

The implications of bite performance for diet in two species of lacertid lizards

A. Herrel, R. Van Damme, B. Vanhooydonck, and F. De Vree

Abstract: One of the performance features that is generally considered crucial to increasing the potential prey spectrum of lizards is bite capacity. In this study we tested whether bite forces may serve as a basis for diet selection in two syntopically occurring lacertid lizards. We did so by measuring bite forces in vivo for a large sample of lizards of the species *Podarcis muralis* and *Lacerta vivipara*. To assess the ecological relevance of the bite forces, we tested the hardness of a number of natural prey items of both species. The results of our study support the predictions of biomechanical models of biting in lizards and indicate that both larger animals and larger headed ones bite harder. Surprisingly, head shape is an excellent predictor of bite performance in the species studied. Moreover, it is demonstrated that bite capacity is a potentially important ecological variable that could be used as a factor in explaining patterns of food-resource use, ontogenetic dietary shifts, and sexual dimorphism in diet.

Résumé : L'une des caractéristiques généralement considérées comme essentielles à l'augmentation de l'amplitude de l'éventail des proies chez les lézards est la force de leur morsure. Au cours de cette étude, nous avons examiné si la force de la morsure peut déterminer le choix des proies chez deux lézards lacertidés qui cohabitent. Pour ce faire, nous avons mesuré la force de la morsure in vivo dans un échantillon important de lézards des espèces *Podarcis muralis* et *Lacerta vivipara*. Nous avons également examiné l'importance écologique de la force des morsures en mesurant la dureté de plusieurs des proies naturelles des deux lézards. Nos résultats corroborent les prédictions des modèles biomécaniques de morsures chez les lézards et indique que les gros lézards et les lézards à grosse tête ont une morsure plus robuste. Étonnamment, la taille de la tête a une excellente valeur prédictive de la performance de la morsure chez les espèces étudiées. Nous démontrons en outre que la force de la morsure peut constituer une variable écologique importante qui pourrait éventuellement servir à expliquer les patterns d'utilisation des ressources alimentaires, les changements dans le régime alimentaire au cours du développement et le dimorphisme sexuel de l'alimentation.

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Introduction

A remarkable finding from many studies investigating patterns of diet utilization and selection in lizards is the apparent overall similarity in diet of related species. True feeding specialists are rare, and most lizards include a large variety of prey in their diet (Greene 1982). Even closely related sympatric species frequently show largely overlapping diets, indicating, at first glance, little selection for divergence in dietary patterns. European lacertids are prime examples of this, and tend to be generalists with overlapping size and habitat ranges (Arnold 1987, 1989). Moreover, most lacertids are considered to be food generalists (Diaz 1995) whose diet closely matches the abundance of prey in the environment (e.g., Nourira 1983; Mou 1987; Sorci 1990; Pollo and Perez-Mellado 1988, 1991). Accordingly, lacertid lizards do not show large morphological differentiations that might indicate potential differences in feeding strategy (Arnold 1987).

However, general correlations between morphology and diet should be treated with caution, as it has been shown pre-

viously that even small morphological differences may have large ecological implications (Moreno and Carrascal 1993; Van Damme et al. 1998). As a direct link between morphology and ecology is not always obvious (or even present), direct testing of the performance of the features related to the function of interest is required (Arnold 1983). One of the performance features that could be crucial for increasing the prey spectrum of lizards is bite force. It has been implied that larger bite forces are important for the inclusion of plant material in the diet (Sokol 1967; Herrel et al. 1998a, 1998b), and it has been demonstrated that larger prey potentially become available through an increase in bite force (Herrel et al. 1999a).

Here we examine bite-force patterns in two lacertid lizards, *Podarcis muralis* (Laurenti 1768) and *Lacerta vivipara* (Jacquin 1787), that occur sympatrically throughout most of Western Europe (Arnold et al. 1978). While *P. muralis* is highly territorial (Edsman 1989), *L. vivipara* is not. However, both species are known to be sexually dimorphic in head size (Arnold 1987). By comparing bite-force patterns with experimentally determined hardness of known prey of both species, we evaluate the potential importance of bite performance in shaping patterns of resource use and sexual dimorphism in head size.

Materials and methods

Animals

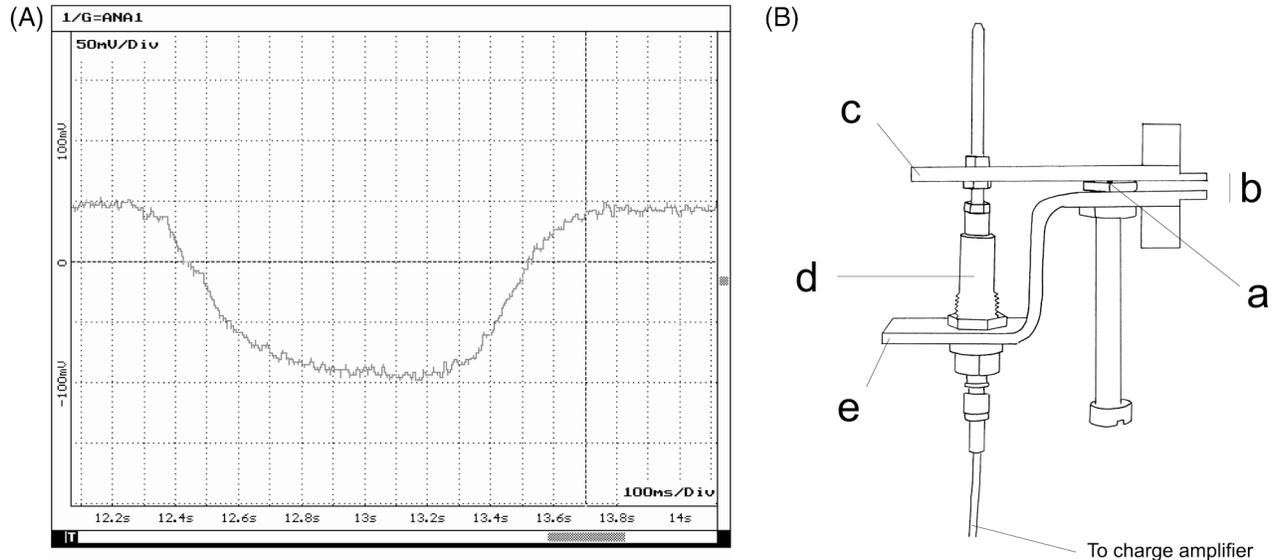
We tested 37 adult *P. muralis* (16 males, body mass 3.13–8.02 g;

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Fig. 1. (A) Representative trace of force recordings made during a prolonged bite of a male *Podarcis muralis*. The actual bite force is measured as the difference between the base line and the maximal downward displacement of the force tracing. (B) Experimental set-up used to register bite forces in vivo. The animal bites on the bite plates (b), which causes the upper plate (c) to rotate, thus exerting pull on the piezoelectric force transducer (d). The distance between the bite plates is adjustable. a, fulcrum; e, holder; modified after Herrel et al. 1999a).



21 females, body mass 2.12–6.72 g) and 36 adult *L. vivipara* (20 males, body mass 2.44–4.00 g; 16 females, body mass 1.23–4.32 g). All animals were caught by hand or noose in Kalmthout (*L. vivipara*) or Hotton (*P. muralis* and *L. vivipara*), Belgium, and transferred to the laboratory at the University of Antwerp. The animals were housed in groups of four in separate terraria and kept on a 12 h light : 12 h dark cycle. Temperatures varied between 28°C (day) and 20°C (night); an incandescent bulb provided a basking place at a higher temperature (40°C). Water and live insects (crickets, mealworms, and grasshoppers) were provided ad libitum. Upon termination of the experiments, all animals were released at their exact site of capture. While in the laboratory, animals were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care.

Bite forces

We measured bite forces in vivo using an isometric Kistler force transducer (type 9203, Kistler Inc., Wintherthur, Switzerland) mounted on a purpose-built holder (Fig. 1) and connected to a Kistler charge amplifier (type 5058A, Kistler Inc.). Biting causes the upper plate to pivot around the fulcrum, and thus pull is exerted on the transducer. Bite forces were recorded using a portable computer equipped with an A/D converter (PC-Scope T512, Imtec GmbH, Backnang, Germany).

We placed all animals in an incubator at 35°C (optimal performance temperature; see Bauwens et al. 1995). After one hour the lizards were captured, which resulted in a very characteristic threat response with the jaws opened maximally. The free end of the holder (bite plates; see Fig. 1) was then placed between the jaws of the animal. This always provoked forceful and prolonged biting. The point of application of bite forces was standardized by mounting acrylic stops on the free end of the holder (see Fig. 1). We repeated these measurements five times for each animal, with an intertrial interval of at least 30 min, which the lizards spent in the incubator. The maximal value obtained during such a recording session was considered to be the maximal bite force for that animal. Bite forces were regressed against snout–vent length (SVL) and head measures for male and female lizards separately. To remove the influence of body size on the variables, we used analyses

of covariance (ANCOVAs) with SVL as covariate. All analyses were calculated using the Statistica (version 5.0) and SPSS (version 5.01) statistical packages.

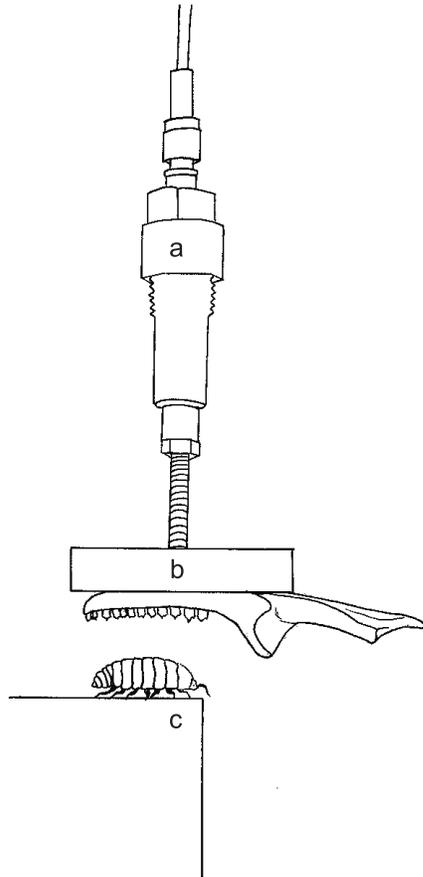
Morphometrics

Just after the experiments, we took the following morphological measurements from each animal: body mass, SVL, head length, head width, head height, and lower-jaw length. Head length was measured from the anterior end of the premaxillary to the posterior edge of the parietal bone. Head width was measured at the widest part of the skull and includes the bulging of the m. pterygoideus. Head height was measured at the highest part of the skull just posterior to the orbita. Lower-jaw length was measured from the anterior end of the dentary bone to the posterior edge of the retroarticular process.

Prey characteristics

The only available data on insect prey hardness are those presented in Herrel et al. (1996), Andrews and Bertram (1997), and Herrel et al. (1999a, 1999b). As these data concern a limited number of prey types, we determined the hardness of additional prey types eaten by the lizards used in this study (Isopoda, Arachnida; see Heulin 1986; Mou 1987). For this purpose we removed the lower jaw of a preserved *P. muralis* specimen and partially embedded it in resin, leaving the tooth rows free. The hardened resin was then mounted on a Kistler force transducer (type 9203, Kistler Inc.) connected to a charge amplifier (model 463A, PCB Piezotronics Inc., New York) and chart recorder (Brush 481 recorder, Gould Inc., Valley View, Ohio). We subsequently crushed the prey items by pushing the jaw onto the prey (oriented transversely to the tooth row) until the teeth penetrated the exoskeleton and structural failure of the prey occurred (Fig. 2). For all prey items tested we recorded the hardness of the hardest part (usually the head and prothorax). Prey types and sample sizes are given in Table 6. We used regression analyses to assess relations between prey size and hardness, and ANCOVAs to compare hardness among prey types using the data gathered here and those from previous studies in which a similar methodology was used (Herrel et al. 1996, 1999a, 1999b). Note, however, that for the data in the former study the

Fig. 2. Experimental procedure employed to determine prey hardness. Note that in the actual experiments the prey was oriented transversely with respect to the tooth rows. To determine prey hardness the lower jaw is slowly pressed against the prey. Simultaneously the forces exerted on the transducer are recorded. Failure of the prey exoskeleton is characterized by a sudden decrease in the force-output curve. *a*, isometric force transducer; *b*, lower jaw of *P. muralis* partially embedded in resin; *c*, prey item.



lower jaw of *Podarcis hispanica* was used and in the latter study the lower jaw of *Gallotia galloti* was used. However, as the dentition is similar in most lacertid lizards, this is not expected to affect the observed prey-hardness patterns greatly.

Feeding experiments

For selected arthropod prey, a series of feeding experiments was conducted using a subset of lizards from both species. The lizards were transferred to a clean test cage and allowed to adjust to their new environment for at least 30 min prior to experimentation. Next, a prey item was introduced into the cage, the feeding behaviour of the animals was observed, and the handling time and number of bites needed to process (i.e., crush and transport) an item were recorded. Individuals were tested twice for each prey type, with at least 1 day between successive trials. A total of eight different prey types were used and at least three individuals of each species were tested with each prey type. The prey consisted of large crickets (15 ± 3 mm), small crickets (5 ± 3 mm), aphids (10 ± 4 mm), beetles (5 ± 2 mm), small grasshoppers (7 ± 5 mm), spiders (6 ± 3 mm), mealworms (20 ± 3 mm), and ants (8 ± 2 mm). As individual effects were not significant for the variables recorded, data were pooled for all individuals. A second experiment consisted of a prey-preference test. Here, two different prey were

offered simultaneously and we recorded which prey was taken first by the animals. In these experiments large crickets were contrasted with small ones and grasshoppers were contrasted with spiders. These combinations were chosen to evaluate the effects of size (small versus large crickets) and hardness (soft spiders versus hard grasshoppers, both being common items in the diet of both species). Again at least two trials for three individuals per species were conducted.

Results

Morphometrics

On average, the *P. muralis* specimens were larger than the *L. vivipara* specimens (ANOVA, $F_{[1,70]} = 23.41$, $P < 0.001$). Within each species, no difference in SVL was found between the sexes (ANOVA, $F_{[1,70]} = 0.003$, $P = 0.96$). Both species show a positive relationship between head and body measures (except for head height vs. SVL in female *P. muralis*; see Table 1, Fig. 3). Within both species, male lizards have significantly longer, wider, and higher heads than female conspecifics of a similar size (see Tables 2, 3). Additionally, males have significantly longer lower jaws and are generally heavier than similarly sized females (Table 2).

Male and female *P. muralis* have longer and wider heads than *L. vivipara* of the same sex (ANCOVA, slopes, $P > 0.05$; intercepts, $P < 0.05$; see Fig. 3). Head heights do not differ between males of either species (ANCOVA, slopes and intercepts, $P > 0.05$). Yet male *L. vivipara* have head lengths and head heights comparable to those of female *P. muralis* (ANCOVA, slopes and intercepts, $P > 0.05$). In contrast, female *P. muralis* tend to have wider heads (ANCOVA, slopes, $P > 0.05$; intercepts, $F_{[1,38]} = 7.74$, $P < 0.01$) and longer lower jaws than male *L. vivipara* (ANCOVA, slopes, $P > 0.05$; intercepts, $F_{[1,38]} = 9.75$, $P < 0.01$).

Bite forces

In both species bite force increases with SVL, head length, lower-jaw length, head width, and head height (except for head height vs. bite force in male *P. muralis*; see Table 4). This implies that males can bite harder than similarly sized females of the same species (ANCOVA, *L. vivipara*: slopes, $F_{[1,33]} = 0.03$, $P = 0.85$; intercepts, $F_{[1,34]} = 104.94$, $P < 0.001$; *P. muralis*: slopes, $F_{[1,33]} = 0.11$, $P = 0.74$; intercepts, $F_{[1,34]} = 43.41$, $P < 0.001$). However, males do not bite harder than females with a similar head size (head length, head width, head height; see Table 5, Fig. 3), indicating that head shape is similar in the two sexes.

When species are compared, *P. muralis* bite harder than *L. vivipara* of the same sex and of similar body size (ANCOVA, male–male: slopes, $F_{[1,32]} = 2.08$, $P = 0.16$; intercepts, $F_{[1,33]} = 30.25$, $P < 0.001$; female–female: slopes, $F_{[1,34]} = 6.34$, $P < 0.05$; intercepts, $F_{[1,35]} = 11.08$, $P < 0.01$). Bite forces of male *L. vivipara* are similar to those of similarly sized female *P. muralis* (ANCOVA, slopes, $F_{[1,38]} = 3.86$, $P = 0.06$; intercepts, $F_{[1,39]} = 1.89$, $P = 0.18$) (Fig. 3).

Prey hardness

Prey hardness increases with size for most prey types tested (Fig. 4). Only *Tenebrio molitor* (all developmental stages tested) and one of the spiders tested (*Tetragnatha extensa*) do not show such a relationship. The residuals of

Table 1. Allometries of head dimensions (mm) and bite force (N) versus SVL (mm).

Variable	Females			Males		
	Slope	Intercept	r ²	Slope	Intercept	r ²
<i>Podarcis muralis</i>						
Head length	0.87	-0.37	0.84	0.62	-0.01	0.61
Head width	0.57	-0.16	0.53	0.82	-0.54	0.79
Head height	ns	ns	0.09*	0.89	-0.76	0.50
Lower-jaw length	1.18	-0.99	0.79	0.95	-0.53	0.56
Bite force	4.5	-7.4	0.75	4.14	-6.47	0.58
<i>Lacerta vivipara</i>						
Head length	0.52	0.09	0.72	0.73	-0.20	0.71
Head width	0.57	-0.19	0.71	0.68	-0.32	0.62
Head height	0.53	-0.24	0.48	0.87	-0.74	0.61
Lower-jaw length	0.53	0.09	0.76	0.85	-0.40	0.79
Bite force	2.55	-4.21	0.82	2.44	-3.84	0.58

Note: All regressions are based on log₁₀-transformed data.
*Not significantly different from 0.

Table 2. Morphometrics and in vivo bite forces.

Variable	Females	Males
<i>P. muralis</i>		
<i>n</i>	21	16
Body mass (g)	4.40 ± 1.46	4.73 ± 1.29
SVL (mm)	55.55 ± 6.35	56.25 ± 5.56
Head length (mm)	12.00 ± 1.05	14.08 ± 1.30
Head width (mm)	6.90 ± 0.59	7.95 ± 0.75
Head height (mm)	5.36 ± 0.58	6.31 ± 0.77
Lower-jaw length (mm)	11.85 ± 1.72	13.53 ± 1.66
Bite force (N)	11.85 ± 1.72	6.52 ± 3.01
<i>L. vivipara</i>		
<i>n</i>	17	20
Body mass (g)	2.59 ± 0.74	3.04 ± 0.54
SVL (mm)	50.44 ± 5.21	49.69 ± 3.09
Head length (mm)	9.62 ± 0.62	10.90 ± 0.58
Head width (mm)	6.09 ± 0.42	6.79 ± 0.36
Head height (mm)	4.59 ± 0.36	5.43 ± 0.37
Lower-jaw length (mm)	10.04 ± 0.63	11.10 ± 0.66
Bite force (N)	1.42 ± 0.44	2.08 ± 0.42

Note: Values are given as the averages ± standard deviation; *n*, sample size; SVL, snout-vent length.

the log₁₀(hardness) versus log₁₀(mass) relationships varied among prey items (ANOVA, $F_{[1,192]} = 343.78$, $P < 0.001$). Spiders are significantly softer and wood lice generally harder than all other prey tested (Table 6; Tukey's HSD test for unequal sample sizes).

Feeding experiments

All individuals of both species refused to eat ants. As *L. vivipara* refused to eat aphids and beetles, these data were not included in the subsequent analysis. A MANOVA performed on the data from the feeding experiment indicated clear species (Rao's $R_{2,40} = 4.34$; $P < 0.05$) and prey (Rao's $R_{8,80} = 9.02$; $P < 0.01$) effects; interaction effects were not significant (Rao's $R_{8,80} = 1.31$; $P = 0.25$). *Lacerta vivipara* had longer handling times and used a larger number of bites to process prey than did *P. muralis*. For both species of lizards, handling times were equal for large crickets and mealworms,

Table 3. Results of ANCOVAs (with SVL as covariate) testing for differences in head dimensions between the sexes.

	Slope		Intercept	
	$F_{[1,33]}$	<i>P</i>	$F_{[1,34]}$	<i>P</i>
<i>L. vivipara</i>				
Head length	2.13	0.153	150.90	<0.001
Head height	2.26	0.142	106.41	<0.001
Head width	0.45	0.506	99.53	<0.001
Lower-jaw length	5.82	0.022	106.59	<0.001
<i>P. muralis</i>				
Head length	2.21	0.147	75.89	<0.001
Head height	3.30	0.080	20.35	<0.001
Head width	1.92	0.175	50.91	<0.001
Lower-jaw length	0.86	0.36	22.56	<0.001

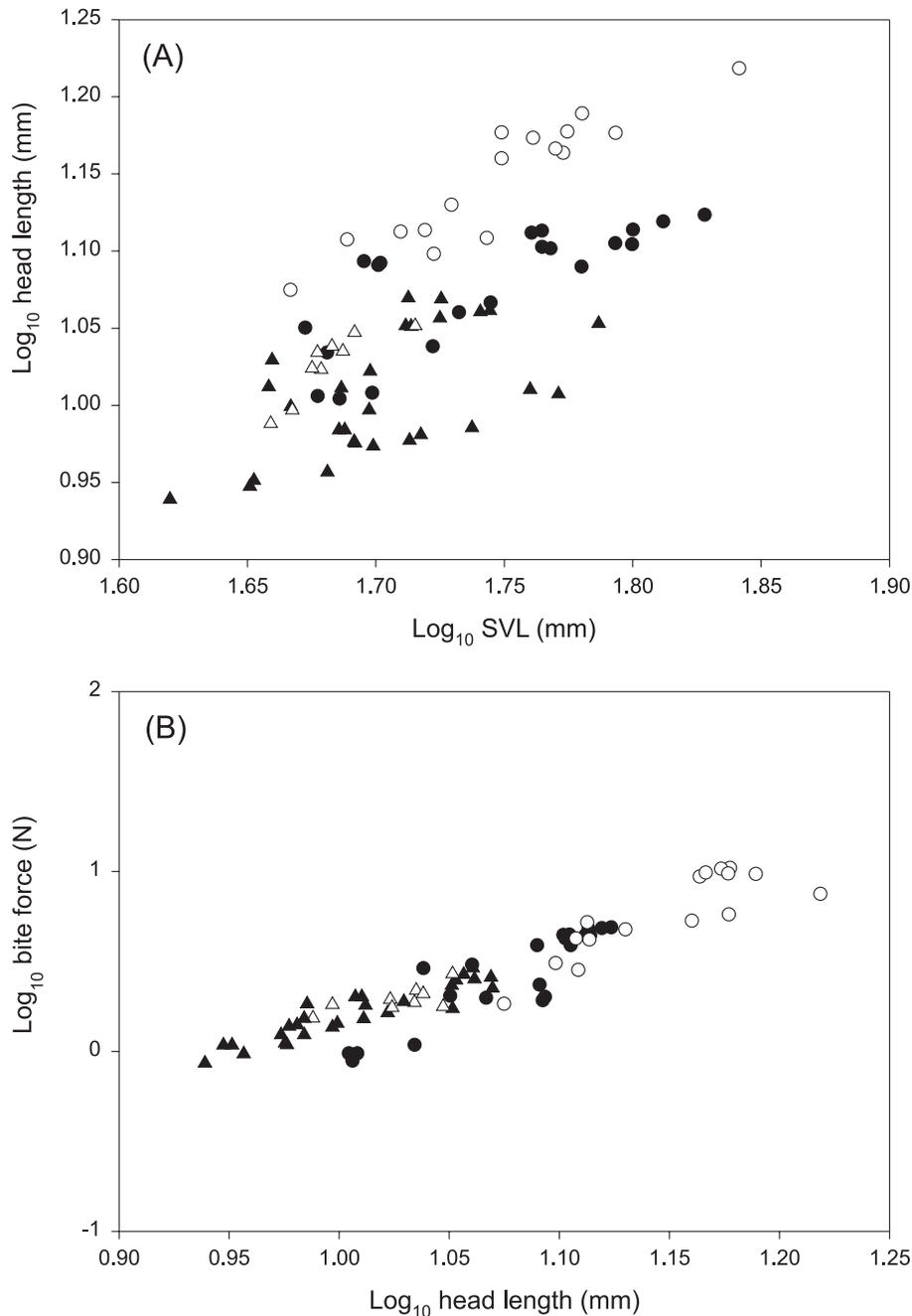
which were both significantly longer than for all other prey offered (see Table 7). Although significantly fewer bites were needed to process small crickets than all other prey, small crickets were largely ignored by individuals of both species (in only one out of six trials did a *P. muralis* eat a small cricket). The largest number of bites was observed for large cricket and mealworm feeding sequences (Table 7).

The results of the prey-preference experiment showed that individuals of both species clearly preferred large over small crickets despite the longer handling times and larger number of bites associated. In all trials, large crickets were captured before small ones. The results of the second prey-preference experiment showed clear differences between the two species. Whereas *P. muralis* preferred grasshoppers over spiders in 67% of all trials, *L. vivipara* preferred spiders over grasshoppers in 85% of all trials.

Discussion

Previous studies of biting in lizards indicated that head size and shape, size and orientation of the jaw-closer muscle, differences in lever arms, and the physiological properties of the jaw muscles can all have an important effect on bite force in lizards (see Herrel et al. 1998a, 1998b, 1999b). The

Fig. 3. Relationships between body and head size (A) and between head size and bite force (B) in *P. muralis* and *Lacerta vivipara*. All head measures show a clear relationship with body size (here head length), but differ between the species and the sexes. Although there are clear inter- and intra-specific differences in bite force (see Results), for a given head size (again head length), the species and sexes no longer differ in bite capacity. Open symbols represent males and closed symbols females. Circles represent *P. muralis* and triangles *L. vivipara*. SVL, snout–vent length.



first implication of those studies, which is supported by the present data, is that for a given head shape, larger lizards are able to bite harder. Secondly, similarly sized lizards with larger heads (length, width, height) are expected, and observed, to bite harder (e.g., compare male and female lizards within species). Given the complexity of the jaw system in lizards, it was not expected that simple external head measures would be such good predictors of bite force. Moreover, as there are no differences in bite force when head

shape is taken into account, differences in bite force are due solely to the increase in overall head size in the lizards examined here. This might have important consequences for field studies, as simple morphometric characters seem to be good predictors of bite capacity in these species.

What are the implications of the bite forces for diet?

The predominant prey classes consumed by both species of lizards considered here are small arthropods such as

Table 4. Allometries of bite force versus head dimensions.

Variable	Females			Males		
	Slope	Intercept	r^2	Slope	Intercept	r^2
<i>P. muralis</i>						
Head length	5.84	-5.87	0.80	4.94	-4.91	0.74
Head width	5.57	-4.24	0.70	4.04	-2.87	0.47
Head height	2.94	-1.71	0.30	ns	ns	0.13
Lower-jaw length	3.83	-3.67	0.95	4.12	-3.89	0.91
<i>L. vivipara</i>						
Head length	4.13	-3.92	0.81	2.85	-2.65	0.60
Head width	3.69	-2.76	0.78	2.26	-1.57	0.37
Head height	2.78	-1.70	0.57	1.87	-1.06	0.42
Lower-jaw length	3.63	-3.49	0.62	2.72	-2.53	0.66

Note: All regressions are based on \log_{10} -transformed data.

Table 5. ANCOVAs of bite-force data.

Covariate (SVL)	Slope		Intercept	
	$F_{[1,33]}$	P	$F_{[1,34]}$	P
<i>L. vivipara</i> : comparisons between the sexes				
Head length	2.89	0.098	0.40	0.53
Head height	1.26	0.27	0.01	0.94
Head width	2.87	0.10	0.75	0.39
Lower-jaw length	1.17	0.29	1.68	0.20
<i>P. muralis</i> : comparisons between the sexes				
Head length	0.76	0.39	0.55	0.46
Head height	0.82	0.37	3.75	0.061
Head width	1.24	0.27	0.28	0.60
Lower-jaw length	0.56	0.46	18.89	<0.001

spiders, crickets, wood lice, and beetles (Avery 1962, 1966; Itämies and Koskela 1971; Koponen and Hietakangas 1972; Strijbosch et al. 1980a, 1980b; Pilorge 1982; Heulin 1986; Mou 1987; Pérez-Mellado and Corti 1993; Richard and Lapini 1993; Roig-Fernandez 1997). As the force needed to crush arthropod prey falls within the range of bite forces observed for both lizard species (Fig. 4), bite performance seems to be an ecologically relevant variable.

As some prey categories are significantly harder than others for a given size, and there is a clear relation between prey size and prey hardness, differences in bite force could influence prey selection in these lizards. In the present case, as bite forces are generally higher for *P. muralis*, the potential prey spectrum is also larger for *P. muralis* than for *L. vivipara* (see Fig. 4). However, the potential prey spectrum might differ from the actual prey eaten, therefore a question arises as to what kinds and size of prey the lizards can be expected to take, based on theoretical reasoning (“optimal” foraging; see McArthur and Pianka 1966; Schoener 1971; Arnold 1993; Emerson et al. 1994; Roughgarden 1995). Apart from a multitude of ecological variables that might influence the availability of prey for lizards, functional determinants of the feeding system are also likely to influence diet. As head size determines bite force, which in turn affects handling time (see Table 7), and as handling time is directly related to energy consumption (Pough and Andrews 1985), having a larger head will reduce the energetic cost of feeding. This

implies that lizards would be expected to minimize handling time by selecting specific prey sizes and (or) types. Moreover, as there are positive relations between prey size and handling time (for a given head size) on the one hand and prey size and energetic content of the prey on the other (Roughgarden 1995), a trade-off seems to occur. Taking into account the fact that most arthropod prey are roughly similar in energetic content (Cummins and Wuycheck 1971), lizards should prefer softer and smaller prey items. However, as an increase in bite force will reduce handling time, tougher prey also become energetically interesting. In summary, for similarly sized lizards, those having lower bite forces (as a result of their smaller head) should select (i) softer and (ii) smaller prey, even if they are not physically constrained to take larger and (or) tougher prey.

Partial support for the above-stated hypotheses (lizards with lower bite forces should select softer and smaller prey) is provided by the results of the prey-preference tests conducted here. When given the choice between two prey items of the same type, the lacertid lizards studied here choose the larger one. However, when provided with two prey types clearly differing in hardness, the species with the lower bite force selects the softer prey item. Additional support can be found in the literature. Whereas the main food categories eaten by *L. vivipara* are typically “soft” prey such as Araneae, Homoptera, and Diptera (Avery 1962, 1966; Itämies and Koskela 1971; Koponen and Hietakangas 1972; Pilorge 1982; Heulin 1986; Roig 1998), *P. muralis* feeds predominantly on “harder” arthropods such as Coleoptera, Isopoda, and Homoptera (Strijbosch et al. 1980a, 1980b; Mou 1987; Richard and Lapini 1993; Pérez-Mellado and Corti 1993). Moreover, in areas where interspecific competition is low, *P. muralis* shows a shift in its diet preference towards softer prey categories such as Arachnida, Diptera, and Gastropoda (Mou and Barbault 1986). Thus there seem to be indications that the food niches of the two lacertid species studied here differ in a way predicted by our observations on bite force and prey-handling behaviour. Although food-niche differentiation, through differences in bite force, could reduce trophic competition between these species, this should be tested explicitly in a syntopic population of *P. muralis* and *L. vivipara*.

The data gathered here may also have implications for the observed ontogenetic dietary shifts in many lizard species. One of the well-documented cases of such a shift in diet in a

Fig. 4. Allometries of prey mass versus prey hardness. The maximal bite forces for male and female *P. muralis* and *L. vivipara* are superimposed. Data for *A. domestica*, *L. migratoria*, and *T. molitor* larvae are taken from Herrel et al. 1996; data for *G. campestris* and the unidentified tenebrionid beetle are taken from Herrel et al. 1999a.

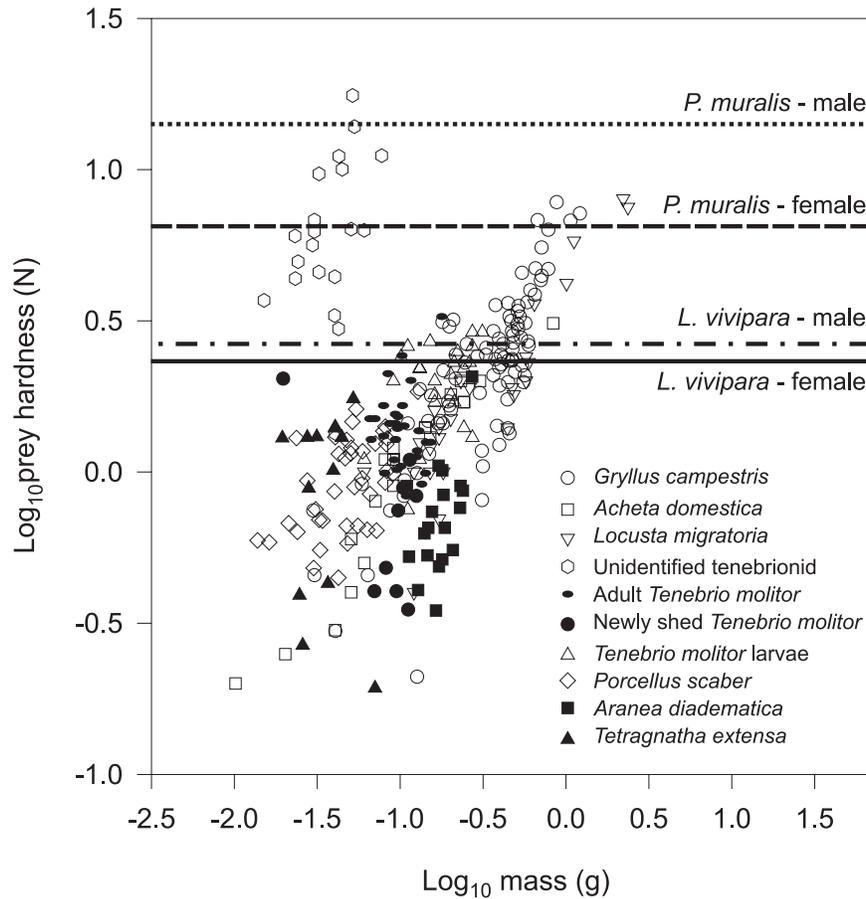


Table 6. Average prey hardness.

Prey	N	Mass (g)	Hardness (N)
<i>Mealworm (Tenebrio molitor)</i>			
Larvae	24	0.18 ± 0.07	2.02 ± 0.58
Adults	29	0.11 ± 0.01	1.51 ± 0.10
Newly shed	12	0.98 ± 0.03	0.85 ± 0.46
<i>Spider (Tetragnatha extensa)</i>			
Fat-bodied spider (<i>Araneus diadematus</i>)	20	0.17 ± 0.04	0.76 ± 0.37
<i>Field cricket (Gryllus campestris)</i>			
House cricket (<i>Acheta domestica</i>)	20	0.15 ± 0.17	1.18 ± 0.72
<i>Grasshopper (Locusta migratoria)</i>			
Isopod (<i>Porcellus scaber</i>)	38	0.51 ± 0.60	2.33 ± 2.01
Unidentified tenebrionid beetle*	20	7.76 ± 1.25 mm (length)	7.01 ± 4.03

Note: Values are given as the average ± standard deviation.

*The unidentified tenebrionid beetle was found completely dried in the field, therefore the average length is reported instead of mass. Forces are expected to be even higher for fresh animals.

lacertid lizard (*Lacerta bilineata*) might be explained by differences in bite performance. In this species juveniles prey mainly upon Orthoptera and spiders, whereas adults eat mainly beetles and isopods (Angelici et al. 1997). These differences in diet correspond nicely to the hardness data for prey items tested here: while spiders are significantly softer

than other prey, wood lice and Coleoptera are generally harder. The smaller juveniles might simply be physically constrained (i.e., have insufficient bite force) to process these harder prey successfully. Presumably the well-known ontogenetic dietary shift from insectivory to partial herbivory in some species (e.g., Castilla et al. 1991) might also be

Table 7. Results of the feeding experiments, showing mean handling times and numbers of bites needed to process selected arthropod prey.

Prey	<i>P. muralis</i>		<i>L. vivipara</i>	
	Handling time (s)	No. of bites	Handling time (s)	No. of bites
Large cricket	41.60 ± 11.37	37.20 ± 5.36	69.33 ± 11.54	56.00 ± 11.15
Small cricket	11.00 ± 0.00	12.00 ± 0.00	7.00 ± 7.07	8.50 ± 2.12
Aphid	19.40 ± 8.32	34.40 ± 13.72	—	—
Beetle	14.00 ± 1.41	25.00 ± 4.24	—	—
Grasshopper	12.75 ± 10.08	16.13 ± 10.29	23.2 ± 27.88	29.40 ± 17.83
Spider	21.57 ± 11.49	21.86 ± 9.69	31.33 ± 25.54	36.67 ± 19.92
Mealworm	61.83 ± 40.86	54.00 ± 12.21	273.00 ± 168.68	143.6 ± 62.65

Note: Values are given as the average ± standard deviation.

explained by differences in bite capacity. Preliminary data on the resistance of plant material to mechanical deformation support this hypothesis (Herrel et al. 1999b).

Sexual dimorphism, territoriality, bite forces, and food-niche separation

Two often-cited hypotheses explaining sexual dimorphism in head size in lizards are (1) sexual selection on males competing for females and (2) natural selection leading to reduced trophic competition between the sexes. One of the implicit assumptions of the latter hypothesis is that the larger headed sex benefits from an increased gape and (or) bite force. Obviously animals with larger heads will be able to open their jaws wider, which gives them an advantage over the other sex. Additionally, the data gathered in this study indicate that within both lacertid species studied here, animals with larger (longer, wider, higher) heads are capable of biting harder. As an increase in bite performance increases the potential prey spectrum for the lizards, and as the toughness of natural prey items of both species overlaps the range of bite forces measured, the basic assumption of this hypothesis is met.

As in most European lacertid species, male–male combat is common, and as males bite and hold onto females during copulation, sexual selection undoubtedly plays an important role in shaping the intraspecific dimorphism in head size. However, once the sexes differ in head size, the correlated increase in bite force creates the possibility of niche divergence between them (but see Herrel et al. 1999a). If such intersexual niche divergence takes place, it can in turn contribute to the maintenance of and (or) increase in sexual dimorphism in head size. Though these two mechanisms are not mutually exclusive, in the case of highly territorial species, where male–male combat is common (such as *P. muralis*; Edsman 1989), sexual selection most likely precedes intersexual niche divergence where it is present.

Lacerta vivipara, on the other hand, seems to be a largely nonterritorial species, and consequently, aggressive male–male interactions are rarely observed. A recent study (Roig-Fernandez 1997) of prey consumption in a Pyrenean population of *L. vivipara* indicated important intersexual differences in diet. While both sexes avoid tougher prey such as Coleoptera and Luloidea and select soft prey such as Aranea and Diptera, only adult males select the larger prey classes (which are harder to crush, and thus require greater bite forces). Although it is tempting to speculate, the question of

whether sexual dimorphism in head size in these lizard species is the direct result of natural selection leading to food-niche separation, or is due to the need for male lizards to bite harder to hold onto the females during copulation, or is just an ancestral trait that is retained in these species can only be resolved by a broad comparative study of the relation between bite-force patterns and sexual dimorphism in head size.

Clearly, bite capacity is an interesting and ecologically relevant performance feature that could help to explain patterns of resource use, niche divergence, and sexual dimorphism in lizards. Unfortunately, the available dietary data often do not provide enough resolution in terms of sexual differences in diet and selection of specific prey types and sizes to allow a critical test of many of the hypotheses proposed here.

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References

- Andrews, C., and Bertram, J.E.A. 1997. Mechanical work as a determinant of prey-handling behavior in the Tokay gecko (*Gekko gecko*). *Physiol. Zool.* **70**: 193–201.
- Angelici, F.M., Luiselli, L., and Rugiero, L. 1997. Food habits of the green lizard, *Lacerta bilineata*, in central Italy and a reliability test of faecal pellet analysis. *Ital. J. Zool.* **64**: 267–272.
- Arnold, E.N. 1987. Resource partitioning among lacertid lizards in southern Europe. *J. Zool. Ser. B*, **1**(4): 739–782.
- Arnold, E.N. 1989. Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old-World family of lizards derived from morphology. *Bull. Br. Mus. (Nat. Hist.) Zool.* **55**: 209–257.
- Arnold, E.N., Burton, J.A., and Oviden, D.W. 1978. Reptiles and amphibians of Britain and Europe. Collins, London.
- Arnold, S.J. 1983. Morphology, performance and fitness. *Am. Zool.* **23**: 347–361.

- Arnold, S.J. 1993. Foraging theory and prey size – predator size relations in snakes. *In* Snakes: ecology and behavior. *Edited by* R.A. Seigel and J.I. Collins. McGraw-Hill, New York. pp. 87–112.
- Avery, R.A. 1962. Notes on the ecology of *Lacerta vivipara* L. *Br. J. Herpetol.* **3**: 36–38.
- Avery, R.A. 1966. Food and feeding habits of the common lizard (*Lacerta vivipara*) in the west of England. *J. Zool.* (1965–1984), **149**: 115–121.
- Bauwens, D., Garland, T., Castilla, A.M., and Van Damme, R. 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioral covariation. *Evolution*, **49**: 848–863.
- Castilla, A.M., Bauwens, D., and Llorente G.L. 1991. Diet composition of the lizard *Lacerta lepida* in central Spain. *J. Herpetol.* **25**: 30–36.
- Cummins, K.W., and Wuycheck, J.C. 1971. Caloric equivalents for investigations in ecological energetics. *Mitt. Int. Ver. Theor. Angew. Limnol.* **18**: 1–160.
- Diaz, J.A. 1995. Prey selection by lacertid lizards: a short review. *Herpetol. J.* **5**: 245–251.
- Edsman, L. 1989. Territoriality and competition in wall lizards. Ph.D. dissertation, University of Stockholm, Stockholm, Sweden.
- Emerson, S.B., Greene, H.W., and Charnov, E.L. 1994. Allometric aspects of predator–prey interactions. *In* Ecological morphology. *Edited by* P.C. Wainwright and S.M. Reilly. University of Chicago Press, Chicago. pp. 123–139.
- Greene, H.W. 1982. Dietary and phenotypic diversity in lizards: why are some organisms specialised? *In* Environmental adaptation and evolution. *Edited by* D. Mossakowski and G. Roth. Gustav Fischer Verlag, New York. pp. 107–128.
- Herrel, A., Van Damme, R., and De Vree, F. 1996. Testing the niche divergence hypothesis by bite force analysis. *Neth. J. Zool.* **46**: 253–262.
- Herrel, A., Aerts, P., and De Vree, F. 1998a. Static biting in lizards: functional morphology of the temporal ligaments. *J. Zool.* (Lond.), **244**: 135–143.
- Herrel, A., Aerts, P., and De Vree, F. 1998b. Ecomorphology of the lizard feeding apparatus: a modelling approach. *Neth. J. Zool.* **48**: 1–25.
- Herrel, A., Spithoven, L., Van Damme, R., and De Vree, F. 1999a. Sexual dimorphism of head size in *Gallotia galloti*; testing the niche divergence hypothesis by functional analyses. *Funct. Ecol.* **13**: 289–297.
- Herrel, A., Verstappen, M., and De Vree, F. 1999b. Modulatory complexity of the feeding repertoire in scincid lizards. *J. Comp. Physiol. A*, **184**: 501–518.
- Heulin, B. 1986. Régime alimentaire estival et utilisation des ressources trophiques dans trois populations de *Lacerta vivipara*. *Acta Oecol.* **7**: 135–150.
- Itämies, J., and Koskela, P. 1971. Diet of the common lizard (*Lacerta vivipara* Jacq.). *Aquilo Ser. Zool.* **11**: 37–43.
- Koponen, S., and Hietakangas, H. 1972. Food of the common lizard (*Lacerta vivipara* Jacquin) on a peat bog in southwestern Finland. *Ann. Zool. Fenn.* **9**: 191–192.
- McArthur, R.H., and Pianka, E.R. 1966. On the optimal use of a patchy environment. *Am. Nat.* **100**: 603–609.
- Moreno, E., and Carrascal, L.M. 1993. Leg morphology and feeding postures in four *Parus* species: an experimental ecomorphological approach. *Ecology*, **74**: 2037–2044.
- Mou, Y.-P. 1987. Ecologie trophique d'une population de lézards des murailles *Podarcis muralis* dans l'ouest de la France. *Rev. Ecol. Terre Vie*, **42**: 81–100.
- Mou, Y.-P., and Barbault, R. 1986. Régime alimentaire d'une population de lézard des murailles, *Podarcis muralis* (Laurent, 1768) dans le sud-ouest de la France. *Amphib.-Reptilia*, **7**: 171–180.
- Nouira, S. 1983. Partage des ressources alimentaires entre deux Lacertidae sympatriques des îles Kerkennah (Tunésie) : *Acanthodactylus pardalis* et *Eremias olivieri*. *Bull. Soc. Zool. Fr.* **108**: 477–483.
- Pérez-Mellado, V., and Corti, C. 1993. Dietary adaptations and herbivory in lacertid lizards of the genus *Podarcis* from western Mediterranean islands (Reptilia: Sauria). *Bonn. Zool. Beitr.* **44**: 193–220.
- Pilorge, T. 1982. Régime alimentaire de *Lacerta vivipara* et *Rana temporaria* dans deux populations sympatriques du Puy de Dôme. *Amphib.-Reptilia*, **3**: 27–31.
- Pollo, C.J., and Perez-Mellado, V. 1988. Trophic ecology of a taxocenosis of Mediterranean species of Lacertidae. *Ecol. Mediterr.* **14**: 131–147.
- Pollo, C.J., and Perez-Mellado, V. 1991. An analysis of a Mediterranean assemblage of three small lacertid lizards in central Spain. *Acta Oecol.* **12**: 655–671.
- Pough, F.H., and Andrews, R.M. 1985. Energy costs of subduing and swallowing prey for a lizard. *Ecology*, **66**: 1525–1533.
- Richard, J., and Lapini, L. 1993. Trophic niche overlap in syntopic populations of *Lacerta horvathi* and *Podarcis muralis* (Reptilia, Lacertidae). *Atti Mus. Civ. Stor. Nat. Trieste*, **45**: 151–157.
- Roig-Fernandez, J.M. 1997. Ecología trófica de una población pirenaica de lagartija de turbera *Zootoca vivipara* (Jacquin, 1787). Tesis de licenciatura, University of Barcelona. Barcelona, Spain.
- Roughgarden, J. 1995. *Anolis* lizards of the Caribbean. Oxford University Press, New York.
- Schoener, T.W. 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* **2**: 369–404.
- Sokol, O.M. 1967. Herbivory in lizards. *Evolution*, **21**: 192–194.
- Sorci, G. 1990. Nicchia trofica di quattro specie di Lacertidae in Sicilia. *Nat. Sicil. Ser. IV, XIV*(Suppl.): 83–93.
- Strijbosch, J.J., Bonnemayer, A.M., and Dietvorst, P.J.M. 1980a. The northernmost population of *Podarcis muralis* (Lacertilia, Lacertidae). *Amphib.-Reptilia*, **1**: 161–172.
- Strijbosch, J.J., Bonnemayer, A.M., and Dietvorst, P.J.M. 1980b. De muurhagedis (*Podarcis muralis*) in Maastricht, Deel 2 : Biotoop en Biotoopgebruik. *Natuurhist. Maandbl.* **60**(12): 240–246.
- Van Damme, R., Aerts, P., and Vanhooydonck, B. 1998. Variation in morphology, gait characteristics and speed of locomotion in two populations of lizards. *Biol. J. Linn. Soc.* **63**: 409–427.