Ecomorphological correlates of habitat partitioning in Corsican lacertid lizards

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Summary

1. Morphological features (i.e. snout–vent length, SVL, mass and limb parameters), locomotor performance (sprint speed, climbing speed, manoeuvrability and endurance) and microhabitat use were measured in three lacertid lizard species. Additionally, microhabitat preference was tested in the laboratory with species kept apart and in combination with each other to assess mutual interference.

2. It was predicted that each species possesses morphological adaptations that allow it to excel in those performance measures relevant in its particular microhabitat.

3. The three species differed in microhabitat use. *Lacerta bedriagae* was mostly seen on boulders, while *Podarcis sicula* occurred among vegetation. *Podarcis tiliguerta* seemed more general in its microhabitat use. The results from the microhabitat preference in the laboratory corresponded well to these field observations.

4. Besides differing in SVL, the three species differed in limb length and diameter, and body mass (all relative to SVL). *L. bedriagae* has long forelimbs, short hindlimbs and a high body mass, while *P. sicula* has short forelimbs, long hindlimbs and a low body mass. *P. tiliguerta* is morphologically intermediate.

5. The differences found in morphology translated partially into performance differences. Only climbing speed and endurance differed among species. *L. bedriagae* excelled in both cases. Considering its microhabitat use, this seemed adaptive.

6. Unexpectedly, the interference experiments suggested that *L. bedriagae* is the least competitive of the three species.

Key-words: Adaptation, locomotion, microhabitat use, performance

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Introduction

It is often assumed that habitat partitioning within a community results from past or present competitive interactions among the constituent species (e.g. Jenssen 1973; Laerm 1974; Schoener 1975; Dunham 1980; Smith 1981; Salzburg 1984; Medel, Marquet & Jaksic 1988; Losos 1994; Leal, Rodríguez-Robles & Losos 1998; Losos & Spiller 1999). After a period of competition, two species might partition the habitat, each species ending up in that part in which it has a competitive advantage over the other. Morphological, physiological or behavioural adaptations are often used to explain the (micro)habitat-dependent dominance. Alternatively, one species might outcompete the second, ousting it to marginal habitats, or driving it to extinction. Again, the superior competitive ability of the first species is usually attributed to the fact that it is better adapted to the respective environment (Losos & Spiller 1999). Therefore, both scenarios assume that the degree of adaptation to the habitat's requirements will determine the outcome of competitive interactions. However,

whether this is indeed the case is seldom tested explicitly. Many studies have attributed variation in morphological, physiological or behavioural traits among syntopic species to differences in habitat use, but inferring adaptation requires more than merely correlating design and ecological parameters (Gould & Lewontin 1979; Arnold 1983). The differences in design should be functional, i.e. they should translate into variation in the ability to carry out ecologically relevant tasks (Huey & Stevenson 1979).

In this paper, we investigate whether differences in microhabitat use exhibited by three species of lacertid lizards (*Podarcis tiliguerta*, Gmelin 1789; *P. sicula campestris*, Rafinesque 1810; and *Lacerta bedriagae*, Camerano 1885) on the Mediterranean island of Corsica are reflected in their general morphology and locomotor performance. Of the three species considered, *P. tiliguerta* seems the most catholic in its microhabitat preference. It can be found in high densities in a wide variety of microhabitats (stone walls, ruins, Mediterranean scrubland, beaches, wood fringes and clearings) from sea-level up to 1800 m altitude (Arnold

& Burton 1978; Schneider 1984; Van Damme *et al.* 1989, 1990; Delaugerre & Cheylan 1992). *Podarcis sicula campestris*, on the other hand, is mostly found in the coastal areas, up to an altitude of 400 m, where it occurs in meadows, maquis, wood fringes, cultivated lands and city parks (Arnold & Burton 1978; Henle & Klaver 1984; Van Damme *et al.* 1990; Delaugerre & Cheylan 1992). It has been introduced on the island by humans (Delaugerre & Cheylan 1992). In contrast, the third species, *L. bedriagae*, has a very restricted distribution on the island and is confined to the high mountain ranges and a few coastal areas. It occurs on large boulders and rocks (Arnold & Burton 1978; Schneider 1984; Castilla *et al.* 1989; Delaugerre & Cheylan 1992).

It has been suggested that where they co-occur, the three species shift their microhabitat use. Where *L. bedriagae* and *P. tiliguerta* are syntopic, the former is more frequently seen on large boulders, the latter on or within small piles of stones and rocks or among dwarf shrubs (Castilla *et al.* 1989; own observations). Where *P. tiliguerta* occurs in sympatry with *P. sicula*, the former is said to concentrate its activity on vertical surfaces (stone walls, rocks), while the latter forages mostly in dense vegetation (Lanza 1955; Arnold & Burton 1978; Henle & Klaver 1984; Van Damme *et al.* 1990). Moreover, Scherer (1904) described aggressive interactions between the two species. The distributions of *L. bedriagae* and *P. sicula* do not overlap on Corsica, and no sympatric populations exist (Delaugerre & Cheylan 1992).

In this paper, we present quantitative data on the microhabitat use of the three species in the field. Because it is often unclear whether individual animals in nature occupy a certain microhabitat because they prefer it, or because they are forced into it by predators or competitors, we also determined microhabitat choice in an experimental set-up. The species were tested separately and in combination with each other to assess mutual interference.

The structural features of the microhabitats occupied by the three species seem to differ sufficiently to warrant morphological differentiation. Moreover, biomechanical considerations suggest that different, conflicting body designs should be selected for in the respective environments. For instance, lizards living in open habitats should have relatively long hindlimbs (Pianka & Pianka 1976; Garland & Losos 1994), and short forelimbs (Snyder 1962; Sukhanov 1968; Losos 1990a). Both short fore- and hindlimbs, on the contrary, would be advantageous in climbing species (Jaksic, Nunez & Ojeda 1980; Pounds 1988; Sinervo & Losos 1991). The body shape of cursorial lizards should be laterally compressed (Snyder 1954; Van Damme, Aerts & Vanhooydonck 1997), while a dorso-ventrally flattened body seems more appropriate for climbing species (Cartmill 1985; Pounds 1988; Miles 1994).

We predict that the three species will show morphological adaptations that allow them to perform better in their respective microhabitat, which, in turn, will be correlated to their competitive ability. As a test for performance ability, we have measured several components of locomotor capacity (level-running and climbing speed, endurance, manoeuvrability). We hypothesize that each species will excel in those performance measures relevant in its particular microhabitat. In other words, *L. bedriagae* is expected to perform best at climbing and have the highest endurance since it occurs in rocky, scarcely vegetated habitats. Morphologically, it is predicted to have short limbs and a high mass. *Podarcis sicula*, on the other hand, is expected to be fast at running and have a high manoeuvrability since it dashes from bush to bush. Short forelimbs and long hindlimbs are supposed to enhance these performance measures. *Podarcis tiliguerta* appears to be more general in its habitat use, and therefore is expected to be intermediate in morphology and performance.

Materials and methods

MICROHABITAT USE IN THE FIELD

The following method was applied of microhabitat quantification for ten individuals of a *P. sicula* population in the Fango valley near Galeria, ten *P. tiliguerta* individuals in the Fango valley near Pirio, and nine *L. bedriagae* individuals at Haut-Asco (all in département Haute-Corse).

Different structural features were quantified at four spots: the spot where the lizard was observed initially, and the end-points of three lines at an angle of 120° and 200 cm from the first one. The direction of these lines was determined haphazardly by throwing a pen on the ground. The lizard sighting location served as the centre of a circle with a radius of 50 cm, the other three points were each the centre of a 100-cm radius circle. At the place where the lizard was spotted, the (1) perch height, (2) distance to nearest cover of stones or rocks and (3) distance to nearest cover by vegetation were measured. Additionally, percentage cover at ground level of stones/rocks, sand, grass/herbs, shrubs and trees (4–8) was quantified by visual estimation, and maximum height of vegetation (9) measured in the four circles. To reduce the number of variables, a principal component analysis (PCA) was performed on the mean values of the four spots (variables 4–9) and the values for the central circle only (variables 1–3). The Broken Stick method was used to determine which factors were significant (Jackson 1993). Factor scores were calculated and used as input for one way analyses of variance (ANOVA, species as factor).

MICROHABITAT PREFERENCE IN THE LABORATORY

For the laboratory experiments, 15 *L. bedriagae* adults (10 males, 5 females), 15 *P. sicula* adults (10 males, 5 females), and 14 *P. tiliguerta* adults (10 males,

Table 1. Measurements in mm (mean ± SD) on the three Corsican lacertid lizard species

Variable	L. bedriagae		P. sicula		P. tiliguerta	
	Males	Females	Males	Females	Males	Females
N	10	5	10	5	10	4
SVL	72·22 ± 6·47	70·76 ± 5·90	68·90 ± 2·40	66·90 ± 1·40	57·57 ± 2·17	55·13 ± 2·89
Mass	10·30 ± 2·73	8·42 ± 2·11	7·57 ± 0·83	5·94 ± 0·68	4·99 ± 0·36	4·22 ± 0·82
Hindlimb span	29·18 ± 2·71	26·57 ± 1·30	28·11 ± 1·45	24·48 ± 0·88	23·15 ± 1·42	21·67 ± 1·62
Femur length	15·31 ± 1·81	13·35 ± 1·01	15·21 ± 0·96	12·78 ± 1·08	12·94 ± 0·48	11·85 ± 1·18
Femur diameter	2·76 ± 0·24	3·09 ± 0·65	2·78 ± 0·34	2·40 ± 0·25	2·15 ± 0·30	2·10 ± 0·18
Tibia length	12·23 ± 1·13	11·02 ± 0·32	12·40 ± 0·48	10·63 ± 0·36	10·04 ± 0·39	9·47 ± 0·93
Tibia diameter	2·90 ± 0·49	2·62 ± 0·55	2·92 ± 0·30	2·48 ± 0·31	2·49 ± 0·25	2·53 ± 0·24
Metatarsus length	4·95 ± 0·59	4·13 ± 0·44	4·88 ± 0·26	4·27 ± 0·36	3·97 ± 0·39	3·78 ± 0·36
Hind toe length	11·68 ± 4·22	11·19 ± 1·26	13·07 ± 0·94	11·46 ± 0·46	11·88 ± 1·08	11·56 ± 1·20
Forelimb span	20·64 ± 1·66	18·40 ± 0·73	18·65 ± 1·24	16·86 ± 0·88	16·36 ± 0·87	15·15 ± 1·51
Humerus length	10·26 ± 1·07	8·96 ± 0·55	8·73 ± 0·55	8·02 ± 0·38	7·43 ± 0·52	7·16 ± 0·57
Humerus diameter	2·20 ± 0·28	2·40 ± 0·22	2·04 ± 0·18	1·60 ± 0·15	1·74 ± 0·12	1·57 ± 0·05
Radius length	8·82 ± 0·56	8·02 ± 0·55	8·17 ± 0·33	7·07 ± 0·32	7·04 ± 0·48	6·76 ± 0·80
Radius diameter	2·14 ± 0·38	1·97 ± 0·32	2·01 ± 0·18	1·71 ± 0·15	1·65 ± 0·13	1·47 ± 0·14
Metacarpus length	3·43 ± 0·34	2·82 ± 0·45	3·08 ± 0·26	2·65 ± 0·25	2·70 ± 0·17	2·27 ± 0·25
Hind toe length	8·23 ± 0·73	7·03 ± 0·13	6·78 ± 0·52	5·99 ± 0·33	6·65 ± 0·67	6·65 ± 0·23

4 females) were collected from the same populations as mentioned above (permit no. 96/403 of the Ministère de l' environnement de la République française). The lizards were transported to the laboratory at the University of Antwerp, Belgium. Five individuals, with species kept apart, were housed in each of nine terraria with a sandy substrate, some rocks and vegetation. A 100-W light bulb provided heat and light for 10 h a day. The lizards were fed live crickets dusted with vitamins daily. Water was always present.

Two sets of microhabitat preference experiments were carried out to elucidate (1) whether the three species prefer a different microhabitat from the one they use under natural conditions when offered a range of microhabitat types to choose from, and (2) whether they change their microhabitat preference in the presence of one of the other species.

In the first experiment, the animals were placed in a large terrarium (16 m^2), in which eight (micro) habitats were present: (1) sand, (2) moss, (3) low grass (*Poa annua*), (4) purple moor grass (*Molinia caerulea*), (5) shrubs (*Lonicera* spp.), (6) logs, (7) a tree trunk and (8) a stone wall. Microhabitats (1) to (5) each had an area of 3 m^2, while the areas of microhabitat (8) and the sum of (6) and (7) were 0·50 m^2. The data for substrates (6) and (7) were pooled in the statistical analyses. Eight 500-W lamps (one above each substrate type) provided light and heat during the experiment, so lizards were able to regulate their body temperatures. Each species was tested in two groups of seven or eight individuals (in total $N = 15$ for *L. bedriagae* and *P. sicula* and $N = 14$ for *P. tiliguerta*), with species kept apart. Each lizard was given an individual dot code on its back (non-toxic paint) for rapid identification. Every 30 min which microhabitat each individual was occupying was observed. The experiment started 1 h after the lizards were introduced into the test terrarium.

In the second experiment, the same experimental set-up and test protocol were used, but individuals of two species (four of each) were placed simultaneously in the terrarium. Two combinations of species were tested: (1) *P. tiliguerta* and *P. sicula*, and (2) *P. tiliguerta* and *L. bedriagae*. The interference between *L. bedriagae* and *P. sicula* was not investigated, since these species do not occur in sympatry on the island.

Whether the species differ in microhabitat preference, and whether microhabitat choice changes when another species is present, were tested by performing a log-linear analysis (hierarchical model) and calculating the Pearson χ^2 statistic.

MORPHOMETRY

The following morphological measurements were taken to the nearest 0·01 mm using digital callipers (Mitutoyo CD-15DC; Mitutoyo (UK) Ltd, Telford, UK) on each individual: snout–vent length (SVL), hindlimb span (measured from hip joint to the distal end of the metatarsus), forelimb span (measured from shoulder joint to the distal end of the metacarpus), length and diameter of the femur, tibia, humerus and radius, length of the metatarsus, metacarpus, second toe of the hindfoot (hereafter referred to as hind toe length), and fourth toe of the forefoot (hereafter referred to as fore toe length). All animals were weighed on an electronic balance (FX-3200; 0·01 g; A & D Instruments, Ltd, Abingdon, UK). Raw data are given in Table 1. All morphological variables were logarithmically (log 10) transformed before statistical analysis.

Whether the three species differ in SVL was tested with a two-way ANOVA (species and sex entered as fixed factors). Since we were particularly interested in shape differences, however, all other measurements were regressed against SVL and the residuals calculated.

These residuals were then entered into a principal component analysis and the resulting factor scores compared with a two-way ANOVA (species and sex entered as factors).

PERFORMANCE

Sprint speed was measured by chasing all individuals down a 2-m long racetrack with a cork substrate. Eight pairs of photocells, placed at 25-cm intervals, registered when a lizard passed. The elapsed time between passing two subsequent cells was stored in the computer and the velocity over each 25 cm was calculated. All animals were tested five times. The highest burst speed over any 25 cm interval was used as an estimate of the animal's maximum sprinting performance.

Climbing capacity was assessed by chasing the animals up a similar racetrack, 1 m long, and tilted to an angle of 70°. The photocells were placed at 15-cm intervals. The lizards were tested on two substrates: (1) a mesh (mesh width = 1 cm) to mimic climbing in vegetation, and (2) smooth schists to mimic climbing on rocks, and were given three trials on each. On each substrate, the highest burst speed over any 15-cm interval was used as a measure of maximum climbing ability.

To estimate manoeuvrability, a 0·5-m long pinboard was placed on the racetrack. This pinboard was made up of 53 sticks, with a diameter of 0·8 mm, positioned in a zigzag pattern. The distance between each pair of sticks, both lengthways and breadthways, was 3·5 cm. In this set-up six pairs of photocells were positioned at 10 cm intervals. All lizards were tested five times. As an estimate of manoeuvrability, the maximum speed over any 10-cm interval was used.

Endurance was quantified as the running time to exhaustion on a treadmill moving at a low and constant speed (0·80 km h^{-1}). An animal was considered exhausted when it did not show a righting response after being placed on its back. All lizards were tested three times. As an estimate of endurance, the maximum running time was used over the three trials.

Prior to experimentation, and between trials, the lizards were placed in an incubator for at least 1 h at 35 °C, which is equal to the selected body temperatures of the three species (Van Damme *et al.* 1990; R. Van Damme, unpublished data). Sprint speed, climbing speed, manoeuvrability and endurance were estimated on different days.

All performance data were logarithmically transformed (log10) prior to analysis. A two-way analysis of variance (species and sex as factors) was performed to test whether the three species differed in sprint speed, climbing speed, manoeuvrability and endurance. In addition, the ANOVA results were compared with the results from a two-way analysis of covariance (species and sex as factors, SVL as covariate) to check whether differences in SVL affect the statistical outcome.

Table 2. Eigenvalues, percentage variation explained, and factor loadings of the significant factors in the principal component analysis on the habitat variables (field). Mean and standard deviation for each species is given for both factors

Variable	PC 1	PC 2
Eigenvalue	4·61	2·08
% variation accounted for	51·26	23·09
Perch height	0·84	−0·03
% stone cover	0·91	0·34
% sand cover	−0·81	−0·03
% grass cover	0·08	−0·65
% shrubs cover	−0·92	0·23
% trees cover	−0·08	−0·79
Max. height vegetation	−0·78	0·34
Distance to nearest rock	−0·92	0·12
Distance to nearest vegetation	0·15	−0·90
Species	Mean ± SD	Mean ± SD
L. bedriagae	0·96 ± 0·10	0·39 ± 0·21
P. sicula	−1·20 ± 0·22	0·24 ± 0·32
P. tiliguerta	0·38 ± 0·55	−0·66 ± 1·57

PC = principal component

Results

MICROHABITAT USE IN THE FIELD

Principal component analysis on the nine microhabitat variables yielded two new variables, which jointly explained 74% of the total variation. The first axis was positively correlated with perch height, and percentage cover by stones or rocks, and negatively correlated with percentage cover by sand, and shrubs, maximum height of the vegetation and the distance to the nearest rock (Table 2). Mean factor scores on this axis differed among the three species (one way ANOVA; $F_{2,25} = 101 \cdot 55$; $P < 0 \cdot 0001$). Sightings of *L. bedriagae* scored positively, of *P. sicula* negatively and of *P. tiliguerta* intermediately on this axis (Table 2). This reflects that *L. bedriagae* individuals were mostly seen on high perches with an open, rocky substrate far away from cover, while *P. sicula* individuals occurred in vegetated patches, close to cover.

The second principal component was negatively correlated with percentage cover by trees, and distance to the nearest vegetation. Mean factor scores differed significantly among species (one way ANOVA; $F_{2,25} = 3 \cdot 46$; $P = 0 \cdot 047$). Sightings of *P. tiliguerta* scored negatively on this axis, *L. bedriagae* positively and *P. sicula* intermediate (Table 2). This means that *P. tiliguerta* individuals were mostly seen near to vegetation, while *L. bedriagae* occurred in open areas.

MICROHABITAT PREFERENCE IN THE LABORATORY

The three species differed significantly in microhabitat preference (log-linear analysis; Pearson $\chi^2_{12} = 68 \cdot 31$; $P < 0 \cdot 0001$), and there was no species by sex interaction effect (Pearson $\chi^2_{12} = 8 \cdot 36$; $P = 0 \cdot 76$) or species by individual interaction effect (Pearson $\chi^2_{168} = 154 \cdot 67$;
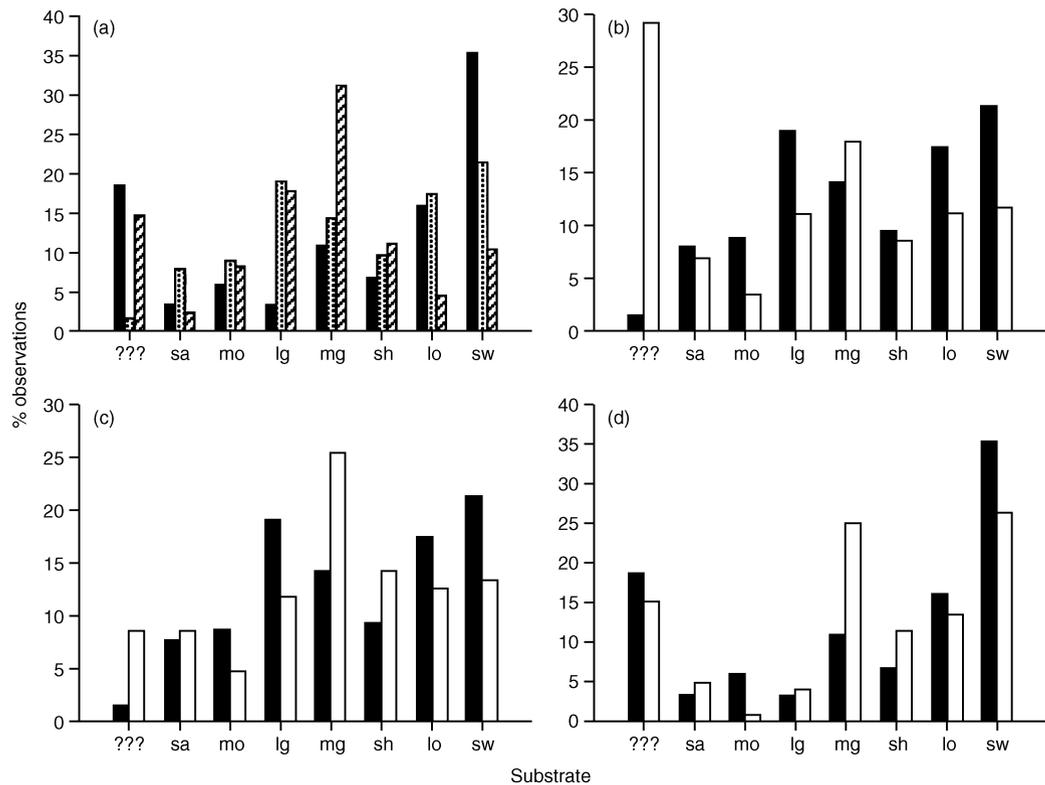
Fig. 1. Microhabitat preference in the experimental set-up, expressed in percentage of observations the lizards were seen in each microhabitat (??? = not seen, sa = sand, mo = moss, lg = low grass, mg = moor grass, sh = shrubs, lo = logs + trunk, sw = stone wall). (a) Microhabitat preference with species kept apart (black bars: *L. bedriagae*, light grey bars: *P. tiliguerta*, dark grey bars: *P. sicula*); (b) microhabitat preference of *P. tiliguerta* in presence of *P. sicula*; (c) microhabitat preference of *P. tiliguerta* in presence of *L. bedriagae*; (d) microhabitat preference of *L. bedriagae* in presence of *P. tiliguerta* (black bars: species kept apart, white bars: two species together).

$P = 0.76$). *Podarcis sicula* preferred the vegetated microhabitats (i.e. low grass and moor grass), while *L. bedriagae* was observed most of the times on the stone wall. *Podarcis tiliguerta* occurred more or less on every substrate (Fig. 1a).

When placing *P. tiliguerta* and *P. sicula* individuals in the test terrarium at the same time, neither of them changed their distribution across the microhabitats compared to when they were tested separately (*P. tiliguerta*: Pearson $\chi^2_6 = 5.71$; $P = 0.46$; *P. sicula*: Pearson $\chi^2_6 = 8.70$; $P = 0.19$). The species by sex interaction was non-significant in both cases (*P. tiliguerta*: Pearson $\chi^2_6 = 3.55$; $P = 0.74$; *P. sicula*: Pearson $\chi^2_6 = 7.17$; $P = 0.31$). However, in the presence of *P. sicula*, *P. tiliguerta* individuals were more often scored as 'not seen' (Fig. 1b).

Podarcis tiliguerta's distribution in the terrarium when *L. bedriagae* was present did not change significantly (Pearson $\chi^2_6 = 11.61$; $P = 0.07$) compared with when observed alone. *Podarcis tiliguerta* individuals, however, seemed to be less active (Fig. 1c). On the contrary, *L. bedriagae* did change its microhabitat use in presence of *P. tiliguerta*: *L. bedriagae* was observed significantly more in the moor grass than when *P. tiliguerta* was absent (Pearson $\chi^2_6 = 14.75$; $P = 0.02$; Fig. 1d). The species by sex interaction was

nonsignificant in both cases (*P. tiliguerta*: Pearson $\chi^2_6 = 8.0$; $P = 0.24$; *L. bedriagae*: Pearson $\chi^2_6 = 8.62$; $P = 0.20$).

MORPHOMETRY

The sampled individuals from the three species differed significantly in SVL (mean ± SD; *P. tiliguerta*: 56.87 ± 2.55 mm; *P. sicula*: 68.23 ± 2.29 mm; *L. bedriagae*: 71.73 ± 6.11 mm; two-way ANOVA, $F = 49.70$; $P < 0.0001$). Sexes did not differ in SVL ($F = 3.00$; $P = 0.09$) and the interaction between sex and species was not significant ($F = 0.06$; $P = 0.95$).

Principal component analysis on the 15 size-free morphological variables yielded three significant variables. Jointly they explained 63% of the total variation. The first axis showed high loadings for residual mass, residual forelimb span, residual humerus and radius length and residual fore toe length (Table 3). A two-way ANOVA on the factor scores revealed a significant difference among species ($F_{2,38} = 21.95$; $P < 0.0001$) and between sexes ($F_{1,38} = 11.71$; $P = 0.002$). There was no interaction (sex × species) effect ($F_{2,38} = 1.86$; $P = 0.17$). *L. bedriagae* scored highly positively, *P. sicula* highly negatively, and *P. tiliguerta* intermediately on this axis (Fig. 2). This suggests that, relative

Table 3. Eigenvalues, percentage of variation explained, and factor loadings of the significant factors in the principal component analysis on the morphological variables

Variable	PC 1	PC 2	PC 3
Eigenvalue	6·10	1·74	1·66
% variation accounted for	40·67	11·59	11·04
Mass	0·72	0·19	0·31
Hindlimb span	0·60	0·62	−0·08
Femur length	0·29	0·81	0·06
Femur diameter	−0·15	−0·14	0·76
Tibia length	0·31	0·78	0·03
Tibia diameter	0·14	0·28	0·49
Metatarsus length	0·13	0·62	−0·21
Hind toe length	0·02	0·81	0·16
Forelimb span	0·76	0·36	−0·09
Humerus length	0·84	0·20	−0·03
Humerus diameter	0·52	0·00	0·67
Radius length	0·75	0·35	0·11
Radius diameter	0·05	0·45	0·68
Metacarpus length	0·31	0·61	0·19
Fore toe length	0·83	0·08	0·00
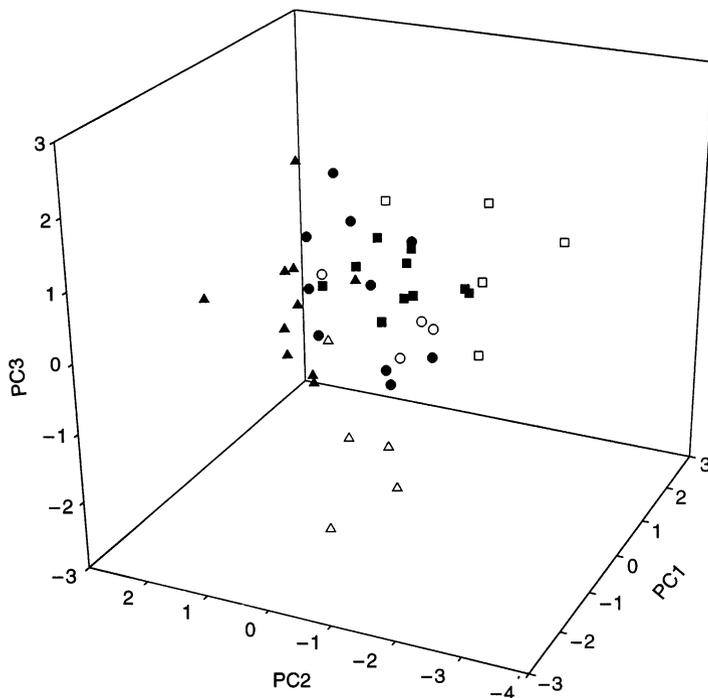
Fig. 2. Position of the three species in 'morphospace' described by the first three principal components. The first principal component correlates positively with residual mass, residual forelimb span, residual humerus, residual radius and residual fore toe length. The second principal component correlates positively with residual femur, tibia and hind toe length. The third principal component correlates positively with femur, humerus and radius diameter. Indicated are the individual factor scores. Symbols refer to species (● *P. tiliguerta*, ■ *L. bedriagae*, ▲ *P. sicula*), symbol fills to sex (white: females, black: males).

to SVL, *L. bedriagae* has the highest mass and longest forelimbs, while *P. sicula* has the lowest mass and shortest forelimbs of the three species. The mean value of this principal component was positive for males and negative for females, which implies that males have a higher relative body mass and longer relative forelimbs than females.

The second principal component was positively correlated with residual femur and tibia length, and residual hind toe length (Table 3). A two-way ANOVA on the factor scores showed a significant effect of species ($F_{2,38} = 8·71$; $P = 0·0007$) and sex ($F_{1,38} = 44·65$; $P < 0·0001$). The sex by species interaction effect was non-significant ($F_{2,38} = 3·26$; $P = 0·05$). *Podarcis sicula* scored positively, *L. bedriagae* negatively and *P. tiliguerta* intermediately on this axis (Fig. 2). This suggests that, relative to SVL, *P. sicula* has the longest hindlimbs, while *L. bedriagae* has the shortest hindlimbs of the three species. The mean value of this principal component was positive in males and negative in females, which implies that males have longer relative hindlimbs than females.

Finally, the third axis was positively correlated with residual femur, humerus and radius diameter (Table 3). A two-way ANOVA on the factor scores revealed a significant interaction ($F_{2,38} = 5·52$; $P = 0·008$) and species effect ($F_{2,38} = 4·01$; $P = 0·03$). The sexes did not differ significantly ($F_{1,38} = 0·56$; $P = 0·46$). *Lacerta bedriagae* scored positively, *P. sicula* negatively and *P. tiliguerta* intermediately on this axis (Fig. 2). This suggests that, relative to SVL, *L. bedriagae* has the thickest limbs and *P. sicula* the most slender ones. The interaction effect indicates that the difference between the sexes is not the same in each species.

PERFORMANCE

Mean maximal sprint speed did not differ among species (Fig. 3a) or between sexes. There was no significant species-by-sex interaction effect. The differences in SVL did not affect the results (Table 4).

Maximal climbing speed on schists, however, differed significantly among the three species. The effects of sex and species-by-sex interaction were non-significant. There was no effect of SVL on the outcome of the analysis (Table 4). *Lacerta bedriagae* is the fastest climber on schists, *P. tiliguerta* the slowest (Fig. 3a), and this is not simply the result of the difference in size.

Maximal climbing speed on mesh differed significantly among species as well (Fig. 3a). There was no significant effect of sex, or of the species-by-sex interaction. However, the differences among species vanished when taking the differences in SVL into account (Table 4).

Manoeuvrability did not differ among species (Fig. 3a) or between sexes, and the species-by-sex interaction was not significant. The difference in SVL did not affect the results (Table 4).

Endurance differed significantly among species. There was no sex effect and the species-by-sex interaction was not significant. Taking the difference in SVL into account did not alter the results (Table 4). *Lacerta bedriagae* had the highest endurance, *P. tiliguerta* the lowest (Fig. 3b).
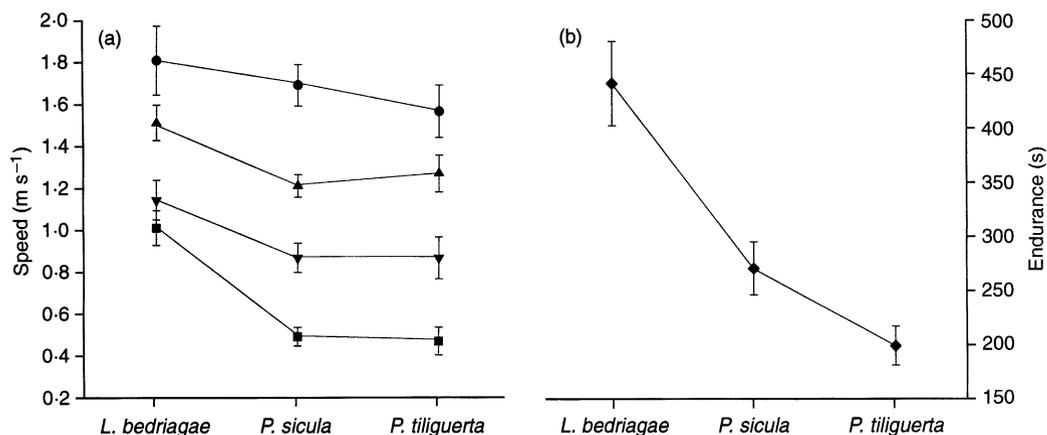
Fig. 3. Performance measures of the three species: (a) sprint speed, climbing speed on schists, climbing speed on mesh, manoeuvrability (b) endurance. All are expressed in absolute terms ((a) m s^{-1}, (b) s). Indicated are species means and standard errors. Symbols refer to performance measures (● sprint speed, ■ climbing speed on schists, ▲ climbing speed on mesh, ▼ manoeuvrability, ◆ endurance).

Table 4. Results from the two-way ANOVA and ANCOVA on the five performance measures. Given are the degrees of freedom, *F*-values and significance levels

Variable	Effect	ANOVA			ANCOVA		
		df	*F*	*P*	df	*F*	*P*
Sprint speed	Species	2, 35	0·54	0·59	2, 34	0·56	0·58
	Sex	1, 35	0·42	0·52	1, 34	0·54	0·47
	Interaction	2, 35	0·33	0·72	2, 34	0·35	0·71
Climbing speed (schists)	Species	2, 37	13·77	<0·0001	2, 36	3·67	0·04
	Sex	1, 37	2·28	0·14	1, 36	1·61	0·21
	Interaction	2, 37	2·65	0·08	2, 36	2·56	0·09
Climbing speed (mesh)	Species	2, 37	3·45	0·04	2, 36	1·76	0·19
	Sex	1, 37	3·06	0·09	1, 36	2·70	0·11
	Interaction	2, 37	0·73	0·49	2, 26	0·68	0·51
Manoeuvrability	Species	2, 31	2·97	0·07	2, 30	2·87	0·07
	Sex	1, 31	0·49	0·49	1, 30	0·82	0·37
	Interaction	2, 31	0·45	0·64	2, 30	0·51	0·60
Endurance	Species	2, 38	18·91	<0·0001	2, 37	6·24	0·005
	Sex	1, 38	2·96	0·09	1, 37	3·00	0·09
	Interaction	2, 38	2·73	0·08	2, 37	2·69	0·08

Discussion

MICROHABITAT USE AND INTERACTIONS AMONG SPECIES

Our field data on the microhabitat use of the three lizard species fit the qualitative habitat descriptions given in earlier papers. *Lacerta bedriagae* individuals were most often seen on large boulders and rocks, far away from cover (cf. Castilla *et al*. 1989; Delaugerre & Cheylan 1992), while *P. sicula* individuals occurred mostly among vegetation and close to hiding places, consisting of rocks (cf. Van Damme *et al*. 1990; Delaugerre & Cheylan 1992). *Podarcis tiliguerta* seemed to be less particular about its microhabitat use (cf. Van Damme *et al*. 1989, 1990; Delaugerre & Cheylan 1992).

The laboratory observations of microhabitat use

(with species kept apart) correspond remarkably well to those made in the field. This may imply that microhabitat choice in the field is not constrained by external factors such as predation or interspecific competition (that is, lizards are not driven out of their 'preferred' microhabitats). Alternatively, lizards in the laboratory set-up may not be optimizing their microhabitat use. For instance, past experiences with predators or competitors in particular microhabitats may keep lizards from using those microhabitats, even in unrestrained conditions. Association of particular (otherwise favourable) microhabitats with danger or competition may also be innate. In this case, microhabitat preference could be considered a 'fixed' behaviour (*sensu* Stein 1979; Sih 1987).

Although the overall microhabitat use of *P. sicula* and *P. tiliguerta* remained unaffected by the presence or absence of one another, *P. tiliguerta* became more

secretive in the presence of *P. sicula*. Moreover, individuals from the latter species were repeatedly seen to chase *P. tiliguerta* individuals in the test terrarium. This suggests that *P. sicula* is the more aggressive species of the two. On the island, however, *P. sicula* and *P. tiliguerta* seem to be able to coexist stably by using different microhabitats (Van Damme *et al.* 1990; Delaugerre & Cheylan 1992), and the distribution of *P. sicula*, which was introduced by humans, appears to be slowly expanding on the island (Delaugerre & Cheylan 1992). Possibly, *P. tiliguerta*'s secretive behaviour in the test terrarium is only a first step in trying to avoid competition with the agonistic *P. sicula*, which may, in the long term, result in a partition of potential microhabitats.

When *L. bedriagae* and *P. tiliguerta* were placed together into the experimental set-up, the former species shifted its microhabitat preference from the stone wall to the vegetation. Moreover, where they co-occur we have seen *P. tiliguerta* individuals actively chasing *L. bedriagae* individuals away. The observed microhabitat shift and chases suggest that *P. tiliguerta* and *L. bedriagae* are competing for the same spots. If so, these competitive interactions may influence the species distribution on Corsica to a great extent. Presently, *L. bedriagae* has the most restricted distribution on the island, occurring only at high elevations. Moreover, Delaugerre & Cheylan (1992) have suggested that *P. tiliguerta* is expanding its distribution at the cost of *L. bedriagae*.

However, we do not have data on which other factors (e.g. predation, intraspecific competition, temporal variation in resource availability, parasites) may come into play under natural conditions and how important they are in structuring this community (Dunham 1980; Barbault & Maury 1981; Smith 1981; Adler 1985; Schall 1992; Schall & Vogt 1993; Holt & Lawton 1994; Leal *et al.* 1998). Therefore, our results must be interpreted with caution.

MORPHOMETRY – LOCOMOTOR PERFORMANCE – MICROHABITAT USE

Interspecific differences

Do the differences in microhabitat use among the three Corsican species correlate with morphological and performance differences?

Out of the five performance measures we took, only climbing speed on schists and endurance differed among species. The largest species, *L. bedriagae*, excelled in both cases, even when taking its size into account. Therefore, size does not seem to be a determinant of performance capacity, and hence cannot be considered adaptive to the different microhabitat requirements. Moreover, on a larger scale, i.e. within the family of the lacertids, no evolutionary relationship was found between size variation and differences in microhabitat use (Vanhooydonck & Van Damme 1999).

The limbs of *L. bedriagae* seem well suited for climbing on smooth surfaces. Having short hind legs is supposed to enhance climbing ability by placing the centre of gravity closer to the substrate and thus increasing stability on inclined surfaces (Cartmill 1985; Pounds 1988; Losos 1990b). Furthermore, in contrast to level-running where the forelimbs are largely inactive (see further), the forelimbs give active support in ascending: they pull the animal toward the vertical surface, while the hind legs push off it. Therefore, the long forelimbs prevent the lizard from toppling back (Autumn *et al.* 1998; Zaaf *et al.* 1999). Also, stout legs (i.e. high diameter) imply thicker (and therefore stronger) bones and/or thicker muscles. Because the cross-sectional area of a muscle is positively correlated to its strength (Alexander 1992), this may suggest that *L. bedriagae* can exert more force, which seems useful if you have to move against gravity. However, other factors (e.g. pinnation angle and moment arms), which we did not quantify in this case, are known to influence climbing capacity (Zaaf *et al.* 1999).

Climbing ability on a mesh seems to be determined by other characteristics than climbing ability on rocky surfaces, since *L. bedriagae*, the best climber on schists, did not perform better on a mesh than the other two species. Possibly, climbing on a mesh constrains the lizard's body shape less because it provides more grip, which makes it easier to climb up.

In contrast to predictions (Kramer 1951; Huey & Hertz 1984; Losos & Sinervo 1989; Sinervo & Losos 1991; Losos, Walton & Bennett 1993; Miles 1994), however, adaptation to one lifestyle (in this case a climbing one) does not seem to compromise other performance capacities in *L. bedriagae*. Firstly, of the three species tested, it has the highest endurance. This may not come as a surprise, since this species occurs mainly in open microhabitat and thus needs to run over great distances to reach safety. Having a high stamina therefore seems to be adaptive. Moreover, while absolute body mass scales negatively with climbing capacity (Hill 1950; Taylor, Caldwell & Rowntree 1972; Huey & Hertz 1982; Cartmill 1985), it has been shown to correlate positively with endurance (Bennett 1980; Garland 1984; Garland & Else 1987; Bennett, Garland & Else 1989; Garland 1994; Beck *et al.* 1995; Autumn *et al.* 1997). *Lacerta bedriagae* falls easily into this pattern, since, of the three species considered, it has the highest absolute body mass.

Additionally, on level surfaces (i.e. sprinting and manoeuvrability) *L. bedriagae* does not perform worse than the two other species. This is quite unexpected given its body shape: based on biomechanical assumptions runners should have long limbs (e.g. Losos & Sinervo 1989; Losos 1990a,b; Sinervo & Losos 1991; Bauwens *et al.* 1995; but see Losos, Papenfuss & Macey 1989; Miles 1994; Van Damme *et al.* 1997). Moreover, high sprinting ability and, especially, manoeuvrability do not seem ecologically relevant for *L. bedriagae*.

Based on *P. sicula*'s limb morphology, we expected it to be a good runner and bad climber. Long hindlimbs are favoured in runners since they increase stride length and hence speed (Pianka & Pianka 1976; Garland & Losos 1994). Furthermore, short forelimbs are believed to be advantageous for these animals because they do not impede the movement of the long hind legs (Snyder 1962; Sukhanov 1968; Losos 1990a). *Podarcis sicula* meets both these requirements. Moreover, good running capacities and high manoeuvrability seem particularly important for *P. sicula*, since it forages among the vegetation and is often seen dashing from bush to bush across sandy patches (Van Damme *et al*. 1990; personal observation). However, the same morphological characteristics (i.e. long hindlimbs, short forelimbs), are detrimental for climbers (see above). Moreover, in nature *P. sicula* is seldom seen to climb stone walls or rocks. Our expectations partially came true: *P. sicula* is the worst climber on schists, but it is not a good runner. Furthermore, it did not perform worse than the other two species when climbing on a mesh. Therefore long hindlimbs and short forelimbs do not seem to have a bad effect on their capacity to climb on mesh. Apparently, by providing more grip, climbing up a mesh is less demanding than climbing up a smooth surface. Moreover, in the field, we have observed *P. sicula* escaping into a tree.

Finally, *P. sicula* had an intermediate endurance. Based on both morphological (i.e. absolute body mass), and ecological data (occurs in more vegetated areas than *L. bedriagae*), we did not expect any differently.

Podarcis tiliguerta appeared to be morphologically and ecologically in between *P. sicula* and *L. bedriagae*. As expected, it proved to be a general 'performer' as well. Only for endurance did *P. tiliguerta* score the lowest. This may not come as a surprise since it has the lowest absolute body mass and seems to occur closest to hiding places consisting of vegetation.

How can the apparent ambiguous relationship between the animals' design and their performance capacity be explained? Firstly, we have focused on one aspect, namely external morphology, only, and in doing so we implicitly assumed all else (e.g. biochemical, physiological variables) to be equal. However, sprint speed is determined by both stride length and frequency (Sukhanov 1968). While stride length is supposed to be correlated with limb length (see Garland & Losos 1994), stride frequency is affected by a variety of physiological and mechanical parameters (e.g. muscle contraction rate, relative muscle mass, proportion of muscle fibre types). If species modulate their speed differently the result may be the same irrespective of the animal's external morphology (see Van Damme, Aerts & Vanhooydonck 1998). We are currently analysing data on the kinematics of level-running to elucidate whether this is indeed the case in *L. bedriagae*, *P. sicula* and *P. tiliguerta*.

Secondly, differences in posture may mask the morphology–performance relationship. Although in general all lizards are considered to be sprawlers, the degree of sprawling may differ among species (see Christian & Garland 1996). Lizards can 'compensate' for differences in limb lengths by placing the limbs parasagital relative to the body, and therefore increase their 'functional' limb length and reduce friction. If *L. bedriagae* were to do this, it would explain why it attains as high sprint speeds with short legs as *P. sicula* does with long legs. This needs further attention.

Lastly, biomechanical considerations do predict differentiation in many of the morphological characters we have examined here, but the applicability of the models to lacertids has recently been questioned (Van Damme *et al*. 1997, 1998; Vanhooydonck & Van Damme 1999). To refine these biomechanical models, and their relation to performance, we need detailed kinematic, morphological and performance data on more species.

Sexual dimorphism

Males and females differ in shape: while males have relatively long hind- and forelimbs and a relatively high body mass, females have relatively short hind- and forelimbs and a relatively low body mass. These morphological differences, however, did not seem to translate into performance or ecological differences. Apparently, the result of the long hindlimbs–long forelimbs–high body mass combination is the same as the short hindlimbs–short forelimbs–low body mass one. Possibly, other factors, such as life-history traits, are more related to the sexual difference in morphology than locomotor behaviour.

Competitive ability

In spite of its larger body size and high-performance capability, *L. bedriagae* seems to be the least competitive species of the three. This follows from both its distribution on the island and the laboratory experiments on habitat preference. In contrast to earlier findings (Schoener 1983; Losos & Spiller 1999) morphology (both size and shape parameters) or locomotor performance do not appear to be good predictors of competitive ability. *Podarcis sicula* and *P. tiliguerta* are very energetic and aggressive animals, while *L. bedriagae* individuals are not. Therefore, differences in aggressiveness might turn out to be more important in determining the outcome of interspecific interactions among these lizards, and hence their distribution, than more traditional measures such as morphological or performance adaptability.

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