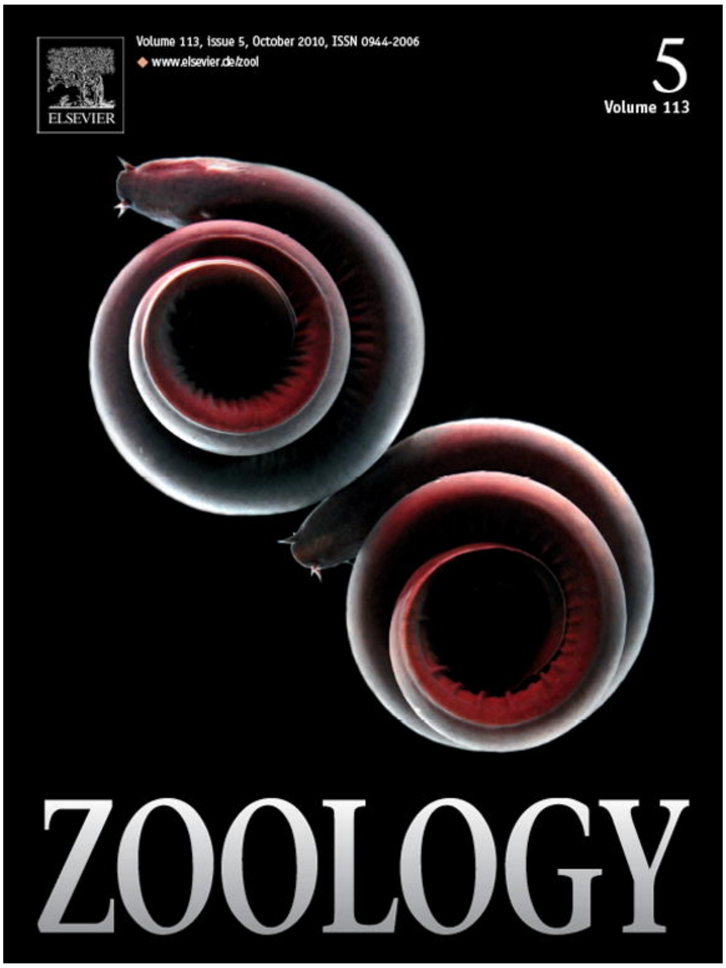

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# Competition with wall lizards does not explain the alpine confinement of Iberian rock lizards: an experimental approach

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## ABSTRACT

Interspecific competition can limit the distribution of species along altitudinal gradients. It has been suggested that Western European rock lizards (genus *Iberolacerta*) are restricted to mountains due to the expansion of wall lizards (*Podarcis*), but there is no experimental evidence to corroborate this hypothesis. This study examines if interference competition with *Podarcis muralis* is a plausible explanation for the alpine confinement of Iberian rock lizards *Iberolacerta cyreni*. In a first experiment, we used an enclosure with four types of microhabitats to investigate whether adult rock and/or wall lizards shifted microhabitat or refuge preferences in the presence of the other species, and to detect aggressive interactions between them. In a second experiment, we staged heterospecific encounters between naïve, laboratory-born juveniles to identify behavioural differences and agonistic interactions. In the enclosure, neither rock nor wall lizards changed their microhabitat preferences in the presence of the other species. Nevertheless, rock lizards increased the diversity of microhabitats and nocturnal refuges used in the single species trials, which had twice the number of conspecifics. Aggressive interactions involved mainly large rock lizard males. Juveniles did not show any interspecific agonistic behaviour, but rock lizards spent more time basking and less time moving. Thus, we found no evidence of competition between both species in terms of habitat shifts or agonistic interactions, although intraspecific interactions seemed to explain the behaviour of adult rock lizards. We conclude that other factors are currently determining the alpine confinement of rock lizards.

## 1. Introduction

Interspecific competition, combined with other biotic and abiotic factors, can limit the distribution of species in potentially suitable habitats (Brown et al., 1996; Pulliam, 2000). While dominant species successfully exploit the shared habitat, subordinate ones can be relegated to suboptimal areas either by their reduced exploitative ability or by direct behavioural interference (Schoener, 1983; Petren et al., 1993). In evolutionary time, competitive exclusion can lead to phenotypic divergence of sympatric species, which diversify their use of resources (Schluter, 2000; Pfennig et al., 2007; Moen and Wiens, 2009). Also, in an effort to minimise overlapping, species can segregate in space by selecting different habitats, a behavioural mechanism which can contribute to generate allopatric distributions (Hess and Losos, 1991; Taniguchi and Nakano, 2000).

Lizards, for their dynamic distribution ranges and moderate dispersal ability, are good models to investigate the role of interspecific competition in community structure. Several studies have demonstrated the crucial role of interspecific competition in the evolution, distribution, and abundance of island lizards (see Case and Bolger, 1991 for a review). For example, success in island colonisation by anoles is seemingly shaped by interspecific competition (Losos et al., 1993; Losos and Spiller, 1999), and the evolutionary radiation and community structure of Caribbean anoles and *Phelsuma* geckos in the Indian Ocean were likely driven by competitive interactions (Losos, 1994; Leal et al., 1998; Harmon et al., 2007).

Although much of the relevant literature concerns island species, elevation has also drawn the attention of biogeographers and evolutionary ecologists seeking to explore the role of interspecific competition in the vertical zonation of organisms (Tannerfeldt et al., 2002; Cadena, 2007; Twomey et al., 2008). For reptiles, the possible effect of competitive interactions on the distribution of species along altitudinal gradients is unclear. While in some cases interspecific competition appears to modify population responses to elevation (Buckley and Roughgarden, 2005, 2006), the altitudinal distribution of other communities seems unrelated to interactions among species (Hofer et al., 1999; Carothers et al., 2001). Nevertheless, studies are still scarce, and further research is needed to

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improve our understanding of how biotic interactions shape lizard assemblages along altitudinal gradients.

West European rock lizards within the genus *Iberolacerta* have small, widely separated ranges in highland areas of the western Mediterranean. They form a monophyletic group with four main units: *I. horvathi* of North-west Croatia and neighbouring regions, the Pyrenean species (*I. bonnali*, *I. aranica* and *I. aurelioi*), the *I. monticola* group from Central Portugal and North-west Spain, and *I. cyreni* of the Iberian Sistema Central, with distinctive populations in Béjar, Gredos and Guadarrama mountain ranges (Carranza et al., 2004). Molecular analyses suggest that *Iberolacerta* has produced few external branches since its initial fragmentation, at approximately the same time when wall lizards (*Podarcis*) diversified into a series of widespread lineages that have persisted until present time (Carranza et al., 2004). Thus, *Iberolacerta* rock lizards may have been restricted to mountains by competition with *Podarcis* (Carranza et al., 2004; Crochet et al., 2004).

This study aims to clarify whether competitive exclusion by wall lizards *P. muralis* is a plausible explanation for the alpine confinement of Iberian rock lizards *I. cyreni*. To detect competition, which among lacertids is mainly manifested as direct behavioural interference rather than indirect exploitation of resources (Downes and Bauwens, 2002), we conducted two experiments. In the first one, we used adult lizards to investigate whether *I. cyreni* and/or *P. muralis* shifted microhabitat or refuge preferences in the presence of the other species, and to detect aggressive interactions. In the second one, we staged heterospecific encounters between pairs of naïve, laboratory-born juveniles of both species to identify behavioural differences which might lead to a competitive advantage of one species over the other.

## 2. Materials and methods

### 2.1. Study system

The lacertid lizards *I. cyreni* and *P. muralis* provide an excellent system to investigate the possible restricting role of competitive exclusion in shaping species distributions. Both are heliothermic, actively foraging, and saxicolous lizards, but they present some morphological differences, *I. cyreni* being slightly larger than *P. muralis* (adult snout–vent length of 73–80 mm and 48–70 mm, respectively). While rock lizards are endemic to the mountains of the Sistema Central in the Iberian Peninsula, wall lizards present a widespread distribution in Central Europe that reaches its south-western limit at the Sierra de Guadarrama (Central Spain), where both species are present. In this mountain range, rock lizards are only found above 1600 m, preferably in rocky outcrops and mixed-shrub formations (Martín and Salvador, 1997; Monasterio et al., 2010), whereas wall lizards occupy lower altitudes (from 1230 m to 2100 m a.s.l.) and a wider range of habitats, including rocky outcrops, oak and pine forests, forest track banks, walls, and other human constructions (Martín-Vallejo et al., 1995; Amo et al., 2007a). The Sierra de Guadarrama presents contrasting seasonal conditions, with cold wet winters and short dry summers. Its mountain bases (1200–1700 m a.s.l.) are covered with deciduous Pyrenean oak (*Quercus pyrenaica)* forests, which are progressively substituted by Scots pine (*Pinus sylvestris*) forests at higher altitudes. These forested areas, which can spread from 1500 m to 2100 m a.s.l., gradually become less dense until vegetation is dominated by a mosaic of dense mixed-shrub formations (of perennial *Juniperus communis* and *Cytisus oromediterraneus*) interspersed with small meadows of *Festuca* and other grasses. These alpine areas above the tree line (1700–2300 m a.s.l.) are also characterised by extensive patches of large granite rocks and scree interspersed among shrub formations (Costa et al., 2005).

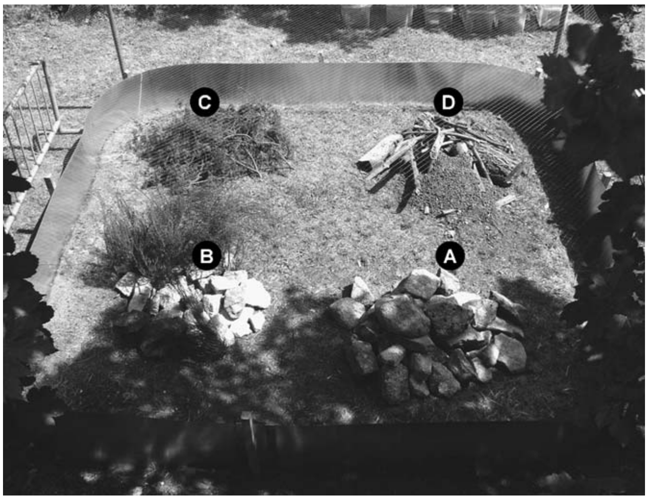

**Fig. 1.** General view of the experimental enclosure used to study microhabitat preferences of adult rock and wall lizards. A = rocks, B = rock–shrub, C = shrub, and D = logs.

### 2.2. Experimental procedure

#### 2.2.1. Adults

For this experiment, we captured 15 adult rock lizards (9 males and 6 females) and 15 wall lizards (5 males and 10 females) in the Sierra de Guadarrama and transported them to 'El Ventorrillo' field station (1500 m), where we weighed and measured (snout–vent length, SVL) them to the nearest 0.1 g and 0.5 mm, respectively. We housed lizards separately in outdoor terraria with a sand substrate, rocks and vegetation. Lizards were fed live crickets every day and they had water available *ad libitum*. Capture methods, housing conditions and release procedures were appropriate for these species, and we observed no adverse effect of either the experiment or the housing methods on lizards' health. All individuals were in good condition, both during the experiment and when released at the site of capture.

We carried out an experiment during June and July 2007 to ascertain the microhabitat preferences of both species, either alone or together, when different microhabitats were offered. For that purpose, we used an outdoor enclosure (4 m × 4 m) with four types of distinct, representative microhabitats (Fig. 1): bare rocks (hereafter rocks), rocks with *C. oromediterraneus* shrubs (hereafter rock–shrub), *J. communis* shrub (hereafter shrub), and logs with gravel (hereafter logs). Sun was available from 09:00 h until 17:30 h (Greenwich Mean Time), allowing lizards to thermoregulate normally. To characterise the thermal environment, we placed four electronic temperature recording devices (tidbits; Onset Computer Corp., Pocasset, MA, USA) on the top of and inside each type of microhabitat. We programmed data loggers to register temperature hourly during 8 days (for tidbits on top of microhabitats) or 10 days (for tidbits inside refuges). Insect prey was naturally available in the enclosure, and we observed lizards feeding on several occasions.

Our experimental design compared the behaviour of lizards when each species was alone in the enclosure and when both species were together. In the first treatment (each species alone), we introduced different combinations of 10 individuals of either rock or wall lizards in the enclosure. In the second treatment, we placed simultaneously different combinations of 5 individuals of each species in the enclosure. To decide which individuals were to be used in each combination, we used the following criteria: (1) we tried to keep constant the proportion of males and females in all cases; (2) we maintained the same proportion of large (72–75 mm

SVL) and small (<68 mm SVL) male rock lizards; and (3) whenever possible, we tried to change all the individuals which were used in consecutive sampling sessions of 2–3 days (see below). Therefore, our design implies that most individuals were used more than once (only two lizards were used just once, 16 individuals were used twice, and 11 individuals were used three times). However, each individual yielded one single data for each treatment (i.e., no pseudoreplication was committed), because the proportion of use of each microhabitat type and the diversity of microhabitats used were estimated pooling together all observations for each individual in each treatment. It should be noted that, although 0.625 individuals/m$^2$ is obviously higher than average densities in the field (nevertheless, values up to 1200 individuals/ha have been reported for the related species *Iberolacerta monticola*; Moreira et al., 1998), lizards can reach these and higher concentrations at local patches of rock and shrub habitat (authors, personal observation).

Observations were carried out with binoculars between 8:00 h and 15:00 h, from a 2 m high wall above the enclosure which made it possible to see the totality of the experimental arena without disturbing the lizards. Each individual received a unique paint code on its back to allow recognition. We recorded the microhabitat use by each animal every 30 min. From our experimental setup (Fig. 1), it is clear that open patches of short grass were also available. However, they were never used by lizards except for moving between the four microhabitats offering refuge. In that case, lizards that were crossing open areas at the moment of recording their behaviour were scored as using the microhabitat at which they arrived. Also, when lizards were on the grass patches but in the immediate surroundings of one of the four microhabitats, they were scored as using that microhabitat type. In both treatments, we registered all agonistic interactions observed. Lizard groups were maintained in the enclosure during two or three consecutive days. Before introducing a new group of lizards, we watered the enclosure abundantly to eliminate chemical cues. We also obtained data about the nocturnal refuges used by lizards. This was done in two ways. The first one was to find and capture all lizards while still inactive in the early morning, taking advantage of the fact that we had to change the group of lizards. The second one was to note the microhabitat from which the animals first emerged in the early morning, with the enclosure in full shade and no prior activity recorded during the previous hour.

We analysed data using chi-square tests (with the null hypothesis that the four microhabitat types were used in equal proportions) and general linear models. We calculated the proportion of use of each microhabitat type for each individual in each treatment ($p_i$), and we estimated the diversity of microhabitats used for each individual and treatment by means of $\exp(H')$, the transformed Shannon diversity index (Kempton and Taylor, 1976). To search for differences between species and/or sexes separately for each treatment, we used multivariate analyses of variance (MANOVAs) where the $p_i$'s of the four microhabitat types were included as the dependent variables. To test for treatment effects (only one species vs. both species in the enclosure) we used a within-subjects MANOVA with the differences between treatments as dependent variables, calculated for each lizard and microhabitat type (the null hypothesis for treatment effects is that the intercept of the linear model, i.e. the mean difference between treatments while holding for the effects of all variables in the model, is equal to zero). Therefore, this repeated measures design effectively avoided pseudoreplication, because sample sizes were always equal to the number of lizards, independently of the number of observations per individual and treatment.

We applied a similar procedure to test for differences between species and/or sexes in the use of nocturnal refuges, but pooling together both treatments (each species alone and both species together) to maintain an acceptable sample size (the nocturnal refuges procedure yielded only one datum per day, producing an average sample size of 4.2 observations per individual, vs. the much higher number of observations – one every 30 min – in the case of microhabitat use data). Thus, although it was not possible to compare $p_i$'s between treatments with such a small amount of data (if, for instance, one individual used rocks as a nocturnal refuge four of four times, thus making all the remaining $p_i$'s equal to zero), we could test overall differences between species and sexes.

#### 2.2.2. *Juveniles*

To search for competitive interactions between juvenile rock and wall lizards, we staged short-term interspecific encounters in the laboratory. For that purpose, and as part of an ongoing study on the ecology of eggs and hatchlings, we reared laboratory-born lizards with live crickets and water supplied *ad libitum*. We formed heterospecific pairs of juveniles ($N = 17$ pairs), matched for their body size. We used each individual only once. Since we raised juveniles in individual terraria, they had no social experience previous to this experiment. We placed heterospecific pairs of lizards in a small terrarium (265 mm length × 162 mm width × 150 mm height) that offered rock and sand substrates in equal proportions. A 40-W focal lamp 25 cm above the rock acted as a heat source allowing lizards to bask. After releasing the lizards in the terrarium, we used a camera on a tripod to record their behaviour during 4 min. We tested all pairs in the early morning and before having fed the lizards. After every encounter, we washed and dried the rock and we replaced the sand. In the video recordings, we registered all interactions detected and we measured the amount of time that lizards spent basking (i.e., laying flat on the rock substrate under the lamp), moving or staying motionless outside the basking area. We used repeated measures ANOVAs to test for interspecific differences in the percentage of time spent basking or moving. At the end of the experiment, lizards were released at their mother's site of capture.

## 3. Results

### 3.1. *Adults*

#### 3.1.1. *Body size and body condition*

In our sample of individuals, rock lizards had larger SVL (mean ± 1 SE = 69.3 ± 1.5 mm) and body mass (mean ± 1 SE = 7.9 ± 0.4 g) than wall lizards (SVL: 58.6 ± 1.5 mm; body mass: 5.1 ± 0.4 g), with no sexual size dimorphism in either species (species effect in two-way ANOVAs: SVL: $F_{1,26} = 25.03$, $P < 0.0001$; body mass: $F_{1,26} = 22.75$, $P < 0.0001$; $P > 0.05$ for all sex and interaction effects). Concerning SVL-adjusted body mass, males of a given SVL were heavier than females, but species did not differ significantly (two-way ANCOVA: sex: $F_{1,25} = 7.22$, $P = 0.013$; $P > 0.25$ for the species and interaction effects).

#### 3.1.2. *Microhabitat use*

In both treatments, the two species preferred the rocky microhabitats and avoided the shrub (see chi-square results in Table 1). We did not find any interspecific or sexual differences in the use of microhabitat types, either when the species were alone (MANOVA; species: Wilks' $\lambda = 0.928$, $F_{3,22} = 0.57$, $P = 0.639$; sex: Wilks' $\lambda = 0.905$, $F_{3,22} = 0.76$, $P = 0.523$; interaction: Wilks' $\lambda = 0.787$, $F_{3,22} = 1.98$, $P = 0.146$) or when they were together in the experimental enclosure (MANOVA; species: Wilks' $\lambda = 0.853$, $F_{3,24} = 1.37$, $P = 0.275$; sex: Wilks' $\lambda = 0.960$, $F_{3,24} = 0.33$, $P = 0.807$; interaction: Wilks' $\lambda = 0.966$, $F_{3,24} = 0.28$, $P = 0.839$). Similarly, a repeated measures MANOVA did not reveal differences in microhabitat use between treatments (one- vs. two-species treatment: Wilks' $\lambda = 0.793$, $F_{3,22} = 1.91$, $P = 0.157$), nor did it find any significant species × treatment (Wilks' $\lambda = 0.895$, $F_{3,22} = 0.86$, $P = 0.478$) or sex × treatment (Wilks' $\lambda = 0.963$,

**Table 1**
Habitat selection based on number of observations of rock (*I. cyreni*) and wall (*P. muralis*) lizards under both experimental treatments (one vs. two species in the enclosure). Significant $\chi^2$ values are shown in bold.

| | Only one species in the enclosure | | | | | Both species in the enclosure | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Observed | Expected | $\chi^2$ | d.f. | $P$ | Observed | Expected | $\chi^2$ | d.f. | $P$ |
| *I. cyreni* | | | | | | | | | | |
| Rocks | 84 | 69 | 3.26 | 1 | 0.071 | 80 | 55.75 | **10.55** | 1 | 0.001 |
| Rock–shrub | 87 | 69 | **4.70** | 1 | 0.030 | 77 | 55.75 | **8.10** | 1 | 0.004 |
| Shrub | 43 | 69 | **9.80** | 1 | 0.002 | 17 | 55.75 | **26.93** | 1 | <0.001 |
| Logs | 62 | 69 | 0.71 | 1 | 0.400 | 49 | 55.75 | 0.82 | 1 | 0.366 |
| All | | | **18.46** | 4 | 0.001 | | | **46.40** | 4 | <0.001 |
| *P. muralis* | | | | | | | | | | |
| Rocks | 53 | 41.75 | 3.03 | 1 | 0.082 | 82 | 49.25 | **21.78** | 1 | <0.001 |
| Rock–shrub | 56 | 41.75 | **4.86** | 1 | 0.027 | 47 | 49.25 | 0.10 | 1 | 0.749 |
| Shrub | 24 | 41.75 | 7.55 | 1 | 0.006 | 14 | 49.25 | **25.23** | 1 | <0.001 |
| Logs | 34 | 41.75 | 1.44 | 1 | 0.230 | 54 | 49.25 | 0.46 | 1 | 0.499 |
| All | | | **16.88** | 4 | 0.002 | | | **47.57** | 4 | <0.001 |

$F_{3,22} = 0.28$, $P = 0.838$) interactions. Nevertheless, overall $\chi^2$ values suggested lower selectivity when there was only one species than when both species shared the enclosure (Table 1). Estimates of effect size (results not shown) showed that non-significant differences in microhabitat use were due to the small size of the effects examined rather than to small sample sizes.

When only one species was present in the enclosure, rock lizards showed significantly higher diversities of microhabitat use than did wall lizards (ANOVA; species: $F_{1,24} = 8.59$, $P = 0.007$; sex: $F_{1,24} = 0.68$, $P = 0.417$; interaction: $F_{1,24} = 1.52$, $P = 0.229$). However, this difference disappeared when both species were together (species: $F_{1,26} = 0.39$, $P = 0.539$; sex: $F_{1,26} = 0.19$, $P = 0.670$; interaction: $F_{1,26} = 0.04$, $P = 0.849$). This result was confirmed by a repeated measures ANOVA, which showed a significant treatment × species interaction ($F_{1,24} = 4.94$, $P = 0.036$), meaning that rock lizards, but not wall lizards, were more evenly distributed in the one-species treatment than in the two-species treatment (Fig. 2).

### 3.1.3. *Agonistic interactions*

Although our experiment was carried out in the post-breeding season, when aggressive interactions and territorial behaviour are presumably less intense, we observed twelve agonistic encounters (Table 2). All these chases implicated only males, and only three of them involved wall lizards (one chased by a conspecific and the other two by a rock lizard). In fact, the majority of attacks (10 out of 12) came from the same rock lizard (B4), which was one of the three largest males (SVL = 75 mm) and was particularly aggressive (as judged from the number and intensity of the attacks) with a conspecific male of the same size (A3; see Table 2). This is not unexpected, given the well-known tendency of these lizards to form clear-cut dominance hierarchies (Martín and Salvador, 1993). To analyse these interactions, we considered the effects of microhabitat use by lizards using experimental groups as sampling units (Table 3). This was done because dominance relationships may depend not only on the individual traits of each lizard, but also on social context. In each experimental group containing rock lizards, we scored as dominant the individual which successfully ousted other males from its preferred microhabitat type (i.e., the microhabitat most frequently used), which was almost invariably the rock–shrub microhabitat (Table 3; for the single group in which no aggressions were observed [group B], the largest male [A2M, SVL = 73 mm] was scored as dominant). We then noted the number of males (including the dominant one) which shared the same microhabitat preference, i.e., which coincided in the microhabitat type for which they showed the highest $p_i$. Despite the small sample size (only five experimental groups including rock lizards), the number of aggressive interactions was significantly correlated with the number of males sharing the preferred microhabitat type (rock–shrub or rocks) with the dominant one (Spearman rank's correlation: $r_s = 0.892$, $N = 5$, $P = 0.042$). Thus, intraspecific competition among rock lizards was important for understanding their patterns of habitat use.

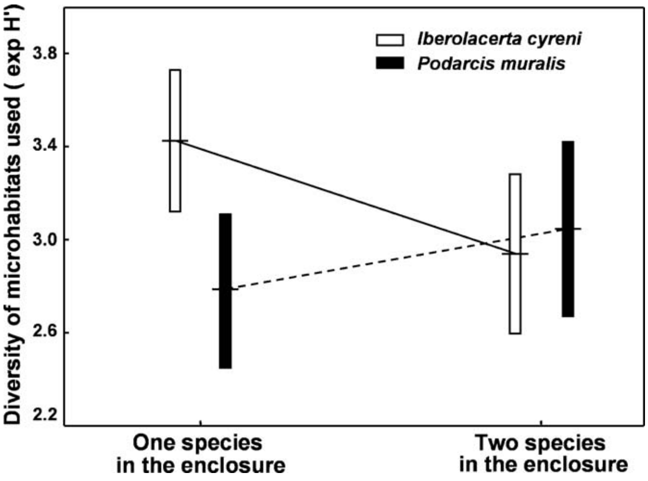

**Fig. 2.** Diversity of microhabitats used ($\exp(H')$) for rock and wall lizards in the one- and two-species treatments. Vertical bars denote 0.95 confidence intervals.

### 3.1.4. *Nocturnal refuges*

We found no significant differences between species or sexes in the use of microhabitat types as nocturnal refuges (MANOVA; species: Wilks' $\lambda = 0.896$, $F_{4,23} = 0.66$, $P = 0.623$; sex: Wilks' $\lambda = 0.949$, $F_{4,23} = 0.31$, $P = 0.870$; interaction: Wilks' $\lambda = 0.964$, $F_{4,23} = 0.22$, $P = 0.926$). Nevertheless, rock lizards used a significantly higher diversity of nocturnal refuges than did wall lizards (ANOVA; species: $F_{1,26} = 17.04$, $P < 0.001$; sex: $F_{1,26} = 1.06$, $P = 0.312$; interaction: $F_{1,26} = 0.88$, $P = 0.357$). Thus, wall lizards used mainly the rocky habitats as nocturnal retreat sites, whereas rock lizards were found in all available types of refuge (Fig. 3). The major difference between both species was that rock lizards also used the shrub as a nocturnal refuge. Interestingly, most of the nocturnal use of this microhabitat type (4 out of 6 observations) corresponded to the dominant male (B4) that won most aggressive interactions with conspecifics (Table 3).

### 3.1.5. *Thermal quality of refuges*

Average temperatures on the surface of the four microhabitat types did not differ significantly after controlling for the effects of time of day (ANOVA with the data in Fig. 4A; time of day: $F_{47,1044} = 110.1$, $P < 0.001$; microhabitat: $F_{3,1044} = 0.41$, $P = 0.745$; interaction: $F_{121,141} = 1.01$, $P = 0.455$), indicating that our results

**Table 2**
Agonistic interactions detected in the experiment: individuals involved (winner is the chasing individual, and loser is the individual ousted by the winner) and number of encounters of each pair.

| Winner | | | | Loser | | | | |
|---|---|---|---|---|---|---|---|---|
| Code | Species | SVL (mm) | Body mass (g) | Code | Species | SVL (mm) | Body mass (g) | No. of encounters |
| B4 | *I. cyreni* | 75 | 11 | A3 | *I. cyreni* | 75 | 10.5 | 4 |
| | | | | D1 | *I. cyreni* | 66 | 8 | 2 |
| | | | | A2M | *I. cyreni* | 73 | 9.5 | 1 |
| | | | | A5 | *I. cyreni* | 60 | 5.5 | 1 |
| | | | | D5 | *P. muralis* | 60 | 6 | 2 |
| A1 | *I. cyreni* | 72 | 9 | B3 | *I. cyreni* | 60 | 5.5 | 1 |
| D3 | *P. muralis* | 57 | 5.5 | DB5C1 | *P. muralis* | 60 | 6 | 1 |

**Table 3**
Experimental groups that included rock lizards and aggressive interactions among them. The identity of the dominant male, its preferred microhabitat, and the total number of males sharing that preference are also indicated.

| Group code | Treatment | Dominant male | Habitat(s) preferred by dominant male | No. of males in that habitat | No. of aggressive interactions |
|---|---|---|---|---|---|
| A | One species | B4 | Rock–shrub | 1 | 1 |
| B | Two species | A2M | Rock–shrub | 1 | 0 |
| C | Two species | B4 | Rock and rock–shrub | 3 | 4 |
| D | Two species | A1 | Rock–shrub | 2 | 1 |
| E | One species | B4 | Rock–shrub | 3 | 3 |

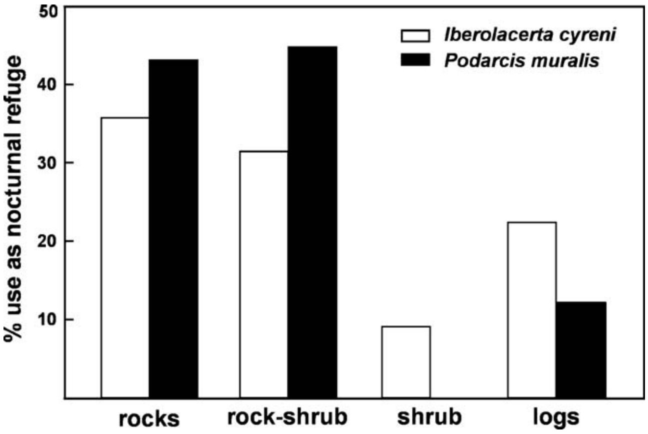

**Fig. 3.** Microhabitats used as nocturnal refuges by rock and wall lizards. Data are given as percentage of observations.

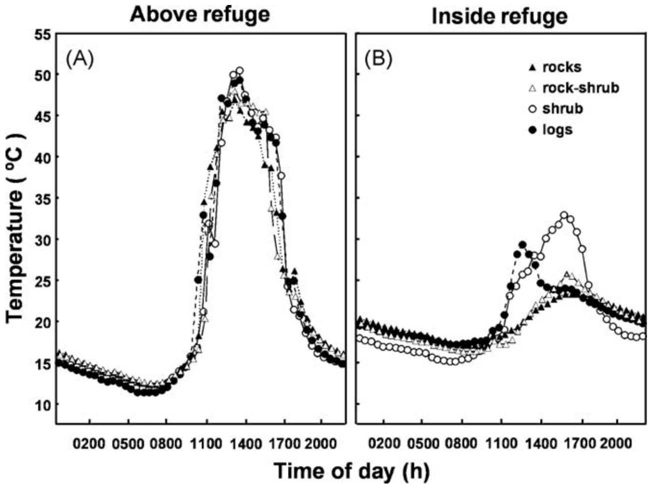

**Fig. 4.** Hourly variation of temperatures (A) on top and (B) inside the refuges offered by each type of microhabitat. Data are based on the readings of four electronic temperature recording devices (tidbits) which were programmed to register temperature hourly during 8 days (for tidbits on top of microhabitats) or 10 days (for tidbits inside refuges).

about microhabitat selection were largely independent of the thermal environment. Nevertheless, microhabitat types offered different thermal qualities as nocturnal refuges (Fig. 4B; time of day: $F_{47,1364} = 34.63$, $P < 0.001$; microhabitat: $F_{3,1364} = 10.24$, $P < 0.001$; interaction: $F_{141,1364} = 3.76$, $P < 0.001$). Although temperatures inside refuges were similar during most of the day, the shrub was the microhabitat type that offered the best thermal quality from the late afternoon to the early evening hours (Fig. 4B).

### 3.2. *Juveniles*

Juvenile lizards did not exhibit significant differences in substrate use, although both species selected positively the rock surface (Table 4: $P = 0.074$ in the corresponding ANOVA with species as the repeated measures factor in staged encounters). Nevertheless, we found differences in activity patterns, because wall lizards spent more time moving around the terrarium than did rock lizards ($P < 0.001$), whereas rock lizards spent more time basking than did wall lizards ($P = 0.001$). We recorded no agonistic interactions in any of the interspecific encounters.

## 4. Discussion

Our results show that neither rock nor wall lizard adults changed their microhabitat preferences in the presence of the other species, as they both selected rocky microhabitats independently of the treatment. Nevertheless, we found that rock lizards increased the diversity of microhabitats and nocturnal refuges used in the single species trials, which had twice the number of conspecifics. Agonistic interactions were scarce and they mainly involved large rock lizard males. Thus, our experimental setup allowed us to detect the

**Table 4**
Behavioural variables (mean ± SE) of rock and wall lizard juveniles in staged encounters. Results from repeated measures ANOVAs are also shown.

| | | Mean ± SE | $F_{1,16}$ | *P* |
|---|---|---|---|---|
| Time spent on rock | *I. cyreni* | 80.93 ± 3.59 | 3.67 | 0.074 |
| | *P. muralis* | 69.82 ± 4.97 | | |
| Time spent moving | *I. cyreni* | 24.90 ± 2.75 | 33.81 | <0.001 |
| | *P. muralis* | 53.97 ± 3.84 | | |
| Time spent basking | *I. cyreni* | 66.76 ± 4.64 | 15.80 | 0.001 |
| | *P. muralis* | 38.58 ± 4.52 | | |

effects of competition on microhabitat use, but such effects seemed to be present only within rock lizards. Similarly, although juveniles did not show any interspecific agonistic behaviour in staged encounters, rock lizard hatchlings spent more time basking and less time moving than wall lizards. According to these results, we discuss the possible roles of inter- and intraspecific competition in shaping the microhabitat selection of these species and the alpine confinement of rock lizards.

Both species showed very similar microhabitat preferences, positively selecting rock and rock–shrub microhabitats and avoiding the shrub. For rock lizards, this is in agreement with morphological adaptations that evidence their specialisation as scansorial rock-dwelling lizards (Arnold, 1973) and with previous field results in the study area (Martín and Salvador, 1997; Amo et al., 2007b; Monasterio et al., 2010). Wall lizards seem also associated with rocks, but they occupy a wider range of habitats throughout their distributional range. In our experiment, rocks and rock–shrub were also the microhabitats preferred by wall lizards. Given the small size of the experimental enclosure, the competitive exclusion hypothesis predicts that rock and wall lizards should compete for these preferred microhabitats, which would produce the displacement of the subordinate species to suboptimal microhabitats. Contrary to this prediction, rock and wall lizards seemed to ignore the presence of each other in the enclosure, and they coexisted without modifying their habitat preferences. Similar experiments with other species have shown that lizards shift their habitat preferences in the presence of a potential competitor (Vanhooydonck et al., 2000) or that competitive displacement increases when habitat availability is reduced (Petren and Case, 1998). Our experiment was successful in detecting intraspecific competition by behavioural interference (see below), meaning that the observed absence of interspecific competition was not due to flaws in the experimental setup. Because we found no changes in the habitat preferences of any of the two species when they were together in the enclosure, we conclude that competitive exclusion by wall lizards is unlikely to explain the alpine confinement of rock lizards. In addition, body size, which has long been demonstrated to affect dominance relationships in lizards (Langkilde and Shine, 2004; Melville, 2002), was larger for rock lizards than for wall lizards, and the interspecific difference in body size found in our data is consistent with the general pattern already known for these species, suggesting that our results are representative of what is supposed to occur in the wild. Moreover, data from a previous field study showed that both lizard species chose microhabitats with shorter distances to the nearest refuge than expected at random, that they both preferred rocks over shrubs as their closest retreat, and that the proportion of observations closer to rocks than to shrubs was higher for rock lizards than for wall lizards (Monasterio et al., 2009).

Our experimental treatment had a significant effect on the diversity of microhabitats used by rock lizards. Rock lizards used all microhabitats more evenly in the one-species than in the two-species treatment—their use of space was more diverse when all individuals in the experimental group were rock lizards. This is consistent with the hypothesis that intraspecific competition influences their microhabitat use. Rock lizard males defend territories intensely during the mating season (May to June), and they often establish dominance hierarchies with neighbouring males by means of aggressive interactions (Martín and Salvador, 1993; Martín and López, 2000; Aragón et al., 2004). Although our experiment was carried out in the post-reproductive season, when agonistic interactions are much reduced (Martín and Salvador, 1993), we can explain our results in terms of territorial behaviour. Thus, rock lizards can avoid undesirable encounters that might lead to agonistic interactions by occupying different types of microhabitats. Engaging in aggressive interactions can be costly (Marler and Moore, 1988), but such costs can be eluded by reducing the number and intensity of fights (Cooper and Vitt, 1987; López and Martín, 2001). In fact, small and subordinate male rock lizards perform less conspicuous activities to avoid fighting with dominant males (Aragón et al., 2004, 2006). In our study, most chases involved *I. cyreni* individuals and were directed from the same male (B4). Moreover, fights were more frequent when more males shared the preferred habitat, suggesting that lizards could avoid aggressions by occupying other microhabitat types. On the other hand, fights involving wall lizards were very scarce and they were never directed from wall to rock lizards, supporting the idea that interspecific competition was negligible. It might be argued that some individuals, especially B4, could have had a disproportionately large effect on the patterns observed. However, dominance hierarchies have been well documented in this species (Martín and Salvador, 1993), which means that a dominant male which starts and wins a large fraction of the intraspecific aggressions is not an unexpected result.

Refuges are valuable resources for reptiles (Huey, 1982; Huey et al., 1989; Díaz et al., 2006), and in some cases it has been found that crevices are strongly defended by dominant lizards, which exclude subordinate species to suboptimal sites (Langkilde et al., 2003, 2005). However, there was no sign of negative interference in the use of nocturnal retreat sites between the species studied. Again, the only noticeable pattern was the higher diversity of refuges used by rock lizards, indicating that individuals of this species were less prone than wall lizards to share their nocturnal retreats. This increased diversity was largely due to the behaviour of the dominant male, who avoided sharing nocturnal refuges with other lizards. Remarkably, this male was also the one that used the shrub microhabitat as a nocturnal refuge more frequently.

Given the major impact that refuge selection can have on the thermal physiology of ectotherms (Huey et al., 1989; Kearney, 2002; Sabo, 2003), it should be noted that the shrub was the warmest refuge during the early evening hours, allowing lizards to attain body temperatures within the preferred thermal range (31.4–35.7 °C; Bauwens et al., 1995) without moving from the shelter. Thus, a lizard could thermoregulate while minimising its exposure to aerial predators, which could have favoured the decision to stay there during the night.

Despite the reduced area shared by heterospecific pairs of juveniles, we detected no agonistic interactions in staged encounters, which supports the results obtained with adults. Because basking opportunities increase energy intake and promote faster growth rates (Sinervo and Adolph, 1989; Niewiarowski and Roosenburg, 1993), juvenile lizards often defend basking sites (Downes and Bauwens, 2002). Although juveniles of both species did not fight over access to basking sites, rock lizards spent more time basking than did wall lizards. This might be indicative of a behavioural preference or a competitive advantage of the former, but not of their hypothesised subordinate condition. It should also be noted that juveniles were matched for their body size; since wall lizard hatchlings are smaller than rock lizard ones, this implies that wall lizard juveniles may have been older than rock lizard ones, and that the competitive ability of the latter may have been underestimated relative to natural encounters.

To conclude, we found no evidence of interspecific competition between rock and wall lizards, either juveniles or adults, in terms of habitat shifts or agonistic interactions. In fact, only intraspecific interactions seemed to explain the behaviour of adult rock lizards in the enclosure. Therefore, we suggest that other factors, different from competitive exclusion by wall lizards, must be currently determining the lower distribution limit of rock lizards. In other words, our results do not support the hypothesis that rock lizards within the genus *Iberolacerta* are confined to high altitude habitats due to the successful radiation and expansion of *Podarcis* (Arnold, 1987; Carranza et al., 2004). However, it could be argued that rock and wall lizards have evolved different specialisations in the past to minimise their present interactions (i.e. the ghost of competition past, sensu Connell, 1980). Nevertheless, other sympatric lizards whose morphological and/or ecological specialisations are thought to have evolved by interspecific competition still respond clearly to competitive exclusion experiments (Leal et al., 1998; Harmon et al., 2007), and our experimental setup allowed us to detect intraspecific competitive interactions. We can thereby conclude that, at least nowadays, interspecific competition is not acting as a barrier for the dispersal of rock lizards, that wall lizards colonise opportunistically the microhabitats they share with rock lizards, and that other factors related to local adaptation are preventing the range expansion of *I. cyreni*. Given the particular conditions of alpine environments (e.g. low temperature), rock lizards could present life history traits that allow them to thrive in mountains, but not at lower altitudes. Previous data suggest that the alpine confinement of Iberian rock lizards is caused by the compromise between environmental thermal quality and refuge availability (Monasterio et al., 2009). To complete these results and explore alternative explanations for the restricted distribution of rock lizards, we recommend further research on the ecophysiology of this species, including the thermal dependence of egg development and the availability and selection of suitable nest sites.

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## References

Amo, L., López, P., Martín, J., 2007a. Natural oak forest vs. ancient pine plantations: lizard microhabitat use may explain the effects of ancient reforestations on distribution and conservation of Iberian lizards. Biodivers. Conserv. 16, 3409–3422.

Amo, L., López, P., Martín, J., 2007b. Habitat deterioration affects body condition of lizards: a behavioral approach with *Iberolacerta cyreni* lizards inhabiting ski resorts. Biol. Conserv. 135, 77–85.

Aragón, P., López, P., Martín, J., 2004. The ontogeny of spatio-temporal tactics and social relationships of adult male Iberian rock lizards, *Lacerta monticola*. Ethology 110, 1001–1019.

Aragón, P., López, P., Martín, J., 2006. Roles of male residence and relative size in the social behavior of Iberian rock lizards, *Lacerta monticola*. Behav. Ecol. Sociobiol. 59, 762–769.

Arnold, E.N., 1973. Relationships of the Palaearctic lizards assigned to the genera *Lacerta*, *Algyroides* and *Psammodromus* (Reptilia: Lacertidae). Bull. Br. Mus. Nat. Hist. 25, 291–366.

Arnold, E.N., 1987. Resource partition among lacertid lizards in southern Europe. J. Zool. Lond. (Biol.) 1, 739–782.

Bauwens, D., Garland, T., Castilla, A.M., Van Damme, R., 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological and behavioural covariation. Evolution 49, 848–863.

Brown, J.H., Stevens, G.C., Kaufmann, D.M., 1996. The geographic range: size, shape, boundaries and internal structure. Annu. Rev. Ecol. Syst. 27, 597–623.

Buckley, L.B., Roughgarden, J., 2005. Effect of species interactions on landscape abundance patterns. J. Anim. Ecol. 74, 1182–1194.

Buckley, L.B., Roughgarden, J., 2006. A hump-shaped density–area relationship for island lizards. Oikos 113, 243–250.

Cadena, C.D., 2007. Testing the role of interspecific competition in the evolutionary origin of elevational zonation: an example with *Buarremon* brush-finches (Aves, Emberizidae) in the neotropical mountains. Evolution 61, 1120–1136.

Carothers, J.H., Jaksic, F.M., Marquet, P.A., 2001. Altitudinal zonation among lizards of the genus *Liolaemus*: questions answered and unanswered questions. Rev. Chil. Hist. Nat. 74, 313–316.

Carranza, S., Arnold, E.M., Amat, F., 2004. DNA phylogeny of *Lacerta* (*Iberolacerta*) and other lacertine lizards (Reptilia: Lacertidae): did competition cause long-term mountain restriction? Syst. Biodivers. 2, 57–77.

Case, T.J., Bolger, D.T., 1991. The role of interspecific competition in the biogeography of island lizards. Trends Ecol. Evol. 6, 135–139.

Connell, J.H., 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35, 131–138.

Cooper, W.E., Vitt, L.J., 1987. Deferred agonistic behavior in a longlived scincid lizard *Eumeces laticeps*. Oecologia 72, 321–326.

Costa, M., Morla, C., Sanz, H., 2005. Los Bosques Ibéricos: Una Interpretación Geobotánica. Editorial Planeta, SA, Barcelona.

Crochet, P.A., Chaline, O., Surget-Groba, Y., Debain, C., Cheylan, M., 2004. Speciation in mountains: phylogeography and phylogeny of the rock lizard genus *Iberolacerta* (Reptilia: Lacertidae). Mol. Phylogen. Evol. 30, 860–866.

Díaz, J.A., Monasterio, C., Salvador, A., 2006. Abundance, microhabitat selection, and conservation of eyed lizards (*Lacerta lepida*): a radiotelemetric study. J. Zool. 268, 295–301.

Downes, S., Bauwens, D., 2002. An experimental demonstration of direct behavioural interference in two Mediterranean lacertid lizard species. Anim. Behav. 63, 1037–1046.

Harmon, L.J., Harmon, L.L., Jones, C.G., 2007. Competition and community structure in diurnal arboreal geckos (genus *Phelsuma*) in the Indian Ocean. Oikos 116, 1863–1878.

Hess, N.E., Losos, J.B., 1991. Interspecific aggression between *Anolis cristatellus* and *A. gundlachi*: comparison of sympatric and allopatric populations. J. Herpetol. 25, 256–259.

Hofer, U., Bersier, L.F., Borcard, D., 1999. Spatial organization of a herpetofauna on an elevational gradient revealed by null model tests. Ecology 80, 976–988.

Huey, R.B., 1982. Temperature, physiology, and the ecology of reptiles. In: Gans, C., Pough, F.H. (Eds.), Biology of the Reptilia, vol. 12, Physiology (C). Academic Press, London, pp. 25–91.

Huey, R.B., Peterson, C.R., Arnold, S.J., Porter, W.P., 1989. Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and thermal consequences. Ecology 70, 931–944.

Kearney, M., 2002. Hot rocks and much-too-hot rocks: seasonal patterns of retreat-site selection by a nocturnal ectotherm. J. Therm. Biol. 27, 205–218.

Kempton, R.A., Taylor, L.R., 1976. Models and statistics for species diversity. Nature 262, 818–820.

Langkilde, T., Shine, R., 2004. Competing for crevices: interspecific conflict influences retreat-site selection in montane lizards. Oecologia 140, 684–691.

Langkilde, T., O'Connor, D., Shine, R., 2003. Shelter-site use by five species of montane scincid lizards in south-eastern Australia. Aust. J. Zool. 51, 175–186.

Langkilde, T., Lance, V.A., Shine, R., 2005. Ecological consequences of agonistic interactions in lizards. Ecology 86, 1650–1659.

Leal, M., Rodriguez-Robies, J.A., Losos, J.B., 1998. An experimental study of interspecific interactions between two Puerto Rican *Anolis* lizards. Oecologia 117, 273–278.

López, P., Martín, J., 2001. Fighting rules and rival recognition reduce costs of aggression in male lizards, *Podarcis hispanica*. Behav. Ecol. Sociobiol. 49, 111–116.

Losos, J.B., 1994. Integrative approaches to evolutionary ecology: *Anolis* lizards as model systems. Annu. Rev. Ecol. Syst. 25, 467–493.

Losos, J.B., Spiller, D.A., 1999. Differential colonization success and asymmetrical interactions between two lizard species. Ecology 80, 252–258.

Losos, J.B., Marks, J.C., Schoener, T.W., 1993. Habitat use and ecological interactions of an introduced and a native species of *Anolis* lizard on Grand Cayman, with a review of the outcomes of anole introductions. Oecologia 95, 525–532.

Marler, C.A., Moore, M.C., 1988. Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards. Behav. Ecol. Sociobiol. 23, 21–26.

Martín, J., López, P., 2000. Social status of male Iberian rock lizards (*Lacerta monticola*) influences their activity patterns during the mating season. Can. J. Zool./Rev. Can. Zool. 78, 1105–1109.

Martín, J., Salvador, A., 1993. Tail loss reduces mating success in the Iberian rock-lizard, *Lacerta monticola*. Behav. Ecol. Sociobiol. 32, 185–189.

Martín, J., Salvador, A., 1997. Microhabitat selection by the Iberian rock lizard *Lacerta monticola*: effects on density and spatial distribution of individuals. Biol. Conserv. 79, 303–307.

Martín-Vallejo, J., García-Fernández, J., Pérez-Mellado, V., Vicente-Villardón, J.L., 1995. Habitat selection and thermal ecology of the sympatric lizards *Podarcis muralis* and *Podarcis hispanica* in a mountain region of Central Spain. Herpetol. J. 5, 181–188.

Melville, J., 2002. Competition and character displacement in two species of scincid lizards. Ecol. Lett. 5, 386–393.

Moen, D.S., Wiens, J.J., 2009. Phylogenetic evidence for competitively driven divergence: body-size evolution in Caribbean treefrogs (Hylidae: *Osteopilus*). Evolution 63, 195–214.

Monasterio, C., Salvador, A., Iraeta, P., Díaz, J.A., 2009. The effects of thermal biology and refuge availability on the restricted distribution of an alpine lizard. J. Biogeogr. 36, 1673–1684.

Monasterio, C., Salvador, A., Díaz, J.A., 2010. Altitude and rock cover explain the distribution and abundance of a Mediterranean alpine lizard. J. Herpetol. 44, 158–163.

Moreira, P.L., Almeida, A.P., Delgado, H., Salgueiro, O., Crespo, E.G., 1998. Bases para a Conservação da Lagartixa-da-montanha (*Lacerta monticola*). Estudos de Biologia e Conservação da Natureza, n° 25. Instituto da Conservação da Natureza, Ministerio do Ambiente, Lisboa.

Niewiarowski, P.H., Roosenburg, W., 1993. Reciprocal transplant reveals sources of variation in growth rates of the lizard *Sceloporus undulatus*. Ecology 74, 1992–2002.

Petren, K., Case, T.J., 1998. Habitat structure determines competition intensity and invasion success in gecko lizards. Proc. Natl. Acad. Sci. U.S.A. 95, 11739–11744.

Petren, K., Bolger, D.T., Case, T.J., 1993. Mechanisms in the competitive success of an invading sexual gecko over an asexual native. Science, New Series 259, 354–358.

Pfennig, D.W., Rice, A.M., Martín, R.A., 2007. Field and experimental evidence for competition's role in phenotypic divergence. Evolution 61, 257–271.

Pulliam, H.R., 2000. On the relationship between niche and distribution. Ecol. Lett. 3, 349–361.

Sabo, J.L., 2003. Hot rocks or no hot rocks: overnight retreat availability and selection by a diurnal lizard. Oecologia 136, 329–335.

Schluter, D., 2000. Ecological character displacement in adaptive radiation. Am. Nat. 156, S4–S16.

Schoener, T.W., 1983. Field experiments on interspecific competition. Am. Nat. 122, 240–285.

Sinervo, B., Adolph, S.C., 1989. Thermal sensitivity of growth rate in hatchling *Sceloporus* lizards: physiological, behavioral and genetic aspects. Oecologia 78, 411–419.

Taniguchi, Y., Nakano, S., 2000. Condition-specific competition: implications for the altitudinal distribution of stream fishes. Ecology 81, 2027–2039.

Tannerfeldt, M., Elmhagen, B., Angerbjorn, A., 2002. Exclusion by interference competition? The relationship between red and arctic foxes. Oecologia 132, 213–220.

Twomey, E., Morales, V., Summers, K., 2008. Evaluating condition-specific and asymmetric competition in a species-distribution context. Oikos 117, 1175–1184.

Vanhooydonck, B., Van Damme, R., Aerts, P., 2000. Ecomorphological correlates of habitat partitioning in Corsican lacertid lizards. Funct. Ecol. 14, 358–368.