Functional and ecological relevance of intraspecific variation in body size and shape in the lizard *Podarcis melisellensis* (Lacertidae)

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Within populations, individual animals may vary considerably in morphology and ecology. The degree to which variation in morphology is related to ecological variation within a population remains largely unexplored. We investigated whether variation in body size and shape among sexes and age classes of the lizard *Podarcis melisellensis* translates in differential whole-animal performance (sprint speed, bite force), escape and prey attack behaviour in the field, microhabitat use and diet. Male and female adult lizards differed significantly in body size and head and limb proportions. These morphological differences were reflected in differences in bite strength, but not in sprint speed. Accordingly, field measurements of escape behaviour and prey attack speed did not differ between the sexes, but males ate larger, harder and faster prey than females. In addition to differences in body size, juveniles diverged from adults in relative limb and head dimensions. These shape differences may explain the relatively high sprint and bite capacities of juvenile lizards. Ontogenetic variation in morphology and performance is strongly reflected in the behaviour and ecology in the field, with juveniles differing from adults in aspects of their microhabitat use, escape behaviour and diet. © 2008 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2008, **94**, 251–264.

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Within natural populations, members of different sexes and ages may vary considerably in their niche use. Males and females, as well as juveniles and adults, have been demonstrated to differ in important aspects of the niche, such as diet (e.g. Durell, Gosscustard & Caldow, 1993; Braña, 1996; Pearson, Shine & How, 2002; Page, McKenzie & Goldsworthy, 2005; Herrel *et al.*, 2006), microhabitat use (e.g. Vidal, Ortiz & Labra, 2002; Both, Edelaar & Renema, 2003; Wolf, Kauermann & Trillmich, 2005; Hellstedt & Henttonen, 2006), and thermal ecology (e.g. Van Damme, Bauwens & Verheyen, 1986; Perez-Mellado & Dela Riva, 1993; Brown & Weatherhead, 2000). It is tempting to ascribe these ecological differences directly to sexual or ontogenetic differences in body size or shape, but theoretical

developments in ecological morphology and empirical observations suggest that the relationship deserves closer inspection.

In the spirit of Arnold's (1983) seminal contribution to ecological morphology, prudent assessments of the relationship between the morphology and the ecology of males and females, or juveniles and adults, requires measurements of whole-animal performance. These measurements will indicate whether the morphological variation observed is functionally and ecologically relevant, i.e. translates into differential performance. For instance, does sexual dimorphism in head size actually contribute to differences in bite performance? This is not self-evident, especially not when structures relevant in a survival context (e.g. aiding feeding or locomotion) are at the same time under sexual selection. Sexual selection for larger heads could, for example, theoretically increase head size in males without affecting muscle mass (Herrel

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et al., 1999), and might thus not be translated into differential bite capacity. A second necessary step is to confirm that the differences in performance have ecological significance, i.e. result in niche segregation. For instance, variation in bite force becomes irrelevant (with regard to feeding ecology) if even the weakest individuals can readily crush all available food items. Moreover, variation in maximal sprint speed may be irrelevant if even the slowest individuals never perform maximally in nature. In this respect, *in situ* performance measurements, behavioural observations, and data on realized niche width are crucial (Irschick *et al*., 2005).

The fact that several empirical studies (e.g. Tu, Wang & Lin, 2000; Luiselli *et al*., 2002; Johnson, McBrayer & Saenz, 2005; Scenna, García de la Rosa & Díaz de Astarloa, 2006) have failed to find ecological niche divergence between sexes or age classes, despite obvious differences in size and shape, suggests that these concerns are warranted. Other studies have reported clear ecological divergence in species that show little differences in morphology (e.g. Gray & Hamer, 2001; Lewis *et al*., 2002; Hellstedt & Henttonen, 2006), lending further support to the notion that the directly linking of morphology with ecology may need to be reassessed.

Although Arnold's (1983) idea to use the performance of the whole animal as a liaison between morphology and ecology has proved very successful in explaining morphological variation among populations or species occupying different niches (see the review in Kingsolver & Huey, 2003), much less attention was given to the ecological correlations of differences between sexes or age classes (see Herrel & Gibb, 2006; for an overview). On the contrary, many studies of ecological morphology have treated intersexual or ontogenetic differences as a nuisance, and have chosen to avoid confounding effects by examining male adult specimens only (e.g. Losos & Irschick, 1994; Irschick *et al*., 1997; Losos, Warheit & Schoener, 1997; Kohlsdorf, Garland & Navas, 2001; Mattingly & Jayne, 2004); others have ignored potential differences and pooled data from different sexes or age classes (e.g. Bonine & Garland, 1999; Melville & Swain, 2000; Zani, 2000; Ribas *et al*., 2004); and still others have failed to mention the sex/age of their study animals (e.g. Irschick *et al*., 1996; Knox, Losos & Schneider, 2001; Kohlsdorf *et al*., 2004). As a consequence, and despite the considerable literature on sexual dimorphism and ontogenetic differences in morphology, we know surprisingly little about the consequences of these differences for whole-animal performance variables (Bonnet, Ineich & Shine, 2005; Lourdais *et al*., 2006).

Here, we examine whether sexual dimorphism in body size and shape in a lacertid lizard, *Podarcis melisellensis*, translates into differences in the whole-animal performance (sprint speed and bite force) and in aspects of the realized niche (diet and microhabitat use). We chose to study sprint speed and bite force as our performance variables in this species (Verwaijen, Van Damme & Herrel, 2002), because of the known sexual differences in limb and head morphology combined with the previously established ecological relevance of these traits (Vanhooydonck, Van Damme & Aerts, 2000; Herrel *et al*., 2001). Recently, Irschick *et al*. (2005) have warned against the uncritical extrapolation of laboratory-measured estimates of performance to field situations, so we also compared the performance of males and females in natural conditions, and evaluated the possibility of compensatory behaviour (Bauwens & Thoen, 1981; Garland & Losos, 1994).

MATERIAL AND METHODS

STUDY ANIMALS

Podarcis melisellensis is a relatively small (adult snout–vent length, SVL, 5.5–6.5 cm), active, heliothermic lacertid lizard that feeds on a variety of arthropods. Adult males can be readily distinguished from adult females by the presence of a swollen tail base (hemipenis); juveniles differ from adults in the size and degree of pigmentation. Subadult lizards of which the sex could not be determined with accuracy were included with the juveniles in our analyses. Lizards were caught by noose or by hand and were transported in cloth bags to the nearby field laboratory, to record morphometrics and conduct performance trials. Animals were kept in individual cloth bags for a maximum of 48 h, after which they were released at the exact site of capture. The individuals used for quantifying morphometrics, sprint speed, bite force, and diet (measured in the field laboratory) were different from the ones used for the field-based analyses of behaviour and performance.

STUDY SITE

All observations and measurements were carried out on the Mediterranean island of Lastovo (Croatia, 42°45′N, 16°53′E) from 23 August to 5 September 2004. The study site is situated among small-scale agricultural fields near the city of Lastovo. The lizards occur mostly on or in the immediate vicinity of the stone walls surrounding small vineyards and abandoned fields. In spring, the neglected fields hold an abundance of ruderal herbs and grasses, interspersed with bushes and trees. In summer, most of the vegetation dries out.

MORPHOMETRICS

Body, head, and limb dimensions were measured *in vivo* using digital callipers (with a precision of 0.01 mm). The SVL was measured from the tip of the snout to the caudal edge of the anal shield. The head length was taken as the distance between the tip of the snout and the caudal edge of the occipital scale. The head width was taken at the widest point of the head, and includes potential bulging of the jaw muscles. The head height was measured at the highest point of the skull, just posterior of the orbits. The 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 quadrate and the anterior edge of the dentary bone. The jaw closing in-lever was estimated by measuring the distance between the quadrate and the coronoid, estimated by the posterior edge of the jugal bone (Herrel *et al.*, 2006).

The following limb dimensions were measured on all lizards: femur length, tibia length, metatarsus length, the length of the longest toe of the hind foot (always the fourth toe), humerus length, radius length, and the metacarpus length. These measurements were used to calculate the total hindlimb length (the sum of all the hindlimb segments) and the total forelimb length (the sum of all forelimb segments) (Herrel, Meyers & Vanhooydonck, 2002). The mass of the lizards was measured using a Pesola spring balance (with a precision of 0.2 g).

PERFORMANCE MEASURES

Sprint speed on a horizontal surface was measured by chasing the lizards as fast as possible along a 2-m racetrack, over a substrate of cork tiles that provided excellent traction. Photocells, positioned at 25-cm intervals along the track, signalled the passing of lizards to a laptop that calculated the sprint speed over each 25-cm section. We raced each individual three times. Each run was scored as 'poor' or 'good' (cf. Van Berkum & Tsuji, 1987; Tsuji *et al.*, 1989; Van Damme, Aerts & Vanhooydonck, 1997). We took the fastest burst speed recorded over any 25-cm interval during all trials as an estimate of an individual lizard's maximum sprinting performance on a flat surface. None of the lizards were consistently scored as 'poor' runners. Prior to every trial, the lizards were placed in a plastic terrarium ($80 \times 40 \times 40$ cm) that was set up with half in the shade and half in the sun, allowing the lizards to thermoregulate and attain their preferred body temperature. We checked the cloacal temperature of the animals at the start of every trial, to see if the body temperature of the lizards was within a predetermined range (33–37 °C) (Castilla, Van Damme & Bauwens, 1999).

Bite forces were measured using an isometric Kistler force transducer (type 9203) mounted on a purpose-built holder and connected to a handheld Kistler charge amplifier with a peak hold function (type 5995). The animals were induced to bite onto two plates, which were set at a fixed distance apart. Biting causes the upper plate to rotate, thus exerting a pull on the piezoelectric force transducer. A full description of the measuring device can be found in Herrel *et al.* (1999, 2001). The bite force of the lizards was recorded five times, as an estimate of the maximal bite capacity, and we used the highest bite force out of the five bites for each individual. Only lizards with body temperatures within the preferred range were tested (following the same procedure used in the sprint protocol). Handling of the lizards typically resulted in a characteristic threat display, with the jaws opened widely. Once the jaws were positioned on the plates, prolonged and forceful biting resulted. In some individuals, the biting had to be induced by gently tapping the lizard on the side of the mouth (Herrel *et al.*, 1999, 2001).

MICROHABITAT USE

Microhabitat use was quantified by recording the structural features of the habitat at places where we sighted undisturbed lizards (Table 1), following the procedures outlined by Castilla & Bauwens (1992). At each site, we recorded what the percentage of rock, sand, herbs, shrubs and trees were within a 50×50-cm quadrant. We also recorded the percentage of vegetation in four height classes (< 10-cm, 10–25-cm, 25–50-cm, and > 50–cm high). Finally, we measured the maximum height of the vegetation, and the distances to the nearest rock and to the nearest hide (e.g. log, rock, or leaves). Upon completion of these measurements, we walked 2 m in a random direction (determined by throwing a pen in the air), and repeated the measurements for a second quadrant. Two additional quadrants were sampled, each at 2-m distance from the original place of sighting, and in the direction of 120° from the first bearing. Additionally, we calculated a horizontal diversity measure (the Shannon–Weaver index, using the percentage coverage of rock, sand, shrubs, and trees) and a vertical diversity index (using the percentages of the different vegetation heights). The means of the measurements for the four quadrants were used as an estimate of a lizard's microhabitat. We transformed all of the percentages $\{y = \arcsin[\sqrt{(x/100)}]\}$ and the heights and distances $[y = \log_{10}(x + 0.5)]$.

Table 1. Mean values per sex and age class for the morphometric, behavioural, performance, and diet variables measured. **The head size is a composite variable (resulting from principal component (PC) analysis), and reflects differences in the six original head measures

	Adult males			Adult females			Juveniles		
	x	SD	n	x	SD	n	x	SD	n
Morphometrics									
Snout–vent length (SVL) (mm)	65.42	1.98	119	57.01	1.66	20	44.61	8.44	40
Mass (g)	6.63	0.75	119	3.83	0.40	20	2.21	1.27	40
Forelimb length (mm)	23.28	1.06	119	18.43	0.65	20	15.84	2.42	40
Hindlimb length (mm)	37.61	1.33	119	29.11	0.76	20	25.51	3.65	40
Head length (mm)	15.17	0.45	119	11.85	0.29	20	10.28	1.42	40
Head width (mm)	8.35	0.34	119	6.46	0.19	20	5.53	0.80	40
Head height (mm)	6.93	0.40	119	5.10	0.25	20	4.29	0.74	40
Lower jaw length (mm)	16.12	0.48	119	12.39	0.33	20	10.63	1.59	40
Jaw closing out-lever (mm)	14.66	0.43	119	11.20	0.27	20	9.61	1.46	40
Jaw closing in-lever (mm)	10.85	0.39	119	8.57	0.19	20	7.40	1.07	40
Head size**	0.64	0.15	119	−0.69	0.11	20	−1.52	0.79	40
Lab performance									
Maximal bite force (N)	12.89	1.55	119	5.92	1.31	20	2.73	1.90	40
Maximal sprint speed (cm s⁻¹)	181.80	44.98	119	166.20	47.55	20	142.69	56.98	40
Field performance									
Approach distance (cm)	133.75	44.00	20	121.86	66.04	21	92.00	58.57	19
Flight distance (cm)	51.80	33.11	20	39.86	24.29	21	47.89	34.34	19
Final distance (cm)	177.55	34.34	20	144.29	71.31	21	124.42	59.19	19
Field escape speed (cm s⁻¹)	106.43	26.20	16	102.17	18.15	7	98.05	36.53	28
Field attack speed (cm s⁻¹)	52.96	31.63	24	44.16	24.03	23	32.25	15.65	16
Diet									
Average prey mass (mg)	29.42	64.88	97	13.37	16.91	19	4.30	4.38	19
Maximal prey mass (g)	56.80	111.31	97	24.57	36.11	19	8.79	8.60	19
Average prey size (mm)	5.81	2.37	96	4.66	1.99	19	3.33	1.48	19
Maximal prey size (mm)	8.37	4.32	96	5.71	3.07	19	5.16	2.37	19
Average prey hardness (N)	0.37	0.34	96	0.23	0.20	19	0.13	0.10	19
Maximal prey hardness (N)	0.75	0.68	96	0.35	0.34	19	0.36	0.31	19

Note: The sprint speed and escape/attack speed values in the table image use the superscript notation cm s^{-1}.

ANTIPREDATOR BEHAVIOUR

We observed the response of individual lizards in the field to a simulated predatory attack, using the following procedure. Once we located an undisturbed lizard, one of us approached it in a straight line and at normal walking speed, until the lizard fled in response to the observer. The instant the lizard ran away from the observer, a pen was dropped on the ground. We then kept walking towards the lizard until it stopped, and marked the positions of the lizard at the start and at the end of the run. We then measured the following characteristics of its flight using a measuring tape: (1) the rectilinear distance between the observer and the lizard at the moment that the lizard noticed the observer (before the actual run) (approach distance); (2) the rectilinear distance between the original position of the lizard and the place where it ran to after noticing the observer (flight distance); and (3) the rectilinear distance between the observer and the spot where the lizard ran to (final distance). We also noted the substrate (rock, ground, or vegetation) and the height of the perch that the lizard was sitting on before and after the flight (Table 1).

ESCAPE SPEED

We filmed lizards escaping simulated attacks in the field, using a Sony digital handycam (type DCR TRV120E, 25 frames s⁻¹). After having recorded the escape response of the lizard, we filmed the entire trajectory once more, but with a tape measure in

view. This allowed us to calculate the natural escape speed of the lizards by dividing the distance travelled by the time needed to do so (Table 1).

PREDATORY ATTACK SPEED

Estimates of predatory attack speeds were obtained by filming undisturbed lizards in the field attacking prey items using a Sony digital handycam (type DCR TRV120E). We fixed a live spider or a cricket to a thin thread that was attached to a fishing rod. We presented the tethered prey item to the lizard, at a distance of about 1 m from its snout. Usually the lizards responded immediately and attacked the prey within seconds. The whole procedure was filmed from a distance of approximately 5 m to avoid disturbance of the lizards by the observer. Following the attack, we filmed the location once more with a measuring tape in view (Table 1). We calculated the speed of the lizards by dividing the distance travelled by the time needed to do so.

DIET

Lizards stomachs were flushed directly after capture using a syringe with a ball-tipped steel needle attached. The size of the syringe and needle was adjusted to suit the size of the animal. Lizards were gently tapped on the sides of the jaw, resulting in a threat response, where the jaws opened widely. A small plastic ring was inserted between the jaws to allow the unhindered flow of water and food out of the digestive tract. The needle was gently inserted into the pharynx and pushed further down the digestive tract until reaching the end of the stomach (the position of the needle could be detected by palpation). Next, water was gently squeezed out of the syringe while massaging the stomach of the lizard. Water was added until the food was regurgitated or pushed out with the water. The stomach contents were placed in individual vials with 70% ethanol. The stomach contents were then analysed down to the larger taxonomical levels for which we could estimate prey hardness (for animal prey), and were measured using a digital calliper (Herrel et al., 2006). The prey items were divided into size classes per taxonomical order (extra large, large, medium, and small). A subset of 20 intact specimens of each subclass and of each taxonomical order, retrieved from the availability samples, were measured and weighed. The average of the length and the mass of this subset was used to define the mass and the length of the prey items in the stomach contents.

We also classified each prey item according to its 'evasiveness'. Sedentary prey items (e.g. caterpillars and molluscs) received an evasiveness score of 1;

walking or running arthropods (e.g. ants and nonflying beetles) obtained a score of 2; jumping prey items (e.g. grasshoppers and crickets) were given a score of 3; and flying insects had a score of 4.

We also estimated prey hardness, by first categorizing the prey as hard [i.e. Coleoptera, Isopoda, Aculeata (without Formicidae), and Mollusca), intermediate (Formicidae and Orthoptera) or soft (all other prey), based on previous measurements of prey hardness for a large sample and the great diversity of arthropod prey (Herrel et al., 1999, 2001; unpubl. data; Aguirre et al., 2003). Next, prey hardness was estimated from previously established relationships between prey hardness and prey length (see Herrel et al., 1999, 2001; unpubl. data; Aguirre et al., 2003) using the following regressions.

1. Soft prey: $\log_{10}$[prey hardness (N)] = 0997*$\log_{10}$[prey length (mm)] – 1379.
2. Intermediate prey: $\log_{10}$[prey hardness (N)] = 1780*$\log_{10}$[prey length (mm)] – 1942.
3. Hard prey: $\log_{10}$[prey hardness (N)] = 1582*$\log_{10}$[prey length (mm)] – 1365.

For each individual, we noted the hardness of the hardest prey item, and the mean prey hardness (over all prey retrieved from the stomach that could be identified and measured) (Herrel et al., 2006).

PREY AVAILABILITY

To obtain an indication of the availability of prey at the site where the lizards were caught, we took sweep samples and set up pitfalls close to the perches or foraging locations of the lizards. The potential prey residing among the vegetation in different microhabitats was sampled ten times for two minutes each using a reinforced sweep net. The sweep samples were transferred to plastic bags and were frozen upon return to the field laboratory. An array of 20 pitfalls (diameter of 10 cm, depth of 10 cm) was set up for 24 h. Pitfalls contained an aquaeous solution of formaldehyde (10%), with a little soap added to reduce the surface tension. After removing all plant material, the availability samples were stored in a plastic container with 70% ethanol. The samples were analysed in the laboratory at the University of Antwerp, and every item was identified and categorized as described above for the stomach contents. From each group we measured (using digital callipers with a precision of 0.01 mm) and weighed (using a Mettler MT5 balance with a precision of 1 µg) a subset of 20 individuals. Before we weighed the selected specimens, the excess ethanol was allowed to evaporate by blotting the insects dry on a tissue and exposing them to the air for five minutes.

All metric variables were $\log_{10}$ transformed prior to analysis. The proportions were arcsine transformed. Absolute differences in metric variables between adult males and females were tested using Student's *t*-tests. When Levene's test indicated an inequality of variances, we used separate-variances *t*-tests. To evaluate whether differences among sexes remained after correcting for size we used analyses of variance, with SVL as a covariate. We checked for possible intersexual differences in allometry by starting with a model that included the sex $\times$ SVL interaction,and reported whether this term contributed significantly to the overall variation. If not, the interaction term was removed from the model, and the test statistics reported here refer to the model without the interaction effect. If adult males and females did not differ in the variable considered, we pooled the data for adult lizards and compared them with the juvenile data to examine the ontogenetic effects. Where we did find intersexual differences, separate tests were used to compare adult males and adult females with juveniles. This procedure implies repeated use of the same dataset in different tests, and therefore somewhat increases the probability of type-I errors. However, we consider this approach more appropriate, as it allows a more direct analysis of sexual dimorphism, which is the major focus of this study. The subsequent comparison with juveniles should be regarded as a first attempt to identify the origin of the sexual dimorphism.

Principal component analyses were used to summarize the microhabitat variables. The orthogonal (varimax) rotation method was used to simplify the interpretation of the new factors.

To test whether the prey eaten by the lizards were taken by chance or actually selected, Ivlev's indices of electivity (*E*) were calculated for the respective size, hardness, and evasiveness classes (Ivlev, 1961). These indices range between –1 and 1: prey classes with negative indices are avoided; those with positive indices are selected.

RESULTS

MORPHOMETRICS

Compared with adult females, adult male *P. meliselensis* have larger mean SVLs (*t*-test, $t_{137} = 18.88$, $P < 0.001$) and body masses ($t_{137} = 20.55$, $P < 0.001$; Table 1). The slopes of the regression lines relating body mass to SVL are similar in the two sexes (ANCOVA, $F_{1,135} = 0.034$, $P = 0.85$), but males weigh more than females at a given SVL ($F_{1,136} = 36.21$, $P < 0.001$). In juveniles, the body mass increases more rapidly with increasing SVL (slope for juveniles,

3.51 ± 0.19; slope for adult males, 2.35 ± 0.13; slope for adult females; 2.44 ± 0.75), but only the difference with adult males is statistically significant (juveniles vs. males, $F_{1,156} = 8.77$, $P = 0.004$; juveniles vs. females, $F_{1,57}$, $P = 0.50$).

The increase in forelimb length with SVL is similar in adult males and females (ANCOVA, $F_{1,135} = 0.25$, $P = 0.62$; Table 1), but males have longer forelimbs than females after correcting for SVL ($F_{1,136} = 51.10$, $P < 0.001$). The relationship between forelimb length and SVL in juveniles is similar to that of adult females (ANCOVA, difference between slopes, $F_{1,57} = 2.89$, $P = 0.10$; difference between intercepts, $F_{1,58} = 0.97$, $P = 0.33$). Compared with adult males, the increase in forelimb length with SVL in juveniles is similar ($F_{1,156} = 0.71$, $P = 0.40$), but juveniles have shorter forelimbs relative to SVL ($F_{1,157} = 44.79$, $P < 0.001$).

The slopes of the relationship between hindlimb length and SVL are similar in adult males and adult females (ANCOVA, $F_{1,135} = 0.35$, $P = 0.56$; Table 1), but males have longer hindlimbs relative to SVL ($F_{1,136} = 40.82$, $P < 0.001$). The slope for juveniles is similar to that for adult males ($F_{1,156} = 2.14$, $P = 0.15$) and adult females ($F_{1,57} = 3.15$, $P = 0.08$), but the limb length relative to SVL is shorter in juveniles than in adult males ($F_{1,157} = 75.35$, $P < 0.001$) and is longer than in adult females ($F_{1,58} = 12.57$, $P = 0.001$).

The sexes and age classes differ significantly in the six measured head variables (Fig. 1, MANCOVA, all $F_{2,177} > 61.91$, all $P < 0.001$; Table 1), but Bonferroni's post-hoc tests demonstrate that males do not differ from juveniles in the several head variables measured (all $P > 0.98$).

The slopes of the relationship between head size (as indicated by the first PC axis of an analysis on all head measures) and SVL are similar in adult males and females ($F_{1,135} = 0.22$, $P = 0.64$), but males have larger heads than females of similar SVL ($F_{1,136} = 281.36$, $P < 0.001$). Slopes for juveniles do not differ from those of adult males ($F_{1,155} = 2.02$, $P = 0.16$) or adult females ($F_{1,56} = 0.69$, $P = 0.41$). Relative to SVL, heads of juveniles are smaller than those of adult males ($F_{1,156} = 1128.84$, $P < 0.001$), but are larger than those of adult females ($F_{1,57} = 7.26$, $P = 0.009$).

PERFORMANCE IN THE LABORATORY

In adult lizards, variation in SVL does not contribute significantly to the variation in maximal sprint speed (ANCOVA, effect of SVL as a covariate, $F_{1,135} = 0.006$, $P = 0.94$; sex $\times$ SVL interaction effect, $F_{1,135} = 0.040$, $P = 0.84$). The mean maximal sprint speed does not differ between the sexes ($F_{1,136} = 2.42$, $P = 0.12$; Table 1). In absolute terms (ms^{-1}), juveniles
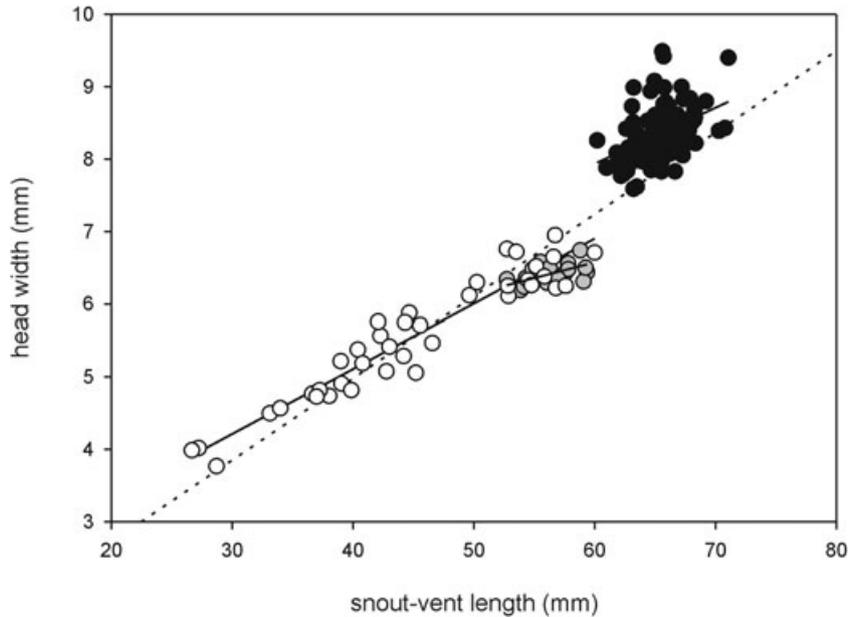
Figure 1. Graph showing the relationship between snout–vent length (SVL) and head width for male, female, and juvenile lizards. The males are indicated by black dots, females by grey dots, and juveniles by white dots. The dashed line is the overall regression line, and the individual regression lines are indicated by solid black lines. Note that the heads of males are much wider than those of females and juveniles.

have lower maximal sprint speeds than adults (t-test, $t_{49.2} = 3.96$, $P < 0.001$). However, when the speed is expressed relative to size (body lengths s^{-1}), juveniles run faster than adults (t-test, $t_{176} = -2.63$, $P = 0.009$).

Adult males have higher bite capacities than adult females (t-test, $t_{20.8} = 15.19$, $P < 0.001$; Table 1). The step-wise elimination of factors starting from an initial model with bite force as the dependent variable, sex as the independent variable, and SVL and all head measurements as covariates, results in a final model with head width ($F_{1,154} = 15.20$, $P < 0.001$), SVL ($F_{1,154} = 49.60$, $P < 0.001$), and sex ($F_{1,154} = 6.53$, $P = 0.012$) as the factors explaining variation in the maximal bite force. As differences between sexes remain significant, this suggests that differences in head width and SVL between adult males and adult females contribute to, but do not completely explain, the differences in the absolute bite force. Comparing adult males with juveniles, using a similar procedure, results in a final model with head length ($F_{1,141} = 56.87$, $P < 0.001$) and SVL ($F_{1,141} = 4.84$, $P = 0.029$) explaining the variation in bite force between the age classes ($F_{1,141} = 2.60$, $P = 0.11$). In the final model comparing bite force in juveniles and adult females, only the head length ($F_{1,54} = 162.43$, $P < 0.0001$) explains a significant level of the variation (age classes, $F_{1,54} = 1.81$, $P = 0.18$).

BEHAVIOUR AND PERFORMANCE IN THE FIELD

In the simulated predation experiment, male and female adult lizards did not differ in mean approach (t-test, $t_{39} = 1.07$, $P = 0.29$; Table 1) or flight distances ($t_{39} = 0.94$, $P = 0.35$), but the distance between the observer and the lizard at the end of the flight was larger in males ($t_{27.4} = 2.64$, $P = 0.014$). In comparison with adults, juvenile lizards took off at smaller approach distances ($t_{27.4} = 2.6$, $P = 0.015$), fled over similar distances ($t_{58} = 0.12$, $P = 0.91$), and stopped at smaller final distances ($t_{58} = 2.54$, $P = 0.014$). Substrate use before and after the experiments did not differ between male and female adults (Fisher's exact tests, before, $P = 0.66$; after, $P = 0.10$; Fig. 2), but juveniles were observed more often in the vegetation than adults (Fisher's exact tests, before, $P = 0.01$; after, $P < 0.001$). Entering substrate use at the onset of the experiment as a factor in the analyses did not help to explain the age-related differences in approach distance and final distance: the age effect remained (approach distance, $F_{1,56} = 5.65$, $P = 0.03$; final distance, $F_{1,56} = 4.62$, $P = 0.04$).

Adult males and females attained similar running speeds while fleeing from simulated attacks in the field (t-test, $t_{21} = 0.20$, $P = 0.84$; Table 1). When speeds are expressed relative to the mean maximum velocities recorded for males and females on the racetrack, males in the field ran at 58.8% ($\pm$ 3.5%)
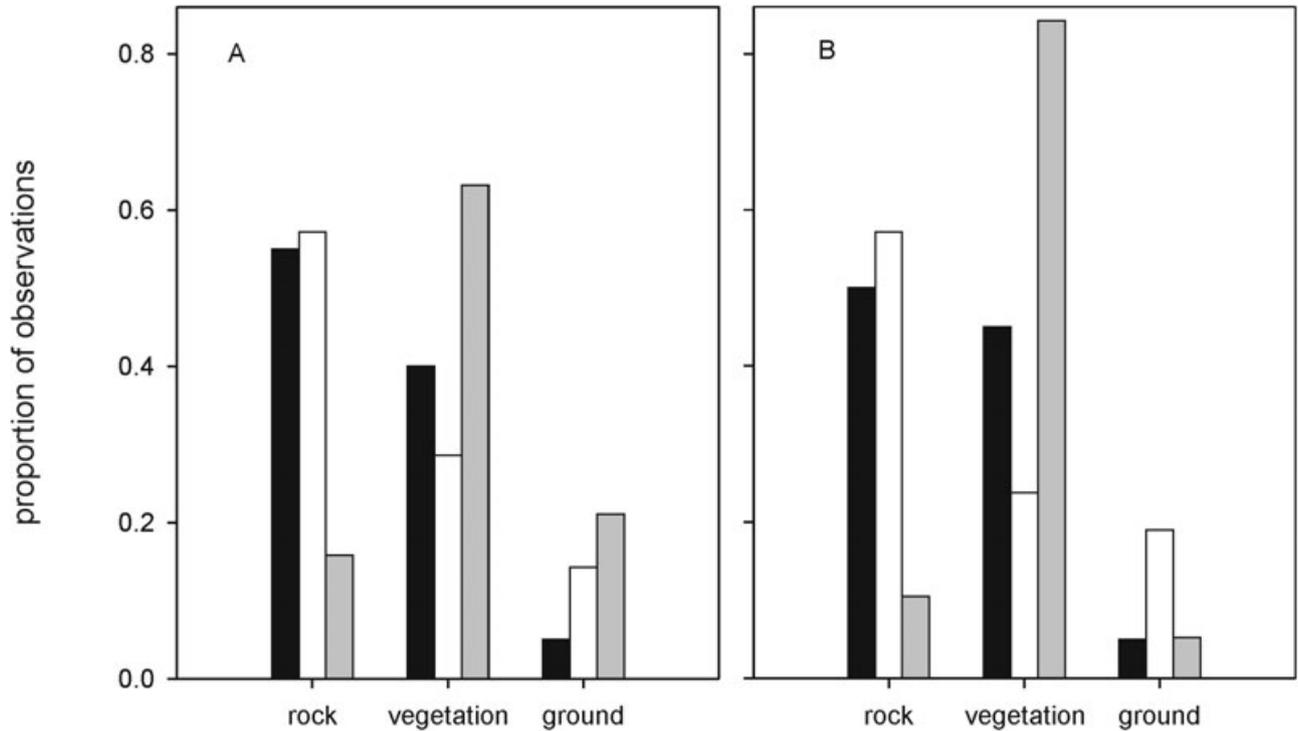
Figure 2. Substrate use of adult male (black bars), adult female (white) and juvenile (grey) *Podarcis melisellensis* before (A) and after (B) the simulated predatory attacks.

and females ran at 61.5% (± 4.1%) of their maximal speed. This difference is not significant ($t_{21} = -0.45$, $P = 0.66$). In absolute terms, the speeds of the juveniles fleeing from the simulated predatory attacks were comparable with those of adults (*t*-test, $t_{45.9} = 1.24$, $P = 0.22$; Table 1), implying that juveniles ran at a higher number of body lengths per second (*t*-test, $t_{37.2} = -4.27$, $P < 0.001$). Compared with the velocity recorded on the racetrack, juveniles in the field fled at 68.72% (± 4.8%) of their maximal speed. This percentage does not differ statistically from that observed for adult lizards ($t_{41.6} = -1.64$, $P = 0.11$).

The maximal speeds recorded for lizards attacking prey in the field also did not differ between adult males and females (*t*-test, $t_{45} = 0.88$, $P = 0.38$; Table 1). Relative to the velocities observed on the racetrack, the attack speeds were remarkably low (males, 29.13 ± 3.5%; females, 26.57 ± 3.0%), and were similar in males and females ($t_{45} = 0.55$, $P = 0.59$). Juveniles attacked prey at lower absolute velocities ($t_{61} = 2.23$, $P = 0.03$), but at similar relative speeds (body lengths s^{-1}, $t_{61} = -0.41$, $P = 0.68$) to adult lizards. Compared with the speeds attained on the racetrack, the attack speeds of juveniles were as low as those of adults (22.60 ± 10.97%, $t_{61} = 1.23$, $P = 0.22$).

MICROHABITAT USE

Principal component analysis reduced the 12 original microhabitat variables to four new ones, jointly explaining 73.87% of the total variation. The first axis (explaining 22.82%) correlated with perch height (−0.65), the percentage coverage by rocks (−0.84), the percentage coverage by herbs (+0.91), and the distance to the nearest hide (+0.63). This axis represents a gradient from open, elevated, rocky microhabitats to closed, low, densely vegetated ones. The second axis (explaining 22.54%) was associated with the percentage coverage by shrubs and trees (+0.72), the percentage coverage by the two higher classes of vegetation (+0.68 and +0.92), and the maximal height of the vegetation (+0.84), hence reflecting a transition from locations lacking tall vegetation to locations covered by canopy. The percentage coverage by vegetation smaller than 10 cm (−0.70), and by vegetation between 10 and 25 cm (+0.82), determines the third axis (explaining 15.41%). Finally, the fourth component correlated with the percentage coverage of sand (+0.90). On all four axes, the scores of adult females were similar to that of males (*t*-tests, all $P > 0.14$). The scores for juveniles on the first principal component were high compared with those of adults (0.43 ± 0.19 and −0.20 ± 0.16, respectively, $t_{58} = 2.37$, $P = 0.02$), indicating that juveniles are found more often in (low)

Table 2. Number of prey items of different mass, hardness, and evasiveness classes found in lizards stomachs (s) and in the sweep samples (a), with the respective Ivlev's indices (E)

| Prey class | a | Adult males | | Adult females | | Juveniles | |
		s	E	s	E	s	E
Prey mass							
< 0.1 mg	19	17	+0.23	2	+0.13	42	+0.87*
0.1–1 mg	170	10	−0.81*	0	−1.00*	9	−0.48*
1–10 mg	483	237	−0.06*	45	+0.07	49	−0.19*
10–100 mg	71	139	+0.56*	13	+0.38	14	+0.14
> 100 mg	19	19	+0.29	2	+0.13	0	−1.00*
Prey hardness							
< 0.14 N	31	25	+0.19	2	−0.12	47	+0.82*
0.14–0.57 N	503	90	−0.51*	24	−0.26*	37	−0.34*
0.57–2.30 N	145	237	+0.50*	27	+0.39*	27	+0.11
2.30–9.27 N	68	51	+0.15	8	+0.18	3	+0.55*
> 9.27 N	15	17	+0.35	1	−0.10	0	−1.00*
Prey evasiveness							
Sedentary	67	24	−0.22*	4	−0.15	58	+0.71*
Walking/running	567	231	−0.15*	45	−0.01	41	−0.35*
Hopping	102	151	+0.46*	12	0.18	15	−0.01
Flying	25	16	+0.07	1	−0.34	0	−1.00*

*Indices that are significantly different from 0 at the significance level $\alpha = 0.05$.

vegetation, whereas adults are typically seen on rocks. Scores on the other three axes do not differ significantly between the two age classes (all $P > 0.62$).

DIET

Male and female adults consumed prey from the five size classes in similar proportions ($\chi_4^2 = 6.73$, $P = 0.15$; Table 2), but both the average ($t_{114} = 2.26$, $P = 0.026$; Table 1) and the maximal prey mass per stomach was larger in males ($t_{114} = 2.67$, $P = 0.009$). Compared with adults, juveniles ate a disproportional large quantity of the smallest prey ($\chi_4^2 = 129.0$, $P < 0.001$; Table 2). The maximal prey size found per stomach was smaller in juveniles than in adult males ($t_{184} = 4.20$, $P < 0.001$), but no difference was found between juveniles and adult females ($t_{101} = 1.45$, $P = 0.15$). Prey consumption was nonrandom with respect to availability in all three sex/age classes (all $\chi_4^2 > 22.5$, $P < 0.0001$; Table 2), with adults selecting larger prey, and juveniles choosing smaller prey when available.

Adult males ate higher proportions of the harder prey items than did females ($\chi^2 = 10.1$, $P = 0.039$; Table 2), but the average hardness of prey items (per stomach) did not differ between males and females ($t_{113} = 1.67$, $P = 0.10$). The hardness of the hardest prey found per stomach was higher in males than in females ($t_{113} = 2.47$, $P = 0.015$). Juveniles clearly ate larger proportions of soft prey items than did adult males ($\chi^2 = 117.0$, $P < 0.001$) or adult females ($\chi^2 = 33.5$, $P < 0.001$). The average prey hardness (per stomach) was substantially lower in juveniles than in adults ($t_{95.8} = 5.67$, $P < 0.001$). Hardness of the hardest prey per stomach differed between juveniles and males ($t_{113} = 2.43$, $P = 0.02$), but not between juveniles and females ($t_{36} = 0.07$, $P = 0.94$). None of the groups ate prey randomly with respect to hardness (males, $\chi^2 = 234$; females, $\chi^2 = 24.3$; juveniles, $\chi^2 = 177$; all $P < 0.0001$). Adults showed a preference for prey of intermediate hardness (0.57–2.30 N) and an avoidance of prey of lower hardness (0.14–0.57 N). Juveniles showed a clear preference for the softest prey.

Adult males ate a greater proportion of prey capable of fast movements than did adult females ($\chi_3^2 = 8.13$, $P = 0.04$; Table 2). Juveniles ate larger proportions of sedentary prey than both adult males ($\chi_3^2 = 145.0$, $P < 0.001$) and adult females ($\chi_3^2 = 36.4$, $P < 0.001$). Female adults consumed prey randomly with respect to their evasiveness ($\chi_3^2 = 2.31$, $P = 0.51$); adult males exhibit a preference for hopping prey ($\chi_3^2 = 83$, $P < 0.001$), whereas juveniles concentrate on sedentary prey ($\chi_3^2 = 148.0$, $P < 0.001$).

DISCUSSION

Our morphometric measurements indicate substantial sexual dimorphism in body size and body shape in

P. melisellensis. Males on average reach larger SVLs than females, and they tend to have higher body masses, longer limbs, and larger head sizes relative to the SVL. Some of these morphological differences contribute to sexual dimorphism in bite capacity, but do not result in differences in maximal sprinting performance. We found little support for ecological or behavioural differences between the sexes in the field: males and females used the same microhabitats, exhibited similar escape behaviour, and fled from predators and attacked prey at similar speeds. However, males ate larger and harder prey items than did females.

In addition to the obvious size differences between juveniles and adults, our data also demonstrate age-related body shape differences, with juveniles having relatively longer limbs than adults. These ontogenetic differences in shape may explain the relatively high sprint capacities of young lizards. In the field, juveniles differ from adults in their microhabitat use, escape behaviour and speed, and diet. Overall, the ecological implications of age-related morphological differences seem more substantial than those of sex-related differences.

FUNCTIONAL SIGNIFICANCE OF SEXUAL DIMORPHISM IN SIZE AND SHAPE

Although sexual size dimorphism is richly documented in lizards (see the review in Cox, Skelly & John-Alder, 2003), whether and how these size differences translate into differences in physiological performance has received much less attention (Cullum, 1998; Lailvaux, Alexander & Whiting, 2003). The few studies that have considered the matter found that male lizards typically run faster than females (Huey & Dunham, 1987; Cullum, 1998; Snell *et al.*, 1988; Dohm *et al.*, 1998; Lailvaux *et al.*, 2003). As speed generally scales positively with SVL (reviewed in Garland & Losos, 1994; but also see, e.g. Garland, 1984; Brodie, 1989), it is commonly assumed that sexual size dimorphism contributes to the difference in sprint speed between the sexes. Where body size cannot fully explain the differences in performance, additional factors have been proposed, such as differences in stockiness (Cullum, 1998), body composition (Cullum, 1998), and relative hindlimb length (Snell *et al.*, 1988). Our findings of no difference in maximal sprint capacity between the two sexes do not support the generality of these earlier observations, even though the degree of sexual size dimorphism in *P. melisellensis* is at least as pronounced as in the species studied in the papers listed. Neither did the observed differences in relative body mass and limb length between male and female *P. melisellensis* lizards translate to noticeable speed differences. Our data

therefore suggest that the morphological differences usually associated with intersexual differences in locomotor performance may be less important than previously thought. Future studies should further examine which proximate factors determine intersexual differences in sprint performance, and why species differ in the degree of sexual dimorphism in sprint performance.

For the feeding system, the relationship between sexual dimorphism in morphology and performance seems more clear-cut. Male *P. melisellensis* lizards tend to have a larger headwidth than females of comparable SVL, and this difference translates into higher bite-force capacities. In this respect, the species resembles other lacertids (Herrel *et al.*, 1999, 2001; but also see McBrayer, 2004) and lizards in general (Herrel *et al.*, 2001, 2006; Herrel & O'Reilly, 2006; Lappin, Hammilton & Sullivan, 2006). However, in *P. melisellensis*, head size alone does not fully explain the sexual dimorphism in bite-force capacity, suggesting that other factors may be involved (e.g. differences in relative muscle mass, degree of pennation, and insertion angles). Similar results were found in *Gallotia galloti* (Herrel *et al.*, 1999); however, in *Podarcis muralis* and *Lacerta vivipara* (Herrel *et al.*, 2001) differences in head size sufficed to explain the sexual dimorphism in bite force. This suggests that selection pressure on bite-force capacity may differ among (closely related) species, or may target different aspects of the feeding system.

ECOLOGICAL SIGNIFICANCE OF SEXUAL DIMORPHISM IN MORPHOLOGY AND PERFORMANCE

Although fundamental to Arnold's (1983) research scheme, tests of the ecological relevance of variation in morphology and whole-animal performance are still relatively rare. However, phenomena such as behavioural compensation (e.g. Bauwens & Thoen, 1981; Hertz, Huey & Garland, 1988; Shaffer & Formanowicz, 1996; Huey, Hertz & Sinervo, 2003), or extraneous performance capacity (Irschick *et al.*, 2005), may create a mismatch between the outcome of laboratory performance tests and actual selection in field conditions.

In accordance with the absence of sexual dimorphism in laboratory sprint speed, we did not observe major differences in escape or attack behaviour between the sexes in the field. This seems to refute the adaptive storyline that the more conspicuous – and hence more vulnerable – males should evolve morphologies that allow them to obtain higher sprint capacities (e.g. larger SVLs and larger relative limb lengths). Moreover, the speeds at which lizards in the field fled from the simulated attacks were low com-

pared with those attained on the racetrack in the laboratory in both males and females. This may indicate that the experimental procedure did not elicit a full escape response in the field; if so, this casts doubts on the value of this widely used method (e.g. Cooper, 1997; Martin, Luque-Larena & Lopez, 2005; Cooper, Perez-Mellado & Hawlena, 2006; Martin *et al.*, 2006). Alternatively, the lizards may be unable to develop maximal speeds in their natural environment, which is clearly more cluttered than the experimental racetrack, or, sprint speed may be ecologically relevant (and hence selected for) in other situations, e.g. during social interactions (e.g. Robson & Miles, 2000; Perry *et al.*, 2004; Peterson & Husak, 2006) or during encounters with more natural enemies, such as birds (*Corvus corax*, *Falco tinnunculus*, etc.), snakes (*Dolichophis caspius*), and mammals (*Martes foina*, *Erinaceus europeus*, etc.). Another possible explanation may be the fact that animals in the field need to make decisions on where to run to, which might reduce the quickness of their response to a stimulus. Our results for *P. melisellensis* do not suggest that sprint speed is relevant in foraging situations, although it might be wise to repeat the experiment with different, more evasive prey types. Potentially, other locomotor traits such as acceleration capacity might be of greater importance than actual sprint speed (Vanhooydonck *et al.*, 2006a; Vanhooydonck, Herrel & Irschick, 2006b).

FUNCTIONAL SIGNIFICANCE OF ONTOGENETIC VARIATION IN SIZE AND SHAPE

As a result of scaling effects, the absolute maximal sprint speed as measured in the racetrack was low in juvenile *P. melisellensis* compared with adults. Comparison of relative sprint speeds between juvenile and adult lizards in our dataset is hampered by the fact that variation in SVL does not explain the variation in the velocity of the latter group, but when speed is simply expressed in $SVL\ s^{-1}$, juveniles ran faster compared with adults. This seems to challenge the general idea that locomotor performance in juvenile animals is compromised by conflicts with the process of growth (Ricklefs, 1979; Carrier, 1996). The enhanced performance of juvenile *P. melisellensis* lizards cannot be attributed to allometric growth of the limbs, as relative limb length is equal or even smaller in juveniles than in adults. The ontogenetic change in locomotor performance must therefore lie in allometric changes of other factors, such as muscular force, contractile velocities, or muscular mechanical advantage (Marsh, 1988; Carrier, 1996). Interestingly, extrapolation of the growth trajectory for limbs in juveniles results in relative limb lengths that are somewhat above those observed in adult females, but

below those observed in adult males. This suggests that the sexual dimorphism in adult limb length results from the differential allocation of energy to limb growth, with males investing more in limb growth and females investing less.

The ontogenetic variation in relative head size mirrors that of limb length, in the sense that extrapolation of the juvenile growth curve for head size results in predicted values that are clearly lower than the actual head sizes of adult males, but are somewhat higher than those of real adult females. The allometric head growth reflected in variation in head length can explain most of the observed differences between juveniles and adults.

ECOLOGICAL SIGNIFICANCE OF ONTOGENETIC VARIATION IN MORPHOLOGY AND PERFORMANCE

As juvenile *P. melisellensis* lizards must negotiate the same predatory environment with lower locomotor capacities, we expected to find some compensatory behaviour. A first hint in this direction is the preference of juveniles for slightly more densely vegetated microhabitats. The vegetation may provide more cover, at least from aerial, visually hunting predators, such as birds. At the same time, by selecting different microhabitats than adult conspecifics, juveniles may be trying to minimize the risk of cannibalism. However, many other factors (e.g. thermal preferences) may be responsible for the observed differences in microhabitat use, and the relevance of these factors will have to be determined by experiments. Juveniles also differed in their escape tactics. It is tempting to ascribe the reduction in approach distance to a shift from a fleeing strategy to one that relies on crypsis, possibly mediated by lower sprint capacities (cf. Bauwens & Thoen, 1981). On the other hand, absolute escape speeds in response to the simulated attacks did not differ significantly between juveniles and adults, suggesting that running juveniles should not be at a higher risk of being caught than adult lizards. Perhaps juveniles rely longer on crypsis because flight is more expensive to them, having to move at more body lengths per second. Given the relatively low prey-attack speeds in both juveniles and adults, it may seem unlikely that reduced locomotor capacities may constrain the diet of the juveniles. However, our diet data show that juveniles eat a disproportionate quantity of sedentary prey. These contradictory results suggest once more that our experiment on foraging speed in the field deserves closer attention (see also above). Our dietary data also suggest strong implications for the reduced bite-force capacity in juveniles. Juvenile *P. melisellensis* lizards eat smaller, softer, and less evasive prey than do adults, and the electivity analyses implicate that

they achieve this by actively selecting such prey types, and may thus potentially avoid competition with adults.

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