

Correlates between morphology, diet and foraging mode in the Ladder Snake *Rhinechis scalaris* (Schinz, 1822)

Juan M. Pleguezuelos, Juan R. Fernández-Cardenete, Santiago Honrubia, Mónica Feriche, Carmen Villafranca
Departamento de Biología Animal, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain,
juanple@ugr.es

Key words: feeding habits, teeth number, tail breakage, Spain

Abstract

In many vertebrates, foraging mode (active *versus* sit-and-wait) is tied to some traits of their natural history such as morphology, type of prey, rate of food acquisition, and survival rate. We explore the correlates between some morphological traits of a Mediterranean colubrid and its feeding ecology and the predation risk, by comparing data on teeth number, tail damage, and diet. A large sample ($n = 368$) of the Ladder Snake, *Rhinechis scalaris* is used. The species feeds almost exclusively on endotherms, mainly mammals (nearly 95% of the diet in mass), which set *R. scalaris* among the most stenophagous snakes in the western Palaearctic. There is also a high percentage of motionless prey in the diet (up to 50% in prey mass), such as nestling birds, mammals and bird eggs. The species is so canalised to a diet based on endotherms that it does not follow the general rule in medium-sized snakes of an ontogenetic dietary shift from ectothermic to endothermic prey; juveniles consumed the smallest endothermic animals: nestling small-mammals. The number of maxillary teeth (mean 15.1), the lowest within the former and large genus *Elaphe*, is likely related to its trophic specialization. *Rhinechis scalaris* also faces an elevated risk of predation, something general in active searcher snakes compared to ambush foragers, as revealed by many individuals with damaged tails (19.9%), the highest within the Iberian community of snakes. We conclude from indirect evidence (high predation on stationary prey, many individuals with damaged tails) that the species is an active searcher and that this foraging mode influences other natural-history traits (i.e. reproductive habits).

Contents

Introduction	179
Material and methods	180
Results	181
Discussion	183

Introduction

In animals, feeding and activity patterns determine not only the amount of energy acquired, but also other life history traits of the species (Stearns, 1992). For instance,

in many vertebrates foraging mode (active *versus* sit-and-wait; Schoener, 1971) influences some natural history traits, such as the rate of food acquisition, or survival rate (Webb *et al.*, 2003). Active foraging strategies normally imply an elevated rate of food acquisition with respect to sit-and-wait strategies (Schoener, 1971), but while the active forager searches for food, it expends energy and increases the risk of injuries from other predators or prey (Greene, 1997). Snakes are good models for investigating the influences of foraging mode in the ecology of organisms: the morphological simplicity of snakes facilitates the analysis of structural shifts (Shine, 2000), they feed almost exclusively on living organisms (Mushinsky, 1987) and they tend to exhibit fixed foraging tactics (Huey and Pianka, 1981). For this reason, many life-history studies seek to understand the relation of these prominent predators to their prey (Mushinsky, 1987; Holycross *et al.*, 2002).

The Ladder Snake, *Rhinechis scalaris*, is a rather large, heavy-bodied colubrid that inhabits the Iberian Peninsula, south-eastern France and the westernmost part of Italy (Cheylan and Guillaume, 1993), being a quasi-Iberian endemic. This species is remarkably differentiated from other European rat snakes (Lenk *et al.*, 2001) and there is evidence for a separate position of this taxon within the genus *Elaphe sensu lato* (*s.l.*), derived in the recent revalidation of the monotypic genus *Rhinechis* Michaelis, 1833 (Utiger *et al.*, 2002). Most previous knowledge of the natural history of this species came from general studies (Valverde, 1967; Vericad and Escarré, 1976), involving small sample sizes. Specific studies on the natural history of *R. scalaris* dealt with diel and seasonal activity (Cheylan, 1986), ontogenetic shift in coloration pattern (Pleguezuelos *et al.*, 1990), movement patterns (Blázquez, 1993) and reproduction (Blázquez, 1994; Pleguezuelos and Feriche, 2006; revision in Cheylan and Guillaume, 1993). Here we study a large sample of free-ranging animals and museum specimens from the south-east-

ern Iberian Peninsula. The goal is to seek for correlates between morphology, diet and foraging mode in this snake. At first we analysed certain morphological traits of the species, such as teeth number and tail breakage. Teeth features in snakes are closely related to diet (Cundall, 1987) and we tried to find any correlates between teeth number and feeding habits. The percentage of individuals with tail breakage would be an indirect evidence of predation pressure in snakes (Turner *et al.*, 1982); in some snakes tail breakage provides an effective defence that favours escape from predators (Savage and Slowinsky, 1996); if *R. scalaris* is an active forager that moves widely, we would expect a high percentage of individuals with damaged tails compared to other species of the Iberian snake community. Secondly, we analysed the taxonomic composition of the diet, with patterns of dietary variation under ontogenetic and sexual cues. Apparently there is no sexual dimorphism in this species, at least not in body length and body mass (Pleguezuelos and Feriche, 2006), but lack of sexual difference in diet is expected (Shine, 1993). With respect to the ontogenetic cue, the specialised diet on endotherms of *R. scalaris* poses a question: how do neonates of this species face up to their first prey, small mammals and birds, being bulky prey for neonates of medium sized snakes? Lastly we studied size-dependent variation in its feeding habits. As *R. scalaris* only preys on relatively bulky prey (small mammals, birds; Valverde, 1967), we would expect the consumption of relatively small-sized prey with respect to its body size.

Material and methods

Study area.– The field study was conducted in the Granada Depression and nearby areas, within a region of approximately 3000 km² in the south-eastern Iberian Peninsula (36°55'–37°20'N, 3°30'–4°15'W), where altitudes range between 450–1200 m asl. Mean annual temperature range between 12.5–14.3°C, and the average yearly rainfall between 355.4–448.0 mm (data from the Cartuja weather station [37°12'N, 3°36'W]). The study area is currently characterised by a mosaic of habitats dominated by cultivated land (olive orchards and cereal crops), mixed areas of evergreen forest and scrubland (*Quercus ilex*) and, to a lesser extent, pine plantations (*Pinus halepensis*, *P. pinaster*).

Sampling.– Field sampling was conducted from 1993 to 2000, within the framework of a larger study on the snake fauna of the region (details in Feriche, 1998). We made searches 3–4 field days per month (c.

six hours each), throughout all months of the year. Specimens killed by local people and road-kills were collected (n = 320). Although the species is difficult to find and catch, some free-ranging live specimens were also captured (n = 25), processed for food items and analysed for getting morphology data (only tail injury, not maxillary teeth count). Specimens from the collections of the Estación Biológica de Doñana, Seville (EBD; n = 20) and Museo Nacional de Ciencias Naturales, Madrid (MNCN; n = 3), collected in the study area, were also analysed. In total, 368 specimens (202 males, 166 females) were examined.

Data collection on morphology and feeding.– In all specimens snout-vent length (SVL) was measured with a cord (± 1 mm) and body mass with an electronic balance (± 0.1 gr.). We checked for tail completeness and classified individuals with undamaged and damaged tails. In specimens collected by the authors, we were sure that tail breakage was the consequence of natural events and not a result of tail grasping during capture. We chose to classify the sub-sample from collections in a conservative way, and thus we did not consider that a tail was damaged if the break-point was not healed. Although it is known that the frequency of tail breakage varies among age classes and between sexes in snakes (Mendelson, 1992), we have for this study pooled the population. Our sample size for analysing this trait was sufficient in *R. scalaris* and it included individuals of all sexes and sizes, so we did not consider it necessary to perform sex or size-corrected comparisons.

Individuals were sexed by dissection in voucher specimens or according to Feriche *et al.* (1993) in live specimens. Stomach contents were checked by making a mid-ventral incision. Live snakes were gently palpated in the fore abdomen to force regurgitation in the case of recently ingested food (not in the rear abdomen to avoid damage of reproductive organs). All reptilian and bird eggs, as well as bird and mammal nestlings, were considered as one item because they were assumed to represent a single feeding event (Rodríguez-Robles and Greene, 1999). Whenever possible, prey items were identified to species level, measured (SVL; ± 1 mm), weighed (± 0.1 g) and the direction of ingestion of the prey (inferred from its orientation in the gut) recorded. Body length and weight of partially digested prey were estimated by comparing it with conspecifics from the study area, considering both traits at the time of ingestion. For the analysis of the ontogenetic shift in diet, four artificial SVL-categories for the snake were used, based upon the need for an analogous

sample size and corresponding to approximately the following ontogenetic stages: i) newborn and immature snakes, ii) males just matured and females close to sexual maturity (males mature at 450 mm SVL, females at 660 mm SVL [Pleguezuelos and Feriche, 2006]), iii) medium-sized adults and iv) large adults (see Table 1 for SVL-range for each category). Distributions of data were checked for normality prior to analyses, and in this article mean values are followed by \pm one standard deviation with alpha set at 0.05. Statistics were performed by STATISTICA 6.0 for WINDOWS PC.

Results

The mean number of maxillary teeth (counting only the left row for each individual) was 15.1 ± 0.7 (range 14-16, $n = 25$). In the study area, 19.9% of the individuals had damaged tails (range 16.2-24.3, 95% confidence interval (CI); $n = 366$).

Of the 368 specimens examined, 81 (22.0%) had prey in their stomach or in the first portion of intestine

and the mean prey number in specimens with stomach contents was $1.16 (\pm 0.58)$. Of the prey, 82 (87.2%) were mammals, 11 (11.7%) were birds, and only one (1.1%) was an ectothermic prey (a lizard clutch). When prey mass was considered, the importance of mammals as prey increased (93.9%) with respect to birds (5.5%) or reptile eggs (0.5%; Table 1. The percentage of newborn mammals in the diet was high (25.5%), as well as the proportion of motionless prey (38.3%).

Mean prey length was 82.6 mm (± 38.6 , $n = 94$) and ranged from 20 mm (bird egg) to 190 mm (juvenile rabbit *Oryctolagus cuniculus*). Mean prey mass was 29.9 gr. (± 40.1 , $n = 94$), ranging from 1.8 g (*Mus spretus* nestling) to 180.0 g (juvenile rabbit). The mean relative prey length (prey SVL/snake SVL) was 0.112 ± 0.043 (range 0.021-0.245; $n = 94$) and mean relative prey mass (prey mass/snake mass) was 0.106 ± 0.080 (range 0.005-0.345, $n = 94$). Most preys were swallowed head-first (83.1%; $n = 65$; 2 \times 2 table with the frequency of prey ingested head- and tail first compared against an equal distribution of frequencies, $\chi^2 = 16.5$, $p < 0.0001$). Prey swallowed tail-first were smaller than those swallowed head-first, both in

Table 1. Prey eaten by the Ladder Snake (*Rhinechis scalaris*) in the Depression of Granada according to four body-size classes.

Prey type	Group I ($n = 79$) SVL < 500 mm		Group II ($n = 93$) SVL 500-699 mm		Group III ($n = 90$) SVL 700-799 mm		Group IV ($n = 106$) SVL > 800 mm		Total ($n = 368$)	
	freq.	mass (g)	freq.	mass (g)	freq.	mass (g)	freq.	mass (g)	freq.	mass (g)
Reptile eggs ^a	-	-	1	17.5	-	-	-	-	1	17.5
Bird eggs	-	-	1	2.4	2	21	1	2.4	4	25.8
Bird nestling ^b	-	-	1	69.0	5	69.6	1	25.0	7	164.6
<i>Suncus etruscus</i>	1	2.2	1	2.3	1	2.0	-	-	3	6.5
<i>Crocidura russula</i>	1	8	2	19.5	-	-	-	-	3	27.5
<i>Neomys anomalus</i>	-	-	1	12.4	-	-	-	-	1	12.4
<i>Talpa occidentalis</i>	-	-	-	-	1	55.0	-	-	1	55.0
<i>Talpa occidentalis</i> litter	-	-	1	18.0	-	-	-	-	1	18.0
<i>Mus</i> sp. ^c	2	12.5	5	67.4	4	65.5	2	33.0	13	178.4
<i>Mus</i> sp. litter ^c	2	23.8	1	7.5	3	30.6	2	18.4	8	80.3
<i>Apodemus sylvaticus</i>	-	-	2	44.3	6	124.6	2	47.0	10	215.9
<i>Apodemus sylvaticus</i> litter	1	6.0	1	4.0	3	30.6	-	-	5	40.6
<i>Rattus rattus</i>	-	-	-	-	-	-	5	613.0	5	613.0
<i>Microtus</i> sp. ^d	-	-	6	155.0	6	192.9	9	181.3	21	529.2
<i>Microtus</i> sp. litter ^d	-	-	1	8.0	-	-	-	-	1	8.0
<i>Elyomis quercinus</i>	-	-	-	-	-	-	1	90.0	1	90.0
<i>Elyomis quercinus</i> litter	1	5.0	-	-	-	-	-	-	1	5.0
<i>Oryctolagus cuniculus</i> juv.	-	-	-	-	-	-	7	1263.0	7	1263.0
<i>Lepus granatensis</i> juv.	-	-	-	-	-	-	1	80.0	1	80.0
TOTAL	8	-	24	-	31	-	31	-	94	3430.7
Individuals with prey	8 (10.1%)		20 (21.5%)		24 (26.4%)		29 (27.1%)			

^a *Lacerta lepida* eggs

^b *Passer domesticus*, *Galerida theklae*, *Petronia petronia*

^c most of the specimens identified were *Mus spretus*

^d 19 *Microtus duodecimcostatus*, 2 *Microtus cabrerai*.

relative prey size and relative prey mass (Mann-Whitney U test; prey SVL/snake SVL, $U = 142.0$; prey mass/snake mass, $U = 141.5$; $p < 0.01$ in both comparisons).

To compare the diet among the four ontogenetic categories, and because of statistical constraints, we reduced the number of different prey-types to five: i) eggs and bird nestlings, ii) newborn mammals, iii) shrews (*Suncus*, *Crocidura*, *Neomys*), iv) small rodents (*Mus*, *Apodemus*, *Microtus*) and v) medium-sized mammals (*Talpa*, *Eliomys*, *Rattus*, *Oryctolagus*, *Lepus*). There was an ontogenetic shift in diet (4×5 table, $\chi^2 = 46.9$, $p < 0.0001$; all *a posteriori* paired χ^2 test also significant at least at the level $p < 0.01$). Newborn and juvenile snakes (group I, Table 1) only fed on the smallest prey species (shrews, juvenile *Mus*) and on newborn mammals; birds appeared as prey only in group II and larger snakes, while the largest prey species (*Talpa*, *Rattus*, *Eliomys*, *Oryctolagus*, *Lepus*) were consumed almost exclusively by group IV (Table 1; Figure 1). None of the eleven newborns found in the field had gut contents and the percentage of individu-

als with prey in their stomachs increased according to size category (Table 1). No clear ontogenetic trend was detected in the importance of newborn mammals as prey: small snakes ingested newborns from small-sized prey, while large snakes fed upon newborns of small and medium-sized prey. Larger snakes took larger prey (Figure 1), though the coefficient of determination of the regression of prey length on snake length was rather low ($r^2 = 0.319$). That is, 68% of the variation in prey length was not explained by the variation in snake length, probably because medium-sized snakes continued to feed on very small prey (bird eggs and nestlings, newborn mammals; Figure 1).

We detected no sexual difference in prey frequency (only sexually mature individuals; because of methodological constraints, the following prey types were pooled: reptile eggs + bird eggs/nestlings, *Suncus* + *Crocidura*, *Oryctolagus* + *Lepus*; 2×9 table, $\chi^2 = 10.77$, $P = 0.2$). Males and females preyed on nestling birds and newborn mammals equally (2×2 table, $\chi^2 = 0.18$, $n = 81$, $P = 0.67$) and there was no intersexual difference in the frequency of snakes with food in their

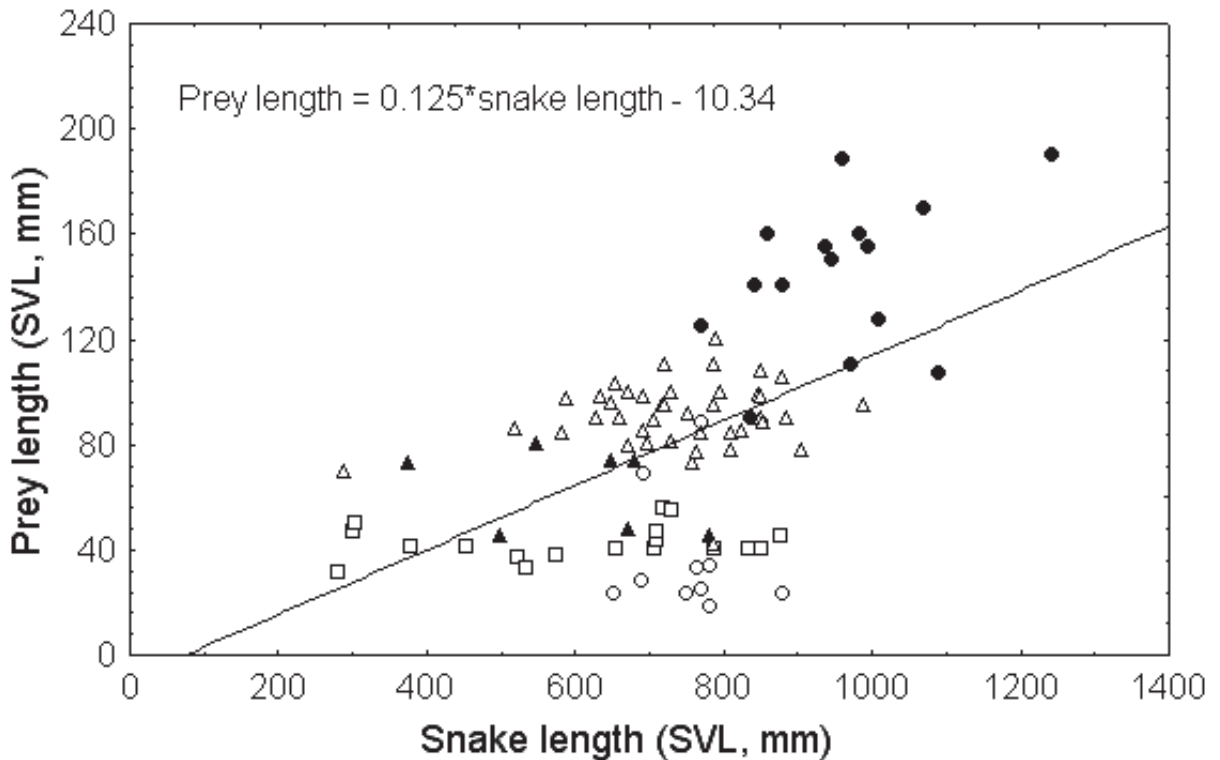


Figure 1. Prey length relative to snake length in the Ladder Snake (*Rhinechis scalaris*) in the Depression of Granada. Different symbols correspond to different prey categories: eggs and nestling birds (open circles), newborn mammals (squares), shrews (solid triangle), small rodents (open triangle), medium-sized mammals (solid circle). For more details, see the text.

stomachs (an index of feeding rate; 2 x 2 table, $\chi^2 = 0.12$, $n = 261$, $p = 0.7$). Males tended to prey on longer and heavier prey than did females, although differences were not significant (ANOVA test, $p < 0.06$ in both comparisons).

Discussion

Feeding ecology.—Mammals are the predominant prey for *R. scalaris* in the south-eastern Iberian Peninsula (nearly 95% of the diet in mass), which set the species among the most stenophagous snakes in western Palaearctic, at least when prey is considered at the level of the traditional vertebrate classes (revision in Böhme, 1993, 1999; Schleich *et al.*, 1996). Birds are the secondary prey; all are captured during their reproductive period (spring time), a general pattern in Mediterranean *Elaphe* s.l. (Filippi *et al.*, 2005). Our results on the diet of the study species coincide in general with previous data (Valverde, 1967; Vericad and Escarré, 1976; Cheylan and Guillaume, 1993).

We also observed a high percentage of stationary prey in our species' diet, suggesting an active foraging strategy (Schoener, 1971), as usual in *Elaphe* s.l. species (Schulz, 1996; Mullin and Cooper, 2000). Evidently, the species frequently raids both mammal and bird nests, although the importance of bird eggs as food was probably underestimated because of difficulties in detecting egg remains in studies of snake diets. As deduced from the nesting ecology of its main prey, *R. scalaris* searches for prey especially in burrows (nests for most of the mammal prey; unpub. data on the authors on radio-tracked individuals).

Although comparative analyses are necessary to define a snake as a specialist predator (Rodríguez-Robles and Greene, 1999), the fact that 49.6% of the prey mass of the diet consists of prey taken in their nest (Table 1) implies that *R. scalaris* somewhat specialises on nest predation. To our knowledge, of all species of *Elaphe* s.l. in western Palaearctic, *R. scalaris* has the highest percentage of nestling prey in its diet (*e.g.* Luiselli and Rugiero, 1993; Rugiero *et al.*, 1998; Filippi *et al.*, 2005). Nest predation is an efficient foraging strategy for snakes. A single nestling, either bird or mammal, accounts for much less prey mass than an adult prey; however, nestlings are not normally alone and the individuals of a brood or a litter considered together would equal the biomass of an adult of the same species, or even more. Moreover, a nestling struggles less effectively (or not at all) than an adult

and handling time may be less for nestling prey than for adult prey (Rodríguez-Robles, 2002). In rat snakes *Elaphe helena* it has been experimentally proven that time to subdue and ingest a prey increases with the size of the prey (Mehta, 2003). An additional advantage of this is that eggs or nestling are food resources seldom shared with other predators in the study area (Valverde, 1967). As deduced from some predictors of body condition in this species, such as the high level of fat bodies (the highest in western Mediterranean colubrids; Feriche, 1998; Fahd, 2001) and the high reproductive frequency (86% of adult females reproduce every year; Pleguezuelos and Feriche, 2006), *R. scalaris* is well fitted to this specialised diet.

Most snakes exhibit spectacular ontogenetic change in body dimensions that provides an excellent point of departure for testing the existence of ontogenetic shifts in diet. *Rhinechis scalaris* is not an exception, since it can increase its body length by up to sixfold and its body weight by up to 120-fold over its ontogenetical stages (unpub. data of the authors). The most interesting finding is that *R. scalaris* did not follow the general rule in the ontogenetic dietary shift of medium-sized snakes – that is, the shift from ectothermic prey (mainly lizards) to endotherms (mainly mammals; Saint Girons, 1980; Pleguezuelos and Moreno, 1990; Rodríguez-Robles and Greene, 1999), a shift that has particularly been observed within *Elaphe* s.l. (Fitch, 1999; Filippi *et al.*, 2005). According to our findings, the feeding habits of *R. scalaris* parallel those of large-sized snakes belonging to other families, such as *Corallus hortulanus* (Henderson, 1993) and *Python regius* (Luiselli and Angelici, 1998). Thus, juveniles are capable of consuming endotherms as adults do, but as the predator's gape size is constrained, their prey are rather small mammals such as *Suncus etruscus* (one of the smallest mammals in the world) or even smaller (*e.g.* nestling mammals). Since none of the newborn snakes found in the field had gut contents, we suggested that they enter the first hibernation period relying only on their large vitellogenic reserves, which fuel growth until the spring of the next calendar year (see also Pleguezuelos and Feriche, 2006).

The high percentage of nestlings in the diet is probably also responsible for the small proportion of variance explained by the correlation between *R. scalaris* body length and prey length. Large snakes, up to 900 mm SVL, continue to feed on very small prey, such as newborn mammals and bird eggs (Figure 1). Hence, the lower limit of prey length does not increase with

snake length (Figure 1). Snakes larger than 900 mm SVL appear to ingest rather large prey, introducing considerable variation in the relationship between prey and snake length. Another aspect that arises from the prey size/predator size relationship is that *R. scalaris* takes relatively small prey. The predator size/prey size relationship in Mediterranean *Elaphe* rat snakes seems rather constant, both at intraspecific and interspecific levels, and set at about 10% of the snake biomass (Capula and Luiselli, 2002; Filippi *et al.*, 2005). We failed to find major sexual differences in the prey type consumed, in accordance with similar SVL and body mass in both sexes (Pleguezuelos and Feriche, 2006).

Rhinechis scalaris showed a strong preference for head-first ingestion, as is usual in snakes (Rodríguez-Robles, 2002). In rat snakes, prey size has significantly affected prey-handling behaviour (Mehta, 2003). The differences in relative prey size between prey swallowed head-first and those swallowed tail-first suggest that this preference must be guided by reduction of resistance and hence, energy cost and handling time (Brown *et al.*, 2003; Mehta, 2003).

Correlates between morphology, diet and foraging mode.— In snakes, studies on the natural diet also provide information on functional morphology (Schwenk, 2000). For instance, teeth characteristics are probably more related to diet than in some other groups of reptiles or vertebrates, as snakes do not use their trophic structures in conspecific rivalry (Shetty and Shine, 2002). Here, we attempt to relate tooth number with feeding ecology in *R. scalaris*. The number of maxillary teeth in *R. scalaris* was among the lowest published for 40 species of *Elaphe* s.l. (reviewed by Schulz, 1996). Reduction in tooth number is a common trend in fossorial and diet-specialised (*i.e.* oophagous) snakes (Gans, 1961; Broadley, 1979; Scanlon and Shine, 1988). However, *R. scalaris* is not fossorial and its diet does not permit it to be classified as oophagous. Simply, this species does not feed upon slippery prey (fish, some reptiles), which require many teeth, or soft contoured prey (adult birds), which implies the need for numerous long teeth (Edmund, 1969). Rather, this species specialises in the consumption of small mammals and probably has the minimum number of teeth needed to seize adult mammals, since highly developed dentition is not necessary for seizing motionless prey (eggs, nestling birds, mammal litter). The reduction in tooth number in *R. scalaris* agrees with their specialised diet on stationary prey, at

least within *Elaphe* s.l. (Schulz, 1996). More data on the link between diet and tooth number are necessary in other taxonomic groups of snakes, an aspect rather well known in many lizard groups (Edmund, 1969).

Being an efficient active forager, as revealed by a high proportion of specimens with prey (Valverde, 1967) and by the highest level of fat bodies among West Mediterranean colubrids (Feriche, 1998; Fahd, 2001) implies some costs during the foraging activity. Studying the spatial ecology of the species by radio-tracking, Blázquez (1993) found that the mean home range of active individuals was 1.83 ha, larger than in other Iberian colubrids (*Malpolon monspessulanus*: 0.39 ha, Blázquez, 1993; *Natrix maura*: 0.18–1.77 ha, Santos and Llorente, 1997). When a snake moves widely, it increases the risk of predation or casualty (Huey and Pianka, 1981; Secor, 1995; Bonnet *et al.*, 1999). Hence, in the study area, although *R. scalaris* represents only 20.6% of the snakes encountered in the field ($n = 1697$), this species accounts for 39.5% of the prey consumed by the short-toed eagle *Circus gallicus*, a raptor specialised in catching snakes (Gil and Pleguezuelos, 2001). This is most striking if we take into account that short-toed eagles are exclusively diurnal and *R. scalaris* somewhat nocturnal (Cheylan, 1986). Indirect evidence of heavy predation pressure is the proportion of individuals with damaged tails (Turner *et al.*, 1982), even though it could indicate inefficient predation (Medel *et al.*, 1988). In the study area, other snakes (*Coronella girondica*, *Hemorrhois hippocrepis*, *Macroprotodon brevis*, *Malpolon monspessulanus*, *Natrix maura*, *Natrix natrix*, *Vipera latastei*) exhibited tail breakage in proportions ranging from 1.1 to 16.4% (n ranged from 91 to 382, depending on the species; unpub. data of the authors). Thus, the percentage of *R. scalaris* individuals with tail breakage proved to be the highest of snakes in the study area, suggesting high predation pressure. The elaborate ontogenetic shift in dorsal pattern of this species (Pleguezuelos *et al.*, 1990) may have also arisen for the concealment of a moving widely species. Thus, our data suggest the existence of a significant mortality cost of active foraging by *R. scalaris*.

We conclude from indirect evidence (high percentage of stationary prey in the diet, many individuals with damaged tails) and direct evidence elsewhere (Blázquez, 1993), that *R. scalaris* is an active searcher and that this foraging mode may be correlated with some natural-history traits of the species (for example high

feeding rate, abdominal fat reserves, frequency of reproduction; this study; Pleguezuelos and Feriche, 2006). A pattern of wide movement in a snake may explain an elevated risk of predation (Gil and Pleguezuelos, 2001). However, unfortunately it may also be correlated with a high vulnerability to anthropogenic mortality (Bonnet *et al.*, 1999), as presently occurs in *R. scalaris* (traffic casualties).

Acknowledgements

We thank J. Cabot and J. González for allowing us to study specimens in collections under their care. Manuel Moreno helped in field sampling. J. Hódar and L. Luiselli contributed with valuable comments on the first draft of the manuscript. K. Setser improved the language style. We thank three anonymous reviewers for their very constructive and detailed suggestions and corrections. The last stage of this study was supported by the Research Award REN2000-1376 GLO of the Spanish MCYT to the senior author and to MF.

References

- Blázquez MC. 1993. Ecología de dos especies de colúbridos, *Malpoina monspessulana* y *Elaphe scalaris* en Doñana (Huelva). Ph. D., Sevilla University.
- Blázquez MC. 1994. Notes on the reproduction of *Elaphe scalaris* (Schinz, 1822) in Southern Spain. *Herpetological Journal* 4: 109-111.
- Böhme W. ed. 1993, 1999. *Handbuch der Reptilien und Amphibien Europas. Schlangen (Serpentes), I & II*. Wiesbaden: Aula-Verlag.
- Bonnet X, Naulleau G, Shine R. 1999. The dangers of leaving home: dispersal and mortality in snakes. *Biological Conservation* 89: 39-50.
- Broadley DG. 1979. Predation on reptile eggs by African snakes of the genus *Prosymna*. *Herpetologica* 35: 338-341.
- Brown C, Foster C, Spivey-White J, Hesletine J. 2003. Feeding behaviour in monitor lizards and snakes; does direction of prey ingestion influence prey handling time? *Herpetological Bulletin* 83: 26-29.
- Capula M, Luiselli L. 2002. Feeding strategies of *Elaphe longissima* from contrasting Mediterranean habitats in central Italy. *Italian Journal of Zoology* 69: 153-156.
- Cheyran M. 1986. Mise en évidence d'une activité nocturne chez le serpent méditerranéen *Elaphe scalaris* (Ophidia, Colubridae). *Amphibia-Reptilia* 7: 181-186.
- Cheyran M, Guillaume CP. 1993. *Elaphe scalaris* (Schinz, 1822) - Treppennatter. In: Böhme W ed. *Handbuch der Reptilien und Amphibien Europas. Band 3/I: Schlangen (Serpentes) I (Typhlopidae, Boidae, Colubridae 1: Colubrinae)*. Wiesbaden: Aula-Verlag, 397-429
- Cundall D. 1987. Functional Morphology. In: Seigel RA., Collins JT., Novak SS. eds., *Snakes, Ecology and Evolutionary Biology*. New York: Macmillan, 106-140.
- Edmund AG. 1969. Dentition. In: Gans C, d'A. Bellairs A, Parson TS. eds., *Biology of the Reptilia*. San Diego: Academic Press 1: 117-200.
- Fahd S. 2001. *Biogéographie, morphologie et écologie des ophiidiens du Rif (Nord du Maroc)*. Tetouan: Ph. D. University of Abdelmalek Essaâdi.
- Feriche M. 1998. *Ecología de la reproducción en colúbridos del sureste de la Península Ibérica*. Ph. D. University of Granada.
- Feriche M, Pleguezuelos JM, Cerro A. 1993. Sexual dimorphism and sexing of mediterranean Colubrids based on external characteristics. *Journal of Herpetology* 27: 357-362.
- Filippi E, Rugiero L, Capula M, Capizzi D, Luiselli L. 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.
- Fitch HS. 1999. *A Kansas Snake Community: Composition and Changes over 50 Years*. Malabar, Florida: Krieger Publishing Co.
- Gans C. 1961. The feeding mechanism of snakes and its possible evolution. *American Zoologist* 177: 217-227.
- Gil JM, Pleguezuelos JM. 2001. Prey and prey-size selection by the Short-toed eagle, *Circaetus gallicus*, during the breeding period in Southeastern Spain. *Journal of Zoology (London)* 255: 131-137.
- Greene HW. 1997. *Snakes. The evolution of Mystery in Nature*. Berkeley: University California Press.
- Henderson RW. 1993. Foraging and diet in West Indian *Corallus enydris* (Serpentes: Boidae). *Journal of Herpetology* 27: 24-28.
- Holycross AT, Painter CW, Prival DB, Swann DE, Schroff MJ, Edwards T, Schwalbe CR. 2002. Diet of *Crotalus lepidus klauberi* (Banded Rock Rattlesnake). *Journal of Herpetology* 36: 589-597.
- Huey RB, Pianka ER. 1981. Ecological consequences of foraging mode. *Ecology* 62: 991-999.
- Lenk P, Joger U, Wink M. 2001. Phylogenetic relationships among European ratsnakes of the genus *Elaphe* Fitzinger based on mitochondrial DNA. *Amphibia-Reptilia* 22: 329-339.
- Luiselli L, Angelici FM. 1998. Sexual size dimorphism and natural history traits are correlated with intersexual dietary divergence in royal pythons (*Python regius*) from the rainforests of southeastern Nigeria. *Italian Journal of Zoology* 65: 183-185.
- Luiselli L, Rugiero L. 1993. Food Habits of the Aesculapian Snake, *Elaphe longissima*, in Central Italy: Do Arboreal Snakes Eat More Birds than Terrestrial Ones? *Journal of Herpetology* 27: 116-117.
- Medel RG, Jiménez JE, Fox SF, Jacksic FM. 1988. Experimental evidence that high population frequencies of lizard tail autotomy indicate inefficient predation. *Oikos* 53: 321-324.
- Mehta RS. 2003. Prey-handling behavior of hatchling *Elaphe helena* (Colubridae). *Herpetologica* 59: 469-474.
- Mendelson JR. III 1992. Frequency of tail breakage in *Coniophanes fissidens* (Serpentes: Colubridae). *Herpetologica* 48: 448-455.
- Mullin SJ, Cooper RJ. 2000. The foraging ecology of the gray ratsnake (*Elaphe obsoleta*) II. Influence of variable habitat structural complexity on snakes foraging for arboreal avian prey. *Amphibia-Reptilia* 21: 211-222.

- Munshinsky HR. 1987. Foraging Ecology. In: Seigel RA, Collins JT, Novak SS, eds. *Snakes, Ecology and Evolutionary Biology*. New York: Macmillan, 302-334.
- Pleguezuelos JM, Feriche M. 2006. Reproductive ecology of a Mediterranean ratsnake, the Ladder Snake *Rhinechis scalaris* (Schinz, 1822). *Herpetological Journal* 16: 177-182.
- Pleguezuelos JM, Moreno M. 1990. Alimentación de *Coluber hippocrepis* Linné, 1758 (Ophidia, Colubridae) en el SE. de la Península Ibérica. *Amphibia-Reptilia* 11: 325-337.
- Pleguezuelos JM, Feriche M, García-Peña H. 1990. Caractères externes et coloration de *Elaphe scalaris* (Schinz, 1822) (Squamata, Colubridae) dans la Péninsule Iberique. *Bulletin de la Société Herpétologique de France* 55: 24-39.
- Rodríguez-Robles JA. 2002. Feeding ecology of North American gopher snakes (*Pituophis catenifer*, Colubridae). *Biological Journal of the Linnean Society* 77: 165-183.
- Rodríguez-Robles JA, Greene HW. 1999. Food habits of the long-nosed snake (*Rhinocheilus lecontei*), a 'specialist' predator? *Journal of Zoology (London)* 248: 489-499.
- Rugiero L, Capizzi D, Luiselli L. 1998. Aspects of the ecology of the leopard snake *Elaphe situla* in southeastern Italy. *Journal of Herpetology* 32: 626-630.
- Saint Girons H. 1980. Selective modifications in the diet of vipers (Reptilia: Viperidae) during growth. *Amphibia-Reptilia* 1: 127-136.
- Santos X, Llorente GA. 1997. Actividad de *Natrix maura* en el Delta del Ebro, analizada mediante técnicas de telemetría. *Revista Espanola de Herpetología* 11: 63-70.
- Savage JM, Slowinski JB. 1996. Evolution of coloration, urotomy and coral snake mimicry in the snake genus *Scaphiodontophis* (Serpentes: Colubridae). *Biological Journal of the Linnean Society* 57: 129-194.
- Scanlon JD, Shine R. 1988. Dentition and diet in snakes: adaptations to oophagy in the Australian elapid genus *Simoselaps*. *Journal of Zoology (London)* 216: 519-528.
- Schleich HH, Kästle W, Kabisch K. 1996. *Amphibians and reptiles of North Africa*. Königstein: Koeltz.
- Schoener TW. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2: 369-404.
- Schulz KD. 1996. A Monograph of the Colubrid Snakes of the Genus *Elaphe* Fitzinger. Königstein: Koeltz.
- Schwenk K. 2000. *Feeding, form Function and Evolution in Tetrapod Vertebrates*. San Diego: San Diego Academic Press.
- Secor SM. 1995. Ecological aspects of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. *Herpetological Monographs* 9: 169-186.
- Shetty S, Shine R. 2002. Sexual divergence in diets and morphology in Fijian sea snakes *Laticauda colubrina* (Laticaudinae). *Australian Ecology* 27: 77-84.
- Shine R. 1993. Sexual dimorphism in snakes. In: Seigel RA, Collins JT eds. *Snakes: Ecology and Behavior*. New York: McGraw Hill, 49-86.
- Shine R. 2000. Vertebral numbers in male and female snakes: the roles of natural, sexual and fecundity selection. *Journal of Evolutionary Biology* 13: 455-465.
- Stearns SC. 1992. *The evolution of natural histories*. Oxford: Oxford University Press.
- Turner FB, Medica PA, Jennrich RI, Maza BG. 1982. Frequencies of broken tails among *Uta stansburiana* in southern Nevada and a test of the predation hypothesis. *Copeia* 1982:835-840.
- Utiger U, Helfenberger N, Schätti B, Schmidt C, Ruf M, Ziswiler W. 2002. Molecular systematics and Phylogeny of old Old and New World ratsnakes, *Elaphe* auct., and related genera (Reptilia, Squamata, Colubridae). *Russian Journal of Herpetology* 9: 105-124.
- Valverde JA. 1967. Estructura de una comunidad de vertebrados terrestres. *Monografías de la Estación Biológica de Doñana* 1: 1-218.
- Vericad JR, Escarré A. 1976. Datos de alimentación de ofidios en el Levante sur ibérico. *Mediterranea* 1: 5-33.
- Webb JK, Brook B, Shine R. 2003. Does foraging mode influence life history traits? A comparative study of growth, maturation and survival of two species of sympatric snakes from southeastern Australia. *Australian Ecology* 28: 601-610.

Received: 8 May 2006.

Accepted: 23 March 2007.