

Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards

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Summary

1. Relationships between morphology, bite force capacity, prey handling efficiency and trophic niche were explored in two sympatric species of lacertid lizards, *Podarcis melisellensis* (Braun 1877) and *Lacerta oxycephala* Duméril & Bibron 1839.

2. Head shape showed little variation, but head size (absolute and relative to snout–vent length, SVL) differed between species and sexes. Males have larger heads than females, both absolute and relative to their SVL. In absolute terms, male *P. melisellensis* have larger heads than male *L. oxycephala*, but the reverse case was true for the females. Relative to SVL, *L. oxycephala* have larger heads than *P. melisellensis*.

3. Bite force capacity was estimated by having the lizards bite on two metal plates, connected to a piezoelectric force transducer. Differences in maximal bite force between species and sexes paralleled differences in absolute head size. Differences in body size and head size explain the higher bite force of males (compared with females), but not the higher bite force of *P. melisellensis* (compared with *L. oxycephala*). Among individual lizards, bite force correlated with body size and head size.

4. Prey handling efficiency, estimated by the time and number of bites needed to subdue a cricket in experimental conditions, also showed intersexual and interspecific variation. This variation corresponded to the differences in maximal bite capacity, suggesting that bite force is a determining factor in prey handling. Among individual lizards, both estimates of handling efficiency correlated with maximal bite force capacity.

5. Faecal pellet analyses suggested that in field conditions, males of both sexes select larger and harder prey than females. There was no difference between the species. The proportion of hard-bodied and large-sized prey items found in a lizard's faeces correlated positively with its bite force capacity.

6. It is concluded that differences in head and body size, through their effect on bite force capacity, may affect prey selection, either directly, or via handling efficiency.

Key-words: Bite performance, Lacertidae, prey handling, sexual dimorphism

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Introduction

Closely related species are thought to be able to coexist only if they specialize in different fractions of the available resources (Gause 1934; Hardin 1960; MacArthur 1968). It is often assumed that such ecological differentiation is followed and aided by changes in morphology, physiology and behaviour that allow the respective species to exploit their specific part of the resources more effectively (Darwin's principle of divergence, Lack 1947; Laerm 1974). In a similar way, within species, sexual dimorphism may evolve to help avoid competition between the sexes. For instance, sexual dimorphism is believed to function in the avoidance

of competition for food (e.g. Schoener 1967; Shine 1986; Watkins 1996).

Early ecomorphological studies have supported these ideas by demonstrating statistical relationships between the morphological features of species or sexes, and the ecological niches they occupy. Critique on the correlative nature of this approach (Arnold 1983; Wainwright 1991) has prompted much research on the causal relationship between morphological and ecological variation. The measurement of whole-animal performance in ecologically relevant functions has become pivotal in this endeavour (Wainwright & Reilly 1994; Irschick & Garland 2001).

In communities of terrestrial vertebrates, ecomorphological research has centred mainly on microhabitat use (Wainwright & Reilly 1994). In lizards, differences in microhabitat use have been related to differences in locomotor capacities, and further to

differences in limb morphology (reviews in Garland & Losos 1994; Van Damme *et al.* 2002). Other dimensions of the ecological niche have received less attention. This is remarkable, since, for instance, differences in diet are often thought to be of prime importance in niche differentiation. Also, in other vertebrate groups (fish: Norton & Brainerd 1993; Norton 1995; Wainwright 1996; birds: Grant 1986) differentiation of trophic morphology has been shown to function in the avoidance of competition.

In this paper, we test the hypothesis that variation in morphology (head size and shape) between and within two species of lacertid lizards produces differences in bite force, prey handling efficiency and, ultimately, diet. *Lacerta oxycephala* Duméril & Bibron 1839 and *Podarcis melisellenis* (Braun 1877) are sympatric on several islands in the Adriatic Sea. The two species are of similar body size and they share the same general body plan. They are also highly similar in many ecological characteristics: both are agile, actively foraging, diurnal, heliothermic lizards with a diet that consists mainly of arthropods. We measured bite capacity because earlier studies on other lacertids have shown that intra- and interspecific variation in head size and shape may affect the maximal force that can be exerted by the jaws (Herrel, Van Damme & De Vree 1996; Herrel, De Grauw & Lemos-Espinal 2001a; Herrel *et al.* 2001b). Variation in bite capacity could be ecologically relevant in at least two ways. It could confine the kind and the size of prey available to the lizard directly. The exoskeleton of arthropods constitutes an impregnable defence to at least some lacertid lizards (Herrel *et al.* 1996, 2001b). Indirectly, bite force may affect the time needed to subdue a prey item, and therefore its profitability. Differences in diet have often been invoked to explain the coexistence of lacertid lizards (e.g. Nouira 1983; Strijbosch 1986; Murray & Schramm 1987; Pollo & Mellado 1988; Sorci 1990), but the morphological and behavioural correlates of these differences have seldom been explored (Herrel *et al.* 2001b).

Materials and methods

MORPHOMETRICS

Head dimensions and snout–vent length (SVL) of 55 *P. melisellenis* (25 males, 13 females, 17 subadults) and 54 *L. oxycephala* (34 males, 13 females, 7 subadults) were measured *in vivo* using digital calipers (Mitutoyo CD20DC, Sakato, Japan). Head length was taken as the distance between the tip of the snout and the caudal edge of the occipital scale. Head width was taken at the widest point of the head, and includes the bulging of the musculus pterygoideus. Head height was measured at the highest point of the skull, just posterior of the orbita. Lower-jaw length was defined as the distance between the anterior end of the dentary bone and the posterior edge of the retroarticular process. Additionally, we estimated the jaw closing out-lever by

measuring the distance between the quadratum and the anterior edge of the dentary bone. The jaw closing in-lever was estimated by measuring the distance between the quadratum and the coronoid, estimated by the posterior edge of the eye.

BITE FORCE

Bite forces were measured using an isometric Kistler force transducer (type 9203, Kistler Inc., Winterthur, Switzerland) mounted on a purpose-built holder and connected to a Kistler charge amplifier (type 5058 A, Kistler Inc.). The animals were induced to bite on two plates, fixed at a distance of 3.65 mm. This causes the upper plate to rotate, thus exerting a pull on the piezoelectric force transducer. The bite forces were recorded using a portable computer equipped with an A/D converter (PC-Scope T512, Imtec GmbH, Backnang, Germany). A full description of the bite measuring device can be found in Herrel *et al.* (2001a,b).

Lizards were kept in individual cloth bags and placed in an incubator at 35 °C for at least 1 h prior to the bite measurements. A lizard was then removed from its bag and held in front of the bite plates. This typically resulted in forceful and prolonged biting. This procedure was repeated five times with each individual lizard, but leaving at least 1 h between successive tests. The maximal value obtained during such a recording session was considered the maximal bite force for that individual lizard.

PREY HARDNESS

In an attempt to assess the ecological relevance of bite capacity in natural conditions, we compared bite forces measured on the lizards to forces needed to crush arthropods. We estimated the hardness of all arthropods collected around the study site and of those found in the lizards' faeces. Because digestive juices (in the lizard's stomach) and the detergent (in the pitfall traps) affect the toughness of the chitin carapax, we were unable to determine the hardness of these items directly. We therefore used two empirical regression equations that relate arthropod size to the force required to crush the thorax. These equations were obtained by applying increasingly stronger forces to the thorax and recording the force exerted at the moment of rupture (see Herrel *et al.* 2001b for details). For 'soft' arthropods, hardness was calculated from a regression equation ($N = 90$, $R^2 = 0.93$) obtained for a range of field crickets (A. Herrel, unpublished data):

$$\log_{10}(\text{hardness, in N}) = 1.7798 * \log_{10}(\text{body length, in mm}) - 1.9421 \quad \text{eqn 1}$$

The hardness of 'hard' arthropods was calculated from a regression equation ($N = 167$, $R^2 = 0.40$) obtained for a variety of beetle species (J. Meyers and L. Aguirre, unpublished data):

$$\log_{10}(\text{hardness, in N}) = 1.5815 * \log_{10}(\text{body length, in mm}) - 1.3650 \quad \text{eqn 2}$$

Adult specimens of Diptera, Hymenoptera, Neuroptera, Lepidoptera, Phasmida, Aranea and Opiliones, and all larvae were considered 'soft' prey items; adult Coleoptera, Dermaptera, Heteroptera, Hemiptera, Chilopoda, Diplopoda and Isopoda were considered 'hard' prey items.

PREY HANDLING

To compare prey handling efficiency between lizard species and sexes, we performed experiments in the laboratory with 17 adult *P. melisellensis* (7 males, 10 females) and 14 *L. oxycephala* (11 males and 3 females). When not being used for experiments, the animals were housed in glass terraria (100 × 50 × 50 cm³), containing a sandy substrate, some rocks and vegetation. Food (crickets, dusted with a commercial mix of calcium and vitamins) and water were available *ad libitum*. A 100-W light bulb was suspended 20 cm above one end of the terrarium and provided light and heat for 10 h a day. Lizards were thus able to regulate their temperature. No more than three animals were put in one terrarium, and the species were kept separate. Two days before the experiments, all food was removed from the terraria, to increase (and standardize) the lizards' motivation to attack prey during the tests. One hour before the start of the observations, a lizard was placed into a test terrarium (50 × 50 × 20 cm³), situated in an environmental chamber (70 × 70 × 70 cm³) at a temperature of 35 °C. After the habituation period, a cricket of known body size was introduced into the terrarium through a slit in the roof of the environmental chamber. The lizard's behaviour was followed and recorded from behind a one-way mirror. We noted the time the lizard needed to subdue and swallow the cricket. Each individual was tested several times, but with at least 3 days between successive trials. Trials in which lizards showed no interest in the 15 min following the introduction of the cricket were terminated and disregarded.

FOOD AVAILABILITY AND DIET

Observations on food availability and diet were performed between 2 and 14 September 2000 on the Mediterranean island of Vis (Croatia, 43.03° N, 16.12° E). The study site is located in and around an old English fortress, situated approximately 20 m above sea level, in the north-east of the island. The stone walls of the fortress constitute the prime microhabitat of *L. oxycephala*; *P. melisellensis* mostly occupies the low herbaceous vegetation in the immediate surroundings of the stronghold.

Arthropod body size distribution at the study site was estimated using pitfall traps (glass jars, 9 cm in diameter and 8 cm high) that were dug into the sub-

strate. The traps were filled up to 2 cm of height with a detergent solution to prevent arthropods from escaping. The traps were inspected daily. In addition, we used an altered leaf blower to suck arthropods from the vegetation and the substrate. All arthropods caught were stored in a 70% ethanol solution until further analysis. Because microhabitat use clearly differed between *L. oxycephala* and *P. melisellensis*, we kept the arthropod samples from the two types of microhabitat separate.

In the laboratory, all arthropods sampled were determined to the family level and their body length was measured using electronic calipers.

Actual prey size distribution was estimated from faecal analyses. Lizards were caught by noose and kept in individual cloth bags until they had defecated (usually within a day). The faeces were stored in individual plastic containers containing a 70% ethanol solution, until further analysis. In the laboratory, faeces were dissected under a binocular microscope and the arthropod remains were determined to the family level. The original size of each prey item was reconstructed using the arthropods collected at the study site as a reference.

Results

MORPHOMETRICS

Head dimensions (summarized in Table 1) were strongly intercorrelated (all $r > 0.75$, $N = 113$, all $P < 0.0001$). Principal component analysis reduced the six original head dimensions to a single new variable (eigenvalue = 5.27), which explained 88% of the total variation. All six original variables had high, positive factor loadings (>0.87) on this first principal component. No other components were extracted (eigenvalues < 1), indicating that the heads of the lizards varied in overall size, but not in shape. In the analyses below, the projections on the first principal component were used as indicators of the lizards' head size.

Adult head size (projections on the first principal component) differed between species (ANOVA, $F_{1,85} = 10.51$, $P = 0.0017$) and between sexes ($F_{1,85} = 337.92$, $P < 0.00001$). The species–sex interaction effect was also significant ($F_{1,85} = 69.67$, $P < 0.00001$). In absolute terms, adult male *P. melisellensis* have larger heads than adult *L. oxycephala*, but the reverse is true in females (Fig. 1). In both species, males have substantially larger heads than females (Fig. 1).

Head size (projections on the first principal component) correlated with size ($r = 0.94$, $P < 0.0001$). With SVL entered as a covariate, head size still differed between the two species (ANCOVA on adults only, $F_{1,84} = 18.05$, $P = 0.00006$) and between the sexes ($F_{1,84} = 72.12$, $P < 0.00001$). The species–sex interaction effect was also significant ($F_{1,84} = 23.14$, $P = 0.000007$). Inspection of the residuals learns that *L. oxycephala* have larger

Table 1. Means and standard deviations of morphometric measures (in mm) and bite forces (in N) of males, females and juveniles of the species studied

		<i>Lacerta oxycephala</i>			<i>Podarcis melisellensis</i>		
		Male	Female	Juvenile	Male	Female	Juvenile
SVL	<i>N</i>	34	13	7	25	13	17
	Mean	58.4	52.9	43.5	60.9	51.3	43.3
	SD	3.0	5.4	5.7	4.3	2.4	4.5
Head length	Mean	15.1	13.2	11.0	14.9	11.5	10.4
	SD	1.0	1.0	1.2	1.1	0.4	0.9
Head width	Mean	8.2	7.1	6.0	8.0	6.0	5.3
	SD	0.9	0.7	0.7	0.7	0.3	0.5
Head height	Mean	5.8	4.9	4.0	6.3	4.7	4.1
	SD	0.9	0.6	0.6	0.7	0.3	0.5
Lower-jaw length	Mean	15.9	13.9	12.0	16.3	12.8	11.3
	SD	0.3	1.1	1.3	1.0	0.5	1.0
Jaw closing outlever	Mean	14.9	13.4	11.1	15.2	11.7	10.5
	SD	0.8	0.7	1.2	1.1	0.4	1.1
Jaw closing inlever	Mean	4.8	4.3	3.4	5.4	3.8	3.5
	SD	0.5	0.4	0.5	0.5	0.3	0.4
Bite force	Mean	5.9	2.9	1.3	6.7	2.4	1.6
	SD	2.0	0.7	0.6	1.4	0.3	0.6

heads, relative to their body size, than *P. melisellensis*. In both species, males have larger relative heads than females, but the dimorphism is more pronounced in *P. melisellensis* (Fig. 1).

BITE FORCE

Absolute bite forces differed between species (Table 1, ANOVA on adults only, $F_{1,85} = 4.28$, $P = 0.04$) and between sexes ($F_{1,85} = 257.4$, $P < 0.00001$). The species–sex interaction effect was also highly significant ($F_{1,85} = 27.17$, $P = 0.000001$). Adult male *P. melisellensis* bite harder than male *L. oxycephala*, but the reverse is

true for the females. In both species, males bite considerably harder than females (Fig. 2).

Both SVL (partial correlation = 0.22, $P = 0.02$) and head size (partial correlation = 0.70, $P < 0.00001$) explain a significant part of the variation in bite force, indicating that larger lizards and lizards with relatively large heads bite harder. When SVL and head size are introduced as covariates into the analysis, bite force no longer differs between sexes ($F_{1,83} = 1.81$, $P = 0.18$). Also, the sex–species interaction effect on bite force is no longer significant ($F_{1,83} = 1.75$, $P = 0.19$). However, the species effect remains significant ($F_{1,83} = 43.82$, $P < 0.00001$). Even when considering its body size and head dimensions, *L. oxycephala* bites less hard than *P. melisellensis*. These results suggest that differences in body size and head size can account for the sexual dimorphism in bite force, but they cannot explain differences between the species.

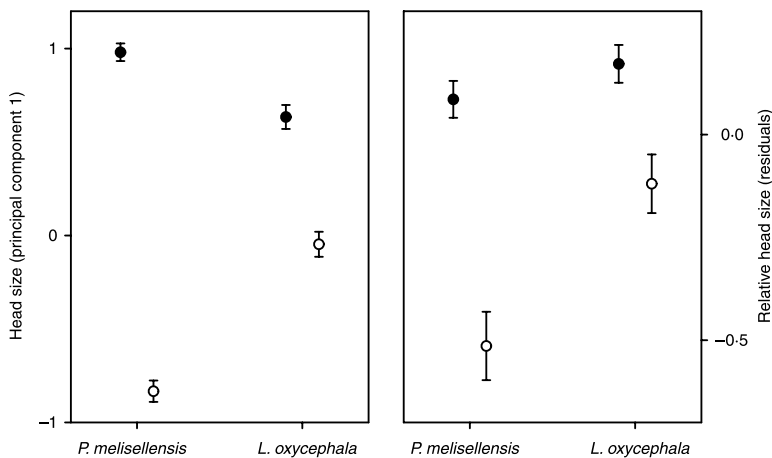


Fig. 1. Head sizes of adult male (●) and female (○) *P. melisellensis* and *L. oxycephala*. Shown is a composite measure of head size, generated by a principal component analysis on six different head measures (see text). The left-hand graph depicts the mean (\pm SE) size estimates for different groups in absolute terms. The right hand graph shows the mean (\pm SE) of the residuals after regressing against \log_{10} SVL.

PREY HANDLING

The time a lizard needed to subdue and swallow a cricket clearly depended on the mass of that cricket (Fig. 3, regression of \log_{10} time on \log_{10} prey mass, on data pooled over all individuals: $r = 0.87$, $N = 163$, $P < 0.00001$). We used the residuals of this relationship to test for differences between sexes and species in handling time. To avoid pseudoreplication, we first calculated average (residual) handling times per individual, thus reducing the data set to 30 points. Analysis of variance on these mean values revealed significant differences between species ($F_{1,26} = 11.68$, $P = 0.002$) and sexes ($F_{1,26} = 14.11$, $P = 0.0009$); the interaction effect was not significant ($F_{1,26} = 1.77$, $P = 0.19$). *Podarcis melisellensis* required less time to subdue a cricket of a given size than did *L. oxycephala*; in both species,

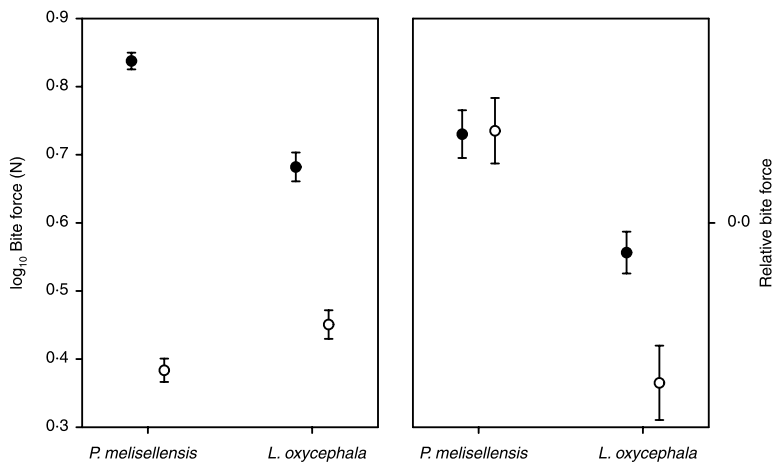


Fig. 2. Bite forces of adult male (●) and female (○) *P. melisellensis* and *L. oxycephala*. On the left, mean (\pm SE) bite forces are given in absolute terms. On the right, bite forces are expressed relative to SVL and head size (residuals of regression against head size and \log_{10} SVL).

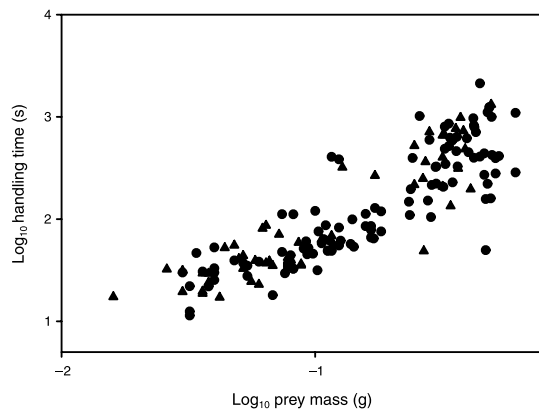


Fig. 3. Effect of prey (crickets) mass on handling time in *P. melisellensis* (●) and *L. oxycephala* (▲).

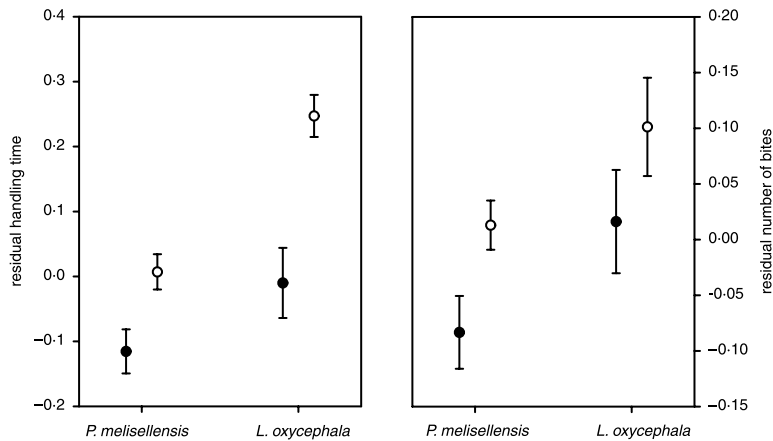


Fig. 4. Handling time (left) and number of bites (right) needed to reduce a cricket in adult male (●) and female (○) *P. melisellensis* and *L. oxycephala*. Handling time and bite number are corrected for prey size by taking the residuals of the regression between \log_{10} handling time (resp. bite number) and \log_{10} prey mass.

ences in bite force, the sexual dimorphism in residual handling time disappeared (ANCOVA, $F_{1,25} = 1.83$, $P = 0.19$). However, the difference between the two species remained significant ($F_{1,25} = 7.98$, $P = 0.009$). Even when correcting for its lower bite performance, *L. oxycephala* takes more time to subdue crickets than does *P. melisellensis*.

The number of bites needed to reduce a cricket also depended on the mass of the prey (regression of the number of bites on prey mass, both \log_{10} -transformed: $r = 0.88$, $N = 163$, $P < 0.0001$). As in our analysis of handling time, we used the residuals of the aforementioned relationship to compare the number of bites between sexes and species. *Lacerta oxycephala* on average needed more bites to reduce a cricket of a given size than did *P. melisellensis* (Fig. 4, ANOVA on mean residuals per individual, $F_{1,26} = 4.55$, $P = 0.04$). In both species, females required more bites than males (Fig. 4, $F_{1,26} = 4.25$, $P = 0.05$). The sex–species interaction effect was not significant ($F_{1,26} = 0.016$, $P = 0.90$). The number of bites needed is negatively correlated with a lizard's bite force ($r = -0.35$, $N = 30$, $P = 0.058$). When differences in bite force are accounted for, the number of bites required no longer differs between sexes ($F_{1,25} = 0.42$, $P = 0.52$) or species ($F_{1,25} = 3.00$, $P = 0.096$), although *L. oxycephala* still tends to need a larger amount of bites than *P. melisellensis*.

DIET

Males of both species had higher proportions of hard-bodied prey in their faeces than females (Fig. 5, ANOVA on adults, $F_{1,70} = 6.90$, $P = 0.01$). The proportions of hard-bodied prey found in the faeces did not differ between both species (Fig. 5, $F_{1,70} = 2.68$, $P = 0.11$). The proportion of hard-bodied prey remains in a lizard's faeces was positively correlated with its bite force (correlation over all individuals sampled, $r = 0.24$, $N = 97$, $P = 0.017$). This was partly, but not entirely, due to the fact that larger lizards ate harder prey (correlation of residual bite forces with proportion of hard-bodied prey: $r = 0.21$, $N = 97$, $P = 0.04$).

Males of both species also had larger proportions of big (>1 cm) prey items in their faeces than females (Fig. 6, ANOVA on adults, $F_{1,70} = 8.52$, $P = 0.004$). Species did not differ in this respect ($F_{1,70} = 0.10$, $P = 0.75$) and the species–sex interaction was also not significant ($F_{1,70} = 0.76$, $P = 0.39$). The proportion of big prey items in a lizard's faeces was positively correlated with its bite force ($r = 0.34$, $N = 97$, $P = 0.00007$) and its residual bite force ($r = 0.26$, $N = 97$, $P = 0.008$).

The relative abundance of hard-bodied vs soft-bodied arthropods differed strongly between the *L. oxycephala* microhabitat (the walls of the fortress and their immediate surroundings) and the *P. melisellensis* microhabitat (the vegetated areas next to the building) (*G*-test, $G = 109.4$, $P < 0.00001$). Samples from the vegetated microhabitat contained a much larger proportion of soft-bodied arthropods (460 of a total 617,

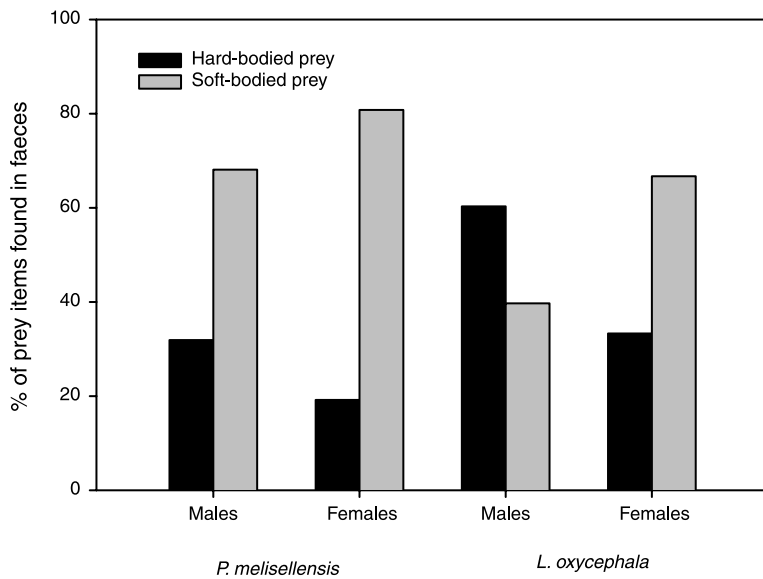


Fig. 5. Proportions of hard- and soft-bodied prey items found in faeces of adult *P. melisellensis* and *L. oxycephala*.

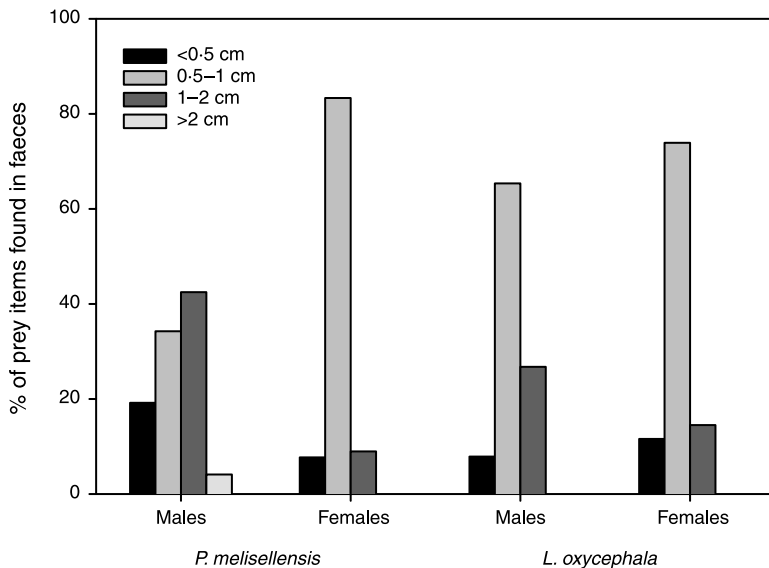


Fig. 6. Proportions of prey size classes found in faeces of adult *P. melisellensis* and *L. oxycephala*.

i.e. 75%) than the samples from the stone wall habitat (109 of a total of 284, i.e. 38%). This difference is highly significant. Arthropods of different sizes (<1 cm vs >1 cm) occurred in similar proportions in the two microhabitats (G -test, $G = 1.08$, $P = 0.30$; walls: 69% small prey items; vegetation: 72% small prey items).

To assess the ecological significance of bite capacity in these lizards, we compared maximal bite performance with the force required to crush arthropods present in the lizard's habitat (Table 2). Adults of both species would be capable of crushing the majority (>85%) of arthropods caught during our sampling efforts, but a substantial percentage of arthropods would be too hard for smaller subadult lizards (Table 2).

Discussion

Despite clear differences in head size, *Podarcis melisellensis* and *Lacerta oxycephala* do not differ in head shape. Similarly, within species, there is sexual dimorphism in head size, but not in head shape. The apparent lack of variation in head shape is surprising for two reasons. First, other studies on lizards have reported considerable variation in skull dimensions (relative to skull length), both between sexes and between closely related species (Herrel *et al.* 1999, 2001a,b). The sample sizes in these studies are similar to ours, so it is unlikely that the non-significance of our tests results from a lack of statistical power. Second, because of obvious differences in substrate use and escape behaviour between the two species, we expected *L. oxycephala* to have a relatively low head compared with *P. melisellensis*. Having a relatively flat head seemed beneficial to species that live on near-vertical surfaces, because it helps keep the centre of mass close to the substrate, and reduces the tendency to topple backwards (Vanhooydonck & Van Damme 1999). Also, low heads are thought to be convenient for lizards that, like *L. oxycephala*, frequently make use of small cracks and crevices in rocks and walls to hide from predators or to pass the night (Arnold 1998; Cooper, van Wijk & Mouton *et al.* 1999; Herrel *et al.* 2001b).

Table 2. Percentage of the number of arthropods collected in the study site that could be crushed by lizards of different species, sex, age and SVL*

	'Small'		'Average'		'Large'	
	SVL (mm)	%	SVL (mm)	%	SVL (mm)	%
<i>Podarcis melisellensis</i>						
Males	56.2	96.1	61.7	96.8	66.1	97.3
Females	46.8	87.8	51.3	89.0	55.0	89.4
Subadults	36.3	68.4	42.7	80.0	51.3	89.5
<i>Lacerta oxycephala</i>						
Males	51.3	91.8	57.5	95.2	64.6	98.4
Females	50.1	90.7	55.0	91.3	60.3	91.6
Subadults	38.0	76.8	42.7	82.9	50.1	89.0

*The total number of arthropods sampled in *P. melisellensis* microhabitat was 621; the number sampled in *L. oxycephala* habitat was 282. Arthropod hardness was estimated from body length (see Materials and methods).

The observation that the two species do not differ in head shape agrees with earlier observations on the conservative nature of general body shape in lacertid lizards (Arnold 1998; Vanhooydonck & Van Damme 1999). Because of the similarity in head shape, we will assume in the rest of the discussion that differences in bite performance, prey handling efficiency and diet between the species and the sexes originate from differences in (relative) head size only. This is probably an oversimplification: the trophic apparatus of lizards is a complex system with many structural and physiological features, only a few of which have been measured in this study. Future in-depth analyses of this system may as yet uncover important shape variation. However, a number of simple and popular predictions on the effect of head shape on bite performance (review in Herrel *et al.* 2001a) do not apply to our study system. For instance, to increase bite force, lizards could evolve wider and higher heads (to accommodate more jaw adductor muscle) or shorter lower jaws (increased out-lever), but this has not occurred in our study species.

The two species show obvious sexual dimorphism in head size, both absolute and relative to SVL. As in most other sexually dimorphic Lacertidae (R. Van Damme, unpublished data), males have larger heads than females. The larger head in male lizards has been associated with intrasexual selection (e.g. male–male combat, territorial conflicts, Trivers 1976; Fitch 1981; Anderson & Vitt 1990; Mouton & van Wyk 1993; Bull & Pamula 1996; Censky 1996), with intersexual selection (copulatory bites; Herrel *et al.* 1996) and with food competition avoidance (Herrel *et al.* 1999, 2001b). All three interpretations rely on the assumption that a larger head results in a higher bite capacity. Our bite force measurements seem to corroborate this hypothesis. Moreover, when differences in SVL and head size are controlled for statistically, differences in bite force between the two sexes disappear. This suggests that the sexual dimorphism in size (SVL and head) suffices to explain differences in bite force.

Sexual dimorphism proved much more pronounced in *P. melisellensis* than in *L. oxycephala*. Shine (1991) has proposed that $(HL_{\text{male,estimated}}/HL_{\text{female,observed}})$ be used as an index of sexual dimorphism in head size. $HL_{\text{male,estimated}}$ is the head length of a male with a SVL equal to that of the average female, as calculated from the regression relating male head length to male SVL (both \log_{10} -transformed). $HL_{\text{female,observed}}$ is the actual average head length for the females. In a set of 34 lacertid species (R. Van Damme, unpublished data), this index varies between 0.97 (in *Acanthodactylus haasi*) and 1.17 (in *Gallotia galloti*). For *P. melisellensis*, the index is 1.11; for *L. oxycephala*, it is 1.05. The functional significance (if any) of the among-species variation in sexual head size dimorphism remains unclear. It could be related to differences in the intensity of intra- and intersexual selection (e.g. due to peculiarities of the respective mating systems) or may reflect variation in the degree of intersexual trophic competition.

Regardless which of these mechanisms is involved, our data suggest that the evolution of sexual dimorphism could be mediated by differential bite force requirements: compared with *L. oxycephala*, the higher degree of head size dimorphism in *P. melisellensis* results in a larger difference in bite force between the sexes.

When controlling for differences in SVL and relative head size, *P. melisellensis* bite harder than *L. oxycephala*. This observation lends further support to our belief that evolutionary changes in bite performance may involve structural modifications beyond changes in overall head size or disproportional changes in the length, height, width of the skull and the jaws (see also above). Changes in pennation angle, in the orientation of the adductor muscles, and in moment arms may all have effects on bite force independent of external head dimensions (see Gans *et al.* 1985; Herrel *et al.* 2001a,b).

The results from our prey handling experiments suggest that the variation in bite force performance may have considerable effects on prey processing efficiency. Lizards that obtained high scores in the bite force measurements required less time and fewer bites to process crickets. The greater handling efficiency of males (compared with females) seems entirely due to their higher bite capacity. On the other hand, the superior efficiency of *P. melisellensis* (compared with *L. oxycephala*) cannot be explained by the difference in bite force only. It is unclear which other morphological, physiological or behavioural factors contribute to the difference between the two species. One may argue that handling time takes but a negligible fraction of the total daily time budget of a lizard, and that therefore the ecological significance of the differences in handling efficiency is limited. Although the time needed to subdue a prey may be substantial (up to 20 min in our experiments, see also Pough & Andrews 1985; De Quieroz *et al.* 1987; Paulissen 1987; Avery & Mynott 1990; Preest 1991; Cruz-Neto, Andrade & Abe 2001), it seems unimportant when compared with the 12 h or so that constitute the daily activity period. Moreover, one or two large prey items will usually fill the daily energy requirements of a lacertid lizard (Avery 1971, 1978; Avery, Bedford & Newcombe 1982). However, several authors have argued that lizards struggling to eat prey in natural conditions are probably more vulnerable to predation, being neither as likely to see a potential predator nor as agile in escaping as an unencumbered lizard (Andrews *et al.* 1987; Avery & Mynott 1990; Pough, Preest & Fusari 1997). Similarly, male lizards struggling with prey may be less likely to notice adversaries entering their territory. In addition, lacertid lizards on occasion steal prey from conspecifics and other species (D. Verwajen, R. Van Damme & A. Herrel, personal observations, both in the laboratory and in the field). The longer it takes a lizard to handle its prey, the more it is exposed to this risk of kleptoparasitism. In this light, handling time may as yet be an ecologically relevant measure.

The maximal bite force that can be exerted by a lizard may also be important in a more direct way. It may determine the range of prey items that can be consumed. For instance, insufficient bite capacity prevents some individuals of *L. vivipara* and *P. muralis* to consume hard-bodied (large) prey items (Herrel *et al.* 2001b). On the other hand, bite forces developed by *G. galloti* suffice to crush the hardest arthropods co-occurring with these lizards in their natural habitat (Herrel *et al.* 1999). Comparison of the bite forces measured in *L. oxycephala* and *P. melisellensis* with the hardness of syntopic arthropods revealed that adults of both species should have no problem crushing most prey items. Differences in prey size and prey type selection between the two species and between the sexes must therefore work through the effect of bite force on handling efficiency, or result from causes not related to bite capacity. In subadult lizards, however, bite force capacity may constrain the range of prey directly. The ontogenetic shifts in diet, observed in many lacertid lizards (Castilla, Bauwens & Llorente 1991; Angelici, Luiselli & Rugiero 1997; Herrel *et al.* 2001b; see also Capel-Williams & Pratten 1978) may well reflect the increase of bite capacity with age.

In conclusion, we have shown that bite force may influence the desirability of prey items for lizards, both directly and indirectly (through its effects on handling time). The latter effect may explain why a variety of other lizard species also need more time to subdue large or hard-bodied prey (Pough & Andrews 1985; Grimmond, Preest & Pough 1994; Andrews & Bertram 1997; Pough, Preest & Fusari 1997; Cooper 2000).

It should be noted that our study constitutes a typical 'two-species comparison', and therefore suffers from a number of statistical and logical problems (Garland & Adolph 1994). Separating the evolutionary relationships between trophic morphology, prey handling efficiency and diet will require a phylogenetically informed analysis of a larger set of species.

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