976; López Jurado & Caballero, 1981), or come from studies carried out in captivity outside their natural distribution area (Saint-Girons, 1980). Although general accounts (Bea & Braña, 1988) state that this species feeds on lizards and small mammals, no study has specifically addressed its foraging ecology.

Vipera latastei is a small-sized viper, with snout-vent length usually not larger than 60.0 cm. It is distributed from north-western Africa (Morocco, Tunisia and Algeria) in the south, to the Iberian peninsula in the north, with the exception of Cantabrian and Pyrenean regions. Despite its former wide distribution in Portugal, it presently only occurs in isolated and small populations, especially in the south (Godinho *et al.*, 1999). This species is threatened mainly by habitat loss, as a consequence of forest fires and intensification of agriculture, and direct human persecution (Brito *et al.*, 2001). Additionally, the Portuguese preliminary conservation status of "Indeterminate" for *V. latastei* (S.N.P.R.C.N., 1991), demonstrates insufficient knowledge concerning this species. Thus, a conservation programme has been established in northern Portugal, which aims to identify priority areas for conservation and to develop management strategies for viper populations and their habitats.

Data on foraging ecology is important because (1) species with very specialized diets usually are unable to use alternative prey types if their habitats are modified or destroyed; and (2) ontogenetic shifts in diet composition may contribute to the endangerment of species, for instance due to declines in a specific prey type needed by a particular age/size class of snakes (Webb & Shine, 1998). Within the framework of the conservation programme for V. latastei, the following questions were asked: (1) is it a size-selective predator and how does prey availability influence the diet composition? (2) Are there ontogenetic shifts in the diet composition? (3) Are there intersexual differences in the diet composition? (4) What is the frequency of feeding and are there seasonal changes in diet composition? These questions should help in understanding the foraging ecology of V. latastei and allow the identification of favourable ecological niches for the species.

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METHODS

STUDY AREA

The study was conducted in the extreme north-western part of the distribution area of V. latastei (Brito & Crespo, 2002), in a National Woodland and Biosphere Reserve, "Mata de Albergaria", Portugal (41°49'N, 8°07'W; elevation c. 750 m a.s.1.), included in a protected area, Parque Nacional da Peneda-Gerês. The area is a series of granite mountains, with altitudes ranging from 50 to 1500 m a.s.l. The climate is Atlantic Mediterranean (Goday, 1953), characterized by wet winters and hot summers. Mean monthly rainfall ranges from 55 mm in July to 457 mm in January (average annual rainfall above 3200 mm/year), and mean air temperature ranges from 7.9 °C in January to 20.4 °C in July (average annual air temperature 14 °C) (INAG, 2002). The vegetation consists mostly of deciduous oak forests (Quercus robur) or mixed deciduous and coniferous forests (Pinus sp.) with arbutus trees (Arbutus unedo). Major shrubs include heath (*Calluna vulgaris* and *Erica*) sp.), gorse (Ulex sp.) and brooms (Cytisus sp.).

FIELD AND ANALYTICAL METHODS

Data were collected between 1998 and 2002 in an area of around 2.300 ha. 135 snakes were caught by hand, sexed by analysing external tail morphology, measured for snout-vent length (SVL), head length (HL), head width (HD), and head height (HH), and permanently marked for future identification by clipping unique combinations of ventral scales. Snakes were palpated to detect prey in the stomach and intestines, but only forced to defecate intestine contents and never forced to disgorge prey; however, prey presence was recorded in such cases. Additionally, 55 road-killed snakes were dissected to collect stomach and intestine prey items. Mammals were identified using identification keys based on the internal structure of hairs (Teerink, 1991). Reptiles, amphibians and invertebrates were identified through their external morphology. Prey items collected from road-killed snakes were measured (body length), whenever their preservation status allowed.

The availability of potential prey was estimated in a smaller area (2.24 ha), and compared with prey data from the vipers captured in this area (64% of the total examined snakes). Due to logistical reasons, prey availability focuses only on small mammals and lizards. Small mammal abundance was estimated using 100 Shermann traps, placed in line at 10 m intervals, baited and surveyed for six nights, in June 1999, 2000 and 2001. This period should correspond to the annual abundance peak of small manimals in this region (Mathias, 1999). Traps were examined in early morning (at about 07:00 to 08:00 hr) and late afternoon (at about 19:00 to 20:00 hr). Lizard abundance was estimated through visual encounter surveys of 1000 m, in the same area at the same time period. Three lacertid lizard species were found in this smaller study area (Podarcis bocagei, *Lacerta schreiberi* and *L. lepida*), but – due to the large size of adult L. schreiberi and L. lepida – only juveniles were considered as potential prey for V. latastei.

The extent of sexual divergence in viper body morphology was quantified according to the methods outlined by Shine (1991*a*). For SVL, the quotient between female SVL and male SVL was found. For HL, HW and HH, a regression equation linking female measures to the SVL was calculated. An estimate of the female head measure was obtained using the mean male SVL. The ratio of female to male head length, at a mean male SVL, provided an index of the extent of sexual size dimorphism in relative head measures (Shine, 1991*a*).

For analysis purposes, snakes were divided into three size categories according to their sexual maturation status: (1) Juveniles and neonates (SVL <30.0 cm); (2) subadults (SVL 30.0-40.0 cm); (3) adults (SVL >40.0 cm) (Brito & Rebelo, 2003). Differences in diet composition were analysed by χ^2 tests and contingency tables (Siegel & Castellan, 1988). To avoid pseudoreplication of data, no snake was included in the analysis more than once. Niche breadth was measured using the standardized Levin's index (B_A) and niche overlap between categories was measured using Pianka's symmetrical equation (O_{jk}) (for details see Krebs, 1989). The relation between snake size and prey size was determined by calculating Kendall's tau (Siegel & Castellan, 1988),

TABLE 1. Sample sizes, body measures and sexual size dimorphism of *Vipera latastei* containing prey. SVL, snout-vent length, HL, head length; HW, head width; HH, head height (all measures in cm); SD, standard deviation; SSD, sexual size dimorphism. See methods for calculation of SSD.

	11	Mean SVL±SD	Mean HL±SD	Mean HW±SD	Mean HH±SD
Males	62	36.3±9.1	2.02±0.36	1.38±0.26	0.76±0.13
Females	39	37.7±8.3	2.12±0.37	1.40 ± 0.30	0.79 ± 0.17
SSD (f/m)	101	1.04	1.01	0.99	1.00
Juveniles	21	25.0±3.7	1.56±0.19	1.02 ± 0.13	0.57±0.06
Subadults	38	34.3±3.2	1.97±0.16	1.33 ± 0.15	0.75±0.11
Adults	42	45.2±4.7	2.37±0.21	1.59±0.22	0.89 ± 0.09
Total	101	36.9±8.8	2.06±0.37	1.39±0.28	0.78±0.15

testing snake SVL against prey length. In the analysis of feeding frequency and seasonal changes in diet composition, data were pooled into three seasons – spring (March to May), summer (June to August) and autumn (September to November). No data were available between December and February due to the low activity levels of *V. latastei* during the winter (Brito, 2003). Feeding frequencies were inferred from the proportion of snakes containing detectable prey items (Shine *et al.*, 1998). Differences in abundance between snake diet and prey availability were analysed by χ^2 tests contingency table tests. A minimum rejection level of α =0.05 was used in all statistical tests.

RESULTS

A total of 190 individual snakes were analysed in this study, of which 101 contained prey (Table 1). The relative number of snakes with and without prey did not differ significantly between sexes ($\chi^2=0.003$, df=1, P=0.954). *V. latastei* preys on four species of small mammal (76% of the total prey items), two lizard species (14%), three amphibian species (5%) and arthropods s.l.

(5 %) (Table 2), and the differences between the frequencies of prey type consumed were significant (χ^2 =116.8, df=3, *P*<0.001). The rodent *Apodemus sylvaticus* was the most frequent prey, representing 40% of the total prey taken. Analysis by sex shows that females take proportionally more mammals than males, but differences were not significant (all size categories: χ^2 =1.74, df=3, *P*=0.628; adults only: χ^2 =1.94, df=2, *P*=0.164). Since there were no inter-sexual differences in the proportion of snakes with and without prey, or in diet composition, sexes were pooled in the subsequent analysis in the three size categories.

There were significant differences in the dietary composition of the three size categories ($\chi^2=17.5$, df=6, P<0.05) (Table 2). Juveniles fed essentially on ectothermic prey (60%), subadults fed on small mammals (74%), mainly insectivores (43%), but also on ectothermic prey (26%), while adults fed almost exclusively on rodents (88%), and only to a small extent on insectivorous (15%) and ectothermic prey (6%). The importance of small mammals in the diet of *V. latastei* increased with snake size, representing 40% of the diet

TABLE 2. Diet composition and niche breadth (B_A) from different sexes and size categories of *Vipera latastei*. Number of prey items and percentage (in parenthesis). See methods for size categories.

	Males	Females	Juveniles	Subadults	Adults	Total
No. snakes examined	117	73	50	70	70	190
% of snakes with prey	53.0	53.4	42.0	58.6	55.7	53.2
Coleopteran	3 (6.3)	1 (2.9)	2 (13.7)	2 (5.7)	-	4 (4.8)
Total Arthropod	3 (6.3)	1 (2.9)	2 (13.3)	2 (5.7)	-	4 (4.8)
Alytes obstetricans	1 (2.1)	-	1 (6.7)	-	-	1 (1.2)
Chioglossa lusitanica	1 (2.1)	-	1 (6.7)	-	-	1(1.2)
Triturus boscai	-	1 (2.9)	-	-	1 (3.0)	1 (1.2)
Unidentified amphibians	1(2.1)	-	-	1 (2.9)	-	1 (1.2)
Total Amphibia	3 (6.3)	1 (2.9)	2 (13.3)	1 (2.9)	1 (3.0)	4 (4.8)
Podarcis bocagei	4 (8.3)	3 (8.6)	1 (6.7)	6 (17.1)	-	7 (8,4)
Podarcis hispanica	1 (2.1)	-	1 (6.7)	-	-	1 (1.2)
Unidentified Lacertidae	3 (6.3)	1 (2.9)	3 (20.0)	-	1 (3.0)	4 (4.8)
Total Reptilia	8 (16.7)	4 (11.4)	5 (33.3)	6 (17.1)	1 (3.0)	12 (14.5)
Crocidura russula	7 (14 6)	5 (14 3)	2 (13 3)	10 (28.6)	_	12 (14 5)
Sorex granarius	2(42)	4 (11.4)	1(67)	5 (14-3)	_	6(72)
Microtus lusitanicus	4 (8.3)	3 (8.6)	2 (13.3)	-	5(152)	7 (8 4)
Apodemus svlvaticus	19 (39.6)	14 (40.0)	1 (6.7)	8 (22.9)	24 (72.7)	33 (39.8)
Unidentified mammals	2 (4.2)	3 (8.6)	-	3 (8.6)	2 (14.3)	5 (6.0)
Total Mammals	34 (70.8)	29 (82.9)	6 (40.0)	26 (74.3)	31 (93.9)	63 (75.9)
Standardized Levin's B _A	0.287	0.142	0.754	0.236	0.044	0.221



FIG. 1. Seasonal variation in the diet composition of *Vipera latastei* from northern Portugal.



FIG. 2. Seasonal changes in the proportion of *Vipera latastei* from northern Portugal containing prey, by sex (A) and by size category (B). See text for size categories.

of juveniles and 94% of adults, while the importance of ectothermic prey decreases with snake size, representing 60% of the diet of juveniles and 6% of adults.

The food niche (B_A) varied between 0.044 for adult snakes to 0.754 for juveniles (Table 2), indicating that adults were more specialized than subadults and juveniles. Food niche differences between all size categories of males and females indicate a greater specialization in females, which consumed proportionally more mammals than the males (Table 2). Niche overlap (O_{jk}) was high between subadults and adults (O_{jk}=0.978), and moderate between juveniles and sub-adults (O_{jk}=0.863), and between juveniles and adults (O_{jk}=0.749). Overlap between all size categories of males and females was very high (O_{jk}=0.993).

(O_{jk} =0.993). There was seasonal variation in diet composition, although this was not significant (χ^2 =8.15, df=6, *P*=0.228) (Fig. 1). Snakes fed on an increasing proportion of mammals, representing 50% of the diet in spring, but 72% in autumn. Reptiles were mostly preyed upon in the spring (25%), while in autumn they were only marginally utilized as prey items (9%). A mphibians were mostly preyed upon in the spring (25%) and autumn (14%).

Analysis of feeding frequency demonstrated significant differences in the proportion of males and females with and without prey from spring to autumn (males: χ^2 =6.49, df=2, *P*=0.039; females: χ^2 =6.66, df=2, *P*=0.036) (Fig. 2A), with both sexes consuming prey more frequently in the summer. There were also differences between the size categories (Fig. 2B), but these were only significant for subadults (χ^2 =6.71, df=2, *P*=0.035) and adults (χ^2 =7.97, df=2, *P*=0.019). These size categories of snakes consumed prey more frequently in the summer.

There was a positive correlation between snake SVL and prey size (Fig. 3) (Kendall's tau = 0.562, P < 0.001). Small snakes ate smaller prey, mostly lizards and insectivorous mammals, but mean prey size shifted at an intermediate body size (SVLs around 40.0 cm), with larger snakes feeding almost exclusively on larger prey.

TABLE 3. Percent frequency of prey types consumed by *Vipera latastei* compared to prey availability.* Indicates significant differences between availability and proportion of prey in the diet (P=0.01).** Indicates prey types which varied significantly in abundance over the study period (P<0.001).

		Consumed			Available	
	1999	2000	2001	1999	2000	2001
Podarcis bocagei	100.0	100.0	100.0	93.8	94.3	97.5
Lacerta schreiberi	-	-	-	6.3	3.8	2.5
Lacerta lepida	-	-	-	0.0	1.9	0.0
Total reptiles	2	5	1	16	53	40
Crocidura russula	50.0	15.4	30.0	20.0	2.0	11.1
Sorex granarius	-	15.4	-	-	-	-
Microtus lusitanicus	-	15.4	-	-	2.0	-
Apodemus sylvaticus	50.0	53.8*	70.0	80.0	96.1**	88.9
Total mammals	4	13	10	15	51	9



FIG. 3. Relationship between Vipera latastei snout-vent length and prey length ($r^2=0.424$, n=19, P=0.003), in northern Portugal.

Estimates of availability of the two main prey types (lizards and small mammals; Table 3), and diet composition analysis indicate that the most common prey (*Podarcis bocagei*, *Crocidura russula* and *Apodemus sylvaticus*) were also the species most frequently preyed upon. Combining data for the three years of study, these three prey species accounted for 88.6% of the diet of the snakes, and their availability represents 97.2% of the total sample. Although available, juveniles of *Lacerta schreiberi* and *L. lepida* were apparently not preyed on, and *Sorex granarius* only marginally so.

DISCUSSION

The diet of V. latastei in the study area follows the general diet pattern of the European Vipera (Bea et al., 1992), with the main prey taken being small mammals. Nevertheless, it is significantly different ($\chi^2=13.41$, df=4, P=0.009) from the diet of this species reported in a study of museum specimens from Spain (Bea & Braña, 1988). For instance, amphibians have never previously been reported as prey for V. latastei. However, in the study area they represent 13% of diet of the juveniles and 3% of the diet of subadults and adults, respectively. Bea & Braña (1988) suggested that V. latastei had a low frequency of small mammals in the diet (58%) compared to other European vipers, while in northern Portugal they play an important role, representing up to 76% of the diet of this viper. These differences in diet composition between studies are probably due to annual and/or seasonal differences in prey availability between regions. For instance, mammal abundance in the smaller study area fluctuated significantly during the three years of study.

Seasonal shifts in dietary composition of snakes are expected due to spatial and temporal changes in prey availability throughout the year, and examples include the viper Vipera ursinii (Agrimi & Luiselli, 1992), the python Liasis fuscus (Madsen & Shine, 1996), and the colubrid Coluber constrictor (Shewchuk & Austin, 2001). V. latastei exhibited seasonal changes in diet composition, with snakes taking an increasing proportion of mammals from spring to autumn. Conversely, there is a decrease in the proportion of lizards taken. Amphibians are mainly preyed upon during spring and autumn. These seasonal shifts are most likely related to fluctuations in the availability of prey. Lizards are especially abundant during their mating season, in spring, and after hatching, in summer, and are thus susceptible to predators (unpublished data). Amphibians should be more available during the spring and autumn, when the climatic conditions enhance their movements (personal observation). The two species of mammal most frequently taken (*Crocidura russula* and *Apodemus sylvaticus*) have their offspring in spring and autumn (Mathias, 1999), thus being more available during these seasons.

Intersexual differences in diet composition have been reported for several snake species, such as the acrochordid Acrochordus arafurae (Houston & Shine, 1993), the pythonid Morelia spilota (Pearson et al., 2002), and the colubrid Natrix maura (Santos & Llorente, 1998). These differences are mainly caused by sexual size dimorphism, females being larger than males, and thus able to feed on larger prey. Such sexual differences in diet composition could also correspond to a higher energetic demand for females, which must devote more resources to their reproductive output (Shine, 1989). Females of V. latastei are larger than males in SVL and relative head length, but the extent of sexual size dimorphism is small compared to other snake species (Shine, 1991a). As expected, there are no significant intersexual differences in the diet composition. The high value of diet overlap between all size categories of males and females further demonstrates the absence of intersexual differences in diet composition.

Overall, V. latastei exhibits a main foraging period in the summer, which should be related to environmental temperature. Winter in this montane study area is rainy and long, thus snakes forage mainly in summer (Brito, 2003), when temperatures should be optimal to enhance digestion (Naulleau, 1982). Juvenile V. latastei had a similar feeding frequency compared to the other size categories, while juveniles of other European viperids have been reported to feed less frequently than sub-adults and adults (Prestt, 1971; Luiselli, 1996). It has been suggested that this can be a direct consequence of the generalized feeding activity of juveniles and/or to gape limitation: juvenile snakes are too small to ingest adult rodents, and thus have a smaller range of prey types which can be ingested (Shine & Madsen, 1997). However, since juveniles are not involved in mating activities, they should maximize the rate of prey intake in order to enhance their growth rates and survival during the hibernation period (e.g. Bonnet, 1997).

Ontogenetic shifts in diet composition are a common pattern in snakes, mainly because they are gape-limited predators (Mushinsky, 1987), and the European Vipera usually exhibit a shift from lizards to small mammals (Saint-Girons, 1980). Juvenile V. latastei feed essentially on ectothermic prey, while adults prey on rodents, and there is a significant correlation between snake size and prey size. This ontogenetic shift in the diet compo-

sition could be explained in two ways. First, differences in energetic content of prey types. Optimal foraging theory predicts that a predator will ignore small prey when densities of large prey are high enough for predator survival (Schoener, 1971). Additionally, the ingestion of numerous small prey would increase capture and handling time compared to the ingestion of fewer large prey. Thus, adult snakes should prefer mammals to lizards, due to the larger size and higher energetic content of manimals. Second, morphology may impose constraints on ingestion capacity in juvenile snakes. Snakes are gape-size limited predators, therefore juveniles are forced to eat small prey. With an increase in snake body size the number and size of ingestible prey types increase, allowing larger snakes to utilize a greater range of prey sizes and taxa (Shine, 1991b).

Nevertheless, lizards are not entirely excluded from the diet of adult *V. latastei*, representing about 6% of prey taken, which is a common pattern in other European viperids (Braña *et al.*, 1988; Luiselli & Agrimi, 1991). Estimates of prey availability demonstrate that both small prey (lizards and insectivorous mammals) and large prey (rodent mammals) are readily available. Faced with this availability of prey, adult snakes should not be entirely forced to shift from lizards to rodent mammals.

In conclusion, *V. latastei* is selective in terms of the species and the size of prey ingested, with larger snakes being more selective than smaller snakes. In addition, larger snakes have a narrower food niche breadth than do smaller snakes. The ontogenetic shift in the dietary habits is mostly due to the morphological constraints imposed on juveniles, which cannot swallow large prey items.

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