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

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...
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lacertids locomotion in

Where ecological adaptations that allow them to perform species (Cartmill 1985; Pounds 1988; Miles 1994). Aerts & Vanhooydonck (1997), while a dorso-ventrally flattened body seems more appropriate for climbing (Snyder 1954; Van Damme, 1991). The body shape of cursorial lizards should Nunez & Ojeda (1980; Pounds 1988; Sinervo & Losos 1990a). Both short fore- and hindlimbs, on the contrary, short forelimbs (Snyder 1962; Sukhanov 1968; Losos, Pianka & Pianka 1976; Garland & Losos 1994), and in open habitats should have relatively long hindlimbs respective environments. For instance, lizards living by the three species seem to differ sufficiently to assess mutual interference. 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 Priro, 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, 5 females), and 14 P. tiliguerta adults (10 males,
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 Université de l’environnement de la République française). 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 sympathy 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 $\chi^2$ 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), 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 foot (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 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 endurance.

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.

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**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

<table>
<thead>
<tr>
<th>Variable</th>
<th>PC 1</th>
<th>PC 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eigenvalue</td>
<td>4.61</td>
<td>2.08</td>
</tr>
<tr>
<td>% variation accounted for</td>
<td>31.26</td>
<td>23.09</td>
</tr>
<tr>
<td>Perch height</td>
<td>0.84</td>
<td>-0.03</td>
</tr>
<tr>
<td>% stone cover</td>
<td>0.91</td>
<td>0.34</td>
</tr>
<tr>
<td>% sand cover</td>
<td>-0.81</td>
<td>-0.03</td>
</tr>
<tr>
<td>% grass cover</td>
<td>0.08</td>
<td>0.65</td>
</tr>
<tr>
<td>% shrubs cover</td>
<td>-0.92</td>
<td>0.23</td>
</tr>
<tr>
<td>% trees cover</td>
<td>-0.08</td>
<td>-0.79</td>
</tr>
<tr>
<td>Max. height vegetation</td>
<td>-0.78</td>
<td>0.34</td>
</tr>
<tr>
<td>Distance to nearest rock</td>
<td>-0.92</td>
<td>0.12</td>
</tr>
<tr>
<td>Distance to nearest vegetation</td>
<td>0.15</td>
<td>-0.90</td>
</tr>
<tr>
<td>Species</td>
<td>Mean ± SD</td>
<td>Mean ± SD</td>
</tr>
<tr>
<td>L. bedriagae</td>
<td>0.96 ± 0.10</td>
<td>0.39 ± 0.21</td>
</tr>
<tr>
<td>P. sicula</td>
<td>-1.20 ± 0.22</td>
<td>0.24 ± 0.32</td>
</tr>
<tr>
<td>P. tiliguerta</td>
<td>0.38 ± 0.55</td>
<td>-0.66 ± 1.37</td>
</tr>
</tbody>
</table>

PC = principal component

**Results**

**MICROHABITAT USE IN THE FIELD**

Principal component analysis on the nine micro-habitat 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; F₁,₁₅₅ = 101.55; P < 0.0001). Sightings of L. bedriagae occurred positively, of P. sicula negatively and of P. tiliguerta intermediate 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; F₁,₁₅₅ = 3.46; P = 0.047). 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 χ² = 8.36; P = 0.076) or species by individual interaction effect (Pearson χ² = 154.67;
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 \( \chi^2 = 5.71; P = 0.46; \) P. sicula: Pearson \( \chi^2 = 8.70; P = 0.19 \)). The species by sex interaction was non-significant in both cases (P. tiliguerta: Pearson \( \chi^2 = 3.55; P = 0.74; \) P. sicula: Pearson \( \chi^2 = 7.17; P = 0.31 \)). 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 \( \chi^2 = 14.75; P = 0.02 \)) 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 \( \chi^2 = 7.17; P = 0.02 \)). The species by sex interaction was nonsignificant in both cases (P. tiliguerta: Pearson \( \chi^2 = 8.02; P = 0.24; \) L. bedriagae: Pearson \( \chi^2 = 8.62; P = 0.20 \)).

**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; 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 (\( F_{1,38} = 21.95; P < 0.0001 \)) and between sexes (\( F_{2,38} = 11.71; P = 0.002 \)). There was no interaction (sex x species) effect (\( F_{2,38} = 1.86; P = 0.17 \)). L. bedriagae scored highly positively, P. sicula highly negatively, and P. tiliguerta moderately on this axis (Fig. 2). This suggests that, relative
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 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*$_{2,38}$ = 8.71; *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* intermediate 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.

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

<table>
<thead>
<tr>
<th>Variable</th>
<th>PC 1</th>
<th>PC 2</th>
<th>PC 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eigenvalue</td>
<td>6.10</td>
<td>1.74</td>
<td>1.66</td>
</tr>
<tr>
<td>% variation accounted for</td>
<td>40.67</td>
<td>11.59</td>
<td>11.04</td>
</tr>
<tr>
<td>Mass</td>
<td>0.72</td>
<td>0.19</td>
<td>0.31</td>
</tr>
<tr>
<td>Hindlimb span</td>
<td>0.60</td>
<td>0.62</td>
<td>-0.08</td>
</tr>
<tr>
<td>Femur length</td>
<td>0.29</td>
<td>0.81</td>
<td>0.06</td>
</tr>
<tr>
<td>Femur diameter</td>
<td>-0.15</td>
<td>-0.14</td>
<td>0.76</td>
</tr>
<tr>
<td>Tibia length</td>
<td>0.31</td>
<td>0.78</td>
<td>0.03</td>
</tr>
<tr>
<td>Tibia diameter</td>
<td>0.14</td>
<td>0.28</td>
<td>0.49</td>
</tr>
<tr>
<td>Metatarsus length</td>
<td>0.13</td>
<td>0.62</td>
<td>-0.21</td>
</tr>
<tr>
<td>Hind toe length</td>
<td>0.02</td>
<td>0.81</td>
<td>0.16</td>
</tr>
<tr>
<td>Forelimb span</td>
<td>0.76</td>
<td>0.36</td>
<td>-0.69</td>
</tr>
<tr>
<td>Humerus length</td>
<td>0.84</td>
<td>0.20</td>
<td>-0.03</td>
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<tr>
<td>Humerus diameter</td>
<td>0.52</td>
<td>0.00</td>
<td>0.67</td>
</tr>
<tr>
<td>Radius length</td>
<td>0.75</td>
<td>0.35</td>
<td>0.11</td>
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<tr>
<td>Radius diameter</td>
<td>0.05</td>
<td>0.45</td>
<td>0.68</td>
</tr>
<tr>
<td>Metacarpus length</td>
<td>0.31</td>
<td>0.61</td>
<td>0.19</td>
</tr>
<tr>
<td>Fore toe length</td>
<td>0.83</td>
<td>0.08</td>
<td>0.00</td>
</tr>
</tbody>
</table>

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*$_{2,38}$ = 44.65; *P* = 0.0001) and sex (*F*$_{1,38}$ = 4.46; *P* = 0.03). The sexes did not differ significantly (*F*$_{2,38}$ = 0.46). *Lacerta bedriagae* scored positively, *P. sicula* negatively and *P. tiliguerta* intermediate 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).
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).

### Table 4. Results from the two-way ANOVA and ANCOVA on the five performance measures

<table>
<thead>
<tr>
<th>Variable</th>
<th>Effect</th>
<th>df</th>
<th>F</th>
<th>P</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sprint speed</td>
<td>Species</td>
<td>2, 35</td>
<td>0.54</td>
<td>0.59</td>
<td>2, 34</td>
<td>0.56</td>
<td>0.58</td>
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<tr>
<td></td>
<td>Sex</td>
<td>1, 35</td>
<td>0.42</td>
<td>0.52</td>
<td>1, 34</td>
<td>0.54</td>
<td>0.47</td>
</tr>
<tr>
<td></td>
<td>Interaction</td>
<td>2, 35</td>
<td>0.33</td>
<td>0.72</td>
<td>2, 34</td>
<td>0.35</td>
<td>0.71</td>
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<tr>
<td>Climbing speed (schists)</td>
<td>Species</td>
<td>2, 37</td>
<td>13.77</td>
<td>&lt;0.0001</td>
<td>2, 36</td>
<td>3.67</td>
<td>0.04</td>
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<tr>
<td></td>
<td>Sex</td>
<td>1, 37</td>
<td>2.28</td>
<td>0.14</td>
<td>1, 36</td>
<td>1.61</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>Interaction</td>
<td>2, 37</td>
<td>2.65</td>
<td>0.08</td>
<td>2, 36</td>
<td>2.56</td>
<td>0.09</td>
</tr>
<tr>
<td>Climbing speed (mesh)</td>
<td>Species</td>
<td>2, 37</td>
<td>3.45</td>
<td>0.04</td>
<td>2, 36</td>
<td>1.76</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td>Sex</td>
<td>1, 37</td>
<td>3.06</td>
<td>0.09</td>
<td>1, 36</td>
<td>2.70</td>
<td>0.11</td>
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<tr>
<td></td>
<td>Interaction</td>
<td>2, 37</td>
<td>0.73</td>
<td>0.49</td>
<td>2, 26</td>
<td>0.68</td>
<td>0.51</td>
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<td>Manoeuvrability</td>
<td>Species</td>
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<td>2.97</td>
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<td>2, 30</td>
<td>2.87</td>
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<td>0.08</td>
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### Discussion

**Microhabitatuse 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; Delaunager & Cheylan 1992), and the distribution of *P. sicula*, which was introduced by humans, appears to be slowly expanding on the island (Delaunager & 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 in 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. Possibly, *L. bedriagae* has the most restricted distribution on the island, occurring only at high elevations. Moreover, Delaunager & 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; Zaal 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 for escaping predators. However, other factors (e.g. pinnation angle and moment arms), which we did not quantify in this case, are known to influence climbing capacity (Zaal 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; Autuman 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 other two species. This is quite unexpected given its body shape: based on biomechanical assumptions runners should have long limbs (e.g. Losos & Sinervo 1989; Losos 1990b; 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*. **365** Ecomorphology of locomotion in lacertids

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 maneuverability 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 chisit, 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 (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 hindlimbs 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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References


a case study with South American Liolaemus. Oecologia 76, 567–569.


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