Journal of Biogeography (*J. Biogeogr.*) (2009) **36**, 1673–1684

ORIGINAL ARTICLE

The effects of thermal biology and refuge availability on the restricted distribution of an alpine lizard

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ABSTRACT

Aim In an effort to disentangle the ecological processes that confine ectotherms to alpine environments, we studied the thermoregulatory and microhabitat selection behaviours of the rock lizard *Iberolacerta cyreni*, which is endemic to some mountains of central Spain, and of the wall lizard *Podarcis muralis*, which is a potential competitor of rock lizards.

Location We chose three areas in the Sierra de Guadarrama (central Spain) that differed in their thermal quality [mean deviation of environmental operative temperatures from the lizards' preferred thermal range (PTR)] and refuge availability: a pine forest (1770 m a.s.l.) in which *P. muralis* was the only species found, and two mixed shrub and rock sites (1770 and 1900 m a.s.l.) where both species were present.

Methods In the field we collected data on refuge availability, sun exposure, body temperature (T_b) and operative temperature (T_e). Thus, we estimated the thermal habitat quality of the areas sampled and the thermoregulation accuracy and effectiveness of both species.

Results The pine forest had the lowest thermal quality and refuge availability. The lower-elevation shrub site offered the best thermal quality, but refuges were much scarcer than at the higher-elevation site. Both species thermoregulated accurately, because mean deviations of body temperature (T_b) from PTR were considerably smaller than those of T_e. *Podarcis muralis* had higher T_b values than did *I. cyreni*, which had similar T_b values at both shrub sites, whereas *P. muralis* had lower T_b values at higher elevation. Overall, the thermoregulatory effectiveness (extent to which T_b values are closer to the PTR than are T_e values) of both species was similar, but whereas *I. cyreni* thermoregulated more efficiently at higher elevation, the opposite was true for *P. muralis*. At the lower-elevation shrub site, *I. cyreni* remained closer to refuges than did *P. muralis*.

Main conclusions Our results suggest that the pine forest belt might prevent the expansion of rock lizards towards lower elevations as a result of its low thermal quality and scarcity of refuges, that the thermoregulatory effectiveness of rock lizards in alpine environments depends more on refuge availability than on thermal habitat quality, and that competition with wall lizards is unlikely to explain either the distribution or the thermoregulatory effectiveness of rock lizards.

Keywords

Altitude, competition, ectotherms, elevation, *Iberolacerta cyreni*, mountains, *Podarcis muralis*, Spain, thermoregulation.

www.blackwellpublishing.com/jbi
doi:10.1111/j.1365-2699.2009.02113.x

INTRODUCTION

The study of altitudinal gradients and their effects on environmental variation and biological diversity is a pervasive topic in ecology (Körner, 2007), but it has become especially relevant in recent years owing to the particular vulnerability of high-elevation ecosystems to global change (Nogués-Bravo *et al.*, 2007). To understand the occurrence of alpine species, we need to consider that current distributions have been modelled by past episodes of geographical isolation that were promoted by climatic changes (Avise *et al.*, 1998; Hewitt, 1999), but also shaped by adaptations to the local conditions found along the altitudinal gradients (Byars *et al.*, 2007; Herrera & Bazaga, 2008). Therefore, disentangling the mechanisms that limit the ranges of montane species requires an understanding of their evolutionary and ecological responses to elevation. This is, however, a complex task given the intricate network of interactions between geophysical (e.g. temperature, solar radiation), environmental (e.g. humidity, seasonality), biotic (e.g. vegetation, competitive exclusion, predation) and even cultural (i.e. habitat exploitation) factors that may be involved.

Temperature, which greatly influences the physiology of organisms, is one of the most important factors to vary with altitude (Körner, 2007). Ectotherms, owing to their pronounced dependence on environmental temperature, are suitable models with which to explore local adaptation and range restrictions in alpine environments (Blanckenhorn, 1998; Bird & Hodkinson, 2005), as well as temperature-related shifts in their altitudinal range that may be associated with global change (Wilson *et al.*, 2005). Lizards are ubiquitous and abundant, can be found in alpine environments, and have often been used as model organisms to assess the ecophysiological and behavioural responses of ectotherms to elevation (Hertz, 1981; Van Damme *et al.*, 1989; Díaz, 1997; Iraeta *et al.*, 2006). Their relatively low mobility does not allow them to migrate long distances (Salvador *et al.*, 2008), and their altitudinal expansion is thus conditioned by their ability to colonize and survive in different types of montane habitats. Thus, habitat specialization, which has been identified as an important determinant of range limits (Holt, 2003), can be particularly selective in alpine lizards. One possible way in which some habitats can preclude lizards from expanding their range, is by their provision of low-quality thermal environments that can lower the effectiveness of thermoregulation and thereby reduce the physiological and ecological performance of the lizards (Huey, 1991; Van Damme *et al.*, 1991; Angilletta *et al.*, 2002).

The evaluation of temperature regulation in field-active small ectotherms in habitats of different thermal quality has been greatly improved in recent years by the experimental protocol developed by Hertz *et al.* (1993), which has been widely used in studies of lizard thermoregulation (Bauwens *et al.*, 1996; Díaz & Cabezas-Díaz, 2004; Blouin-Demers & Nadeau, 2005). This procedure requires data on the body temperatures of field-active animals (T_b values), environmental operative temperatures (T_e values, or the temperatures of randomly distributed models that integrate heat loads in the same way as lizards do), and preferred thermal range (T_{sel}, or the range of temperatures selected by lizards in a laboratory thermal gradient with no thermoregulatory restrictions). These data can be combined to evaluate the thermal quality of the habitat (average difference between available T_e values and T_{sel}), to demonstrate the existence of active thermoregulation (by showing that T_b values are closer to T_{sel} than are T_e values), and to estimate its accuracy (average difference between T_b values and T_{sel}) and effectiveness (extent to which T_b values are closer to T_{sel} than are T_e values).

Apart from thermal quality, habitat types distributed along altitudinal gradients may differ in other aspects that can be very important for the persistence of lizard populations, such as the availability of refuge sites (Huey *et al.*, 1989; Downes & Shine, 1998; Díaz *et al.*, 2006a). This is because biotic interactions such as predation and competition can also be relevant in constraining the occurrence of species, particularly at their lower distributional limits (Brown *et al.*, 1996; Case *et al.*, 2005). Although it is difficult to assess whether lizards are being excluded by the presence of predators and/or competitors, they are among the preferred prey of many vertebrate predators in Mediterranean food webs (Martín & López, 1990), and some lizard species show community structure and/or distribution patterns that seem to be influenced by interspecific competition (Downes & Bauwens, 2002; Harmon *et al.*, 2007).

The Iberian rock lizard *Iberolacerta cyreni* (Müller and Hellmich, 1937) (Reptilia: Lacertidae), which has a restricted distribution in alpine habitats of several mountain ranges in central Spain (Sierras de Guadarrama, Gredos and Béjar), is a good model for the study of the physical (thermal biology) and biological (predator avoidance and competition) factors that set altitudinal limits. This strictly alpine species is listed as Endangered in the IUCN Red List because of its small extent of occurrence and the acute fragmentation of its range. Although it is known that the historical isolation of *Iberolacerta* species in Mediterranean mountain ranges has greatly contributed to their currently fragmented distribution pattern (Carranza *et al.*, 2004; Crochet *et al.*, 2004), the ecological mechanisms that maintain their confinement to high elevations remain unexplored. We suggest two possible, non-alternative explanations. The first one is habitat specialization, which is suggested by the association of *I. cyreni* with high-elevation open rocky areas (Martín & Salvador, 1997). It can be hypothesized that the thermal quality of these mixed-shrub rocky habitats should be higher, owing to the higher availability of solar radiation (which should help to raise environmental temperatures, bringing them closer to the lizards' preferred range), than that of the pine forests that form the immediately lower vegetation belt. However, this pattern might be complicated by the altitudinal thermal gradient, with lower temperatures at higher elevation. Another factor that might cause habitat specialization is refuge availability, because rocks and rock crevices seem essential for successfully combining thermoregulation and predator avoidance (Carrascal *et al.*, 1992; Martín *et al.*, 2003). The second explanation, which has been suggested on the basis of the timing and intensity of speciation events deduced from DNA sequences, is that *Iberolacerta* and most other European rock lizards were restricted to mountains by the spread of *Podarcis* wall lizards (Arnold, 1987; Carranza *et al.*, 2004). However, there is no behavioural, correlational or experimental evidence corroborating current competition between sympatric populations of *Iberolacerta* and *Podarcis*. Therefore, it would be useful to compare the thermoregulatory performance of these taxa along altitudinal gradients, and to examine whether the patterns found are consistent with the predictions of the competitive hypothesis or whether they reflect independent adaptations to environmental gradients.

The aim of this study was to identify the habitat factors that produce an ecological barrier for the expansion of *I. cyreni* towards lower elevation. For that purpose, we selected three habitat types (a pine forest and two mixed-shrub and rock sites at different elevations), we used the protocol of Hertz *et al.* (1993) to characterize their thermal environments and to evaluate thermoregulation by *I. cyreni* and the common wall lizard *Podarcis muralis* (Laurenti, 1768) (Reptilia: Lacertidae), and we estimated refuge availability at each site. Our goals were: (1) to analyse the differences in the extent to which T_e values match T_{sel} values in each habitat; (2) to compare the accuracy and effectiveness of lizard thermoregulation *sensu* Hertz *et al.* (1993); and (3) to discuss whether the altitudinal pattern found suggests competition or independent adaptation. This integrative approach could shed light on the complex ecological interactions that ultimately result in the isolation of rock lizards in alpine environments.

MATERIALS AND METHODS

Study species and study areas

Both *I. cyreni* and *P. muralis* are heliothermic, actively foraging, and saxicolous lacertid lizards. *Iberolacerta cyreni* is slightly larger and more robust [adult snout–vent length (SVL) = 73–80 mm, body mass = 5.0–11.9 g] than *P. muralis* (SVL = 48–70 mm, body mass = 3.3–6.8 g). Whereas *I. cyreni* is endemic to the Sistema Central and is only found between 1600 and 2590 m a.s.l., being most common in rocky outcrops and mixed-shrub formations (Martín & Salvador, 1997), *P. muralis* occupies somewhat lower elevations (from 1230 to 2100 m a.s.l.) and a wider range of habitats, including rocky outcrops, oak, beech and pine forests, forest track banks, walls, and other human constructions (Diego-Rasilla, 2004; Amo *et al.*, 2007a).

Both species coincide at the Sierra de Guadarrama, where *P. muralis* reaches its southwestern distributional limit in the Iberian Peninsula. This mountain range, located in central Spain, extends over 80 km in a south-west to north-east direction, comprising numerous peaks and reaching its highest point at 2428 m a.s.l. Its continental climate is characterized by contrasting seasonal conditions, with cold wet winters and short summer droughts. Average minimum (February) and maximum (July) monthly temperatures are −3.3 and 20.8°C (Puerto de Navacerrada meteorological station, at 1860 m a.s.l.), respectively. The average annual precipitation is 1409 mm.

In the Sierra de Guadarrama, 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 elevations. These forested areas, which can spread from 1500 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 areas above the tree line (1700–2300 m a.s.l.) are also characterized by extensive patches of large granite rocks and scree interspersed among shrub formations.

We used three study sites in the Sierra de Guadarrama: Bola del Mundo (40º46′ N, 3º59′ W; ED50), a densely vegetated mixed-shrub site located at *c.* 1900 m a.s.l (hereafter higher-elevation shrub site); Morcuera (40º49′ N, 3º49′ W; ED50), a sparsely vegetated mixed-shrub area at lower elevation (*c.* 1770 m a.s.l.) and with warmer thermal conditions (hereafter lower-elevation shrub site); and Fuente de los Geólogos (40º46′ N, 4º00′ W; ED50), a pine forest area at *c.* 1770 m a.s.l. (hereafter pine forest site). It is important to note that although both lizard species were present in the mixed-shrub sites, *I. cyreni* was absent from the pine forest area, in which *P. muralis* was the only small lacertid found.

Field sampling

Field sampling took place between May and July, in the activity season of 2007. Data were collected on sunny days between 08:00 and 16:00 h (Mean European Time), covering the main daily activity period of the species. We simultaneously collected data on T_b values, T_e values, and lizard behaviour.

Body temperatures

Lizards ($n = 67$ *I. cyreni*, and $n = 42$ *P. muralis*) were captured by hand or with a noose, and the following data were recorded: time, sun exposure (full sun, sun filtered by vegetation or full shade), gender, and body temperature (T_b) measured immediately after capture with a Miller–Weber quick-reading mercury thermometer (± 0.1°C precision). In addition, microhabitat use at first detection (grass, rock, shrub or open area) and distance to the nearest refuge (rock or dense shrub) were also noted. To ensure equal detection probability among different microhabitats and shaded and sunlit areas, we carefully searched not only in open sunny areas, but also within shrubs and other shaded patches. In all areas, wariness in both species after first capture, combined with our effort to visit different areas each sampling day, reduced the probability of repeated sampling of the same individuals.

Operative temperatures

Data on operative temperatures were obtained using green and unpainted hollow copper cylinders (length = 5 cm, diameter = 1 cm) closed at both ends except for a small fissure that allowed insertion of the sensing tip of an electronic digital thermometer (digi-thermo®; ± 0.1°C precision). These copper models have been widely used to provide estimates of operative temperatures available to lacertid lizards (Belliure *et al.*, 1996; Díaz & Cabezas-Díaz, 2004). The model colours were chosen to match the lizards' absorptivity for solar radiation; in *I. cyreni*, many males and some females have a green dorsal coloration, whereas the remaining *I. cyreni* individuals and all *P. muralis* individuals have a brownish coloration. Thus, we used the mean of the green and unpainted models (one of each type per sampling point) to provide a null hypothesis of no thermoregulation (Hertz, 1992; Hertz *et al.*, 1993). Nevertheless, colour seems to affect temperature only in large-sized animals and has no apparent effect on small ones (Vitt & Sartorius, 1999; Shine & Kearney, 2001). In fact, temperature data of green and unpainted models were highly correlated ($r^2 = 0.95$, $n = 1012$; $T_{\mathrm{unpainted}} = 0.83 + 0.99\ T_{\mathrm{green}}$; $P = 0.289$ for the null hypothesis that the slope is equal to one), being on average 0.6 °C higher for unpainted than for green models. Although we did not compare the models' responses to changing heat loads with those of living animals, we are confident that our procedure is adequate for providing valid null temperature distributions to be used as yardsticks against which to compare lizard body temperatures. Moreover, commercially available electronic temperature recording devices (especially Tidbits™, Onset Computer Corporation, Pocasset, MA, USA; http://www.onsetcomp.com) can be taken as useful proxies for lizard models, which calls into question the notion that models should be designed to mimic lizards in microstructure of scalation, colour and overall morphology (Vitt & Sartorius, 1999). We used Tidbits to register operative temperatures in all study sites and sun exposures, and found that hourly means of Tidbit and model temperatures were highly correlated ($r^2 = 0.88$, $n = 53$, $P < 0.001$). The intercept of the regression of Tidbit on model temperatures ($T_{\mathrm{Tidbit}} = 1.45 + 0.85\ T_{\mathrm{model}}$) was not significantly different from zero ($P = 0.248$), but the slope was smaller than 1 ($P = 0.0009$), indicating that models had faster heating rates than Tidbits and responded more rapidly to changes in heat loads, and that is what makes them more suitable to estimate operative environmental temperatures in the highly variable alpine thermal environment.

Fourteen pairs of copper models per sampling day were used to estimate T_e values at each study site. Models were distributed at random locations separated on average by *c.* 20 m, using two models (one green and one unpainted) at each sampling point. Models were dropped on the ground and positioned with their inferior surface contacting the substrate. Temperatures from all models were registered at hourly intervals. In addition to T_e, we also recorded the distance to the nearest rock, to the nearest shrub and to the nearest refuge (which is the shortest of the two former distances), the weather at the moment of measurement (cloudy vs. sunny), and, if sunny, exposure to sun (as defined above). The random distribution of models with respect to microhabitats and sun/shade patches provides the null hypotheses of no thermoregulation (Hertz *et al.*, 1993; Bauwens *et al.*, 1996; Díaz & Cabezas-Díaz, 2004) against which the selectivity of lizards can be evaluated.

Preferred body temperatures

The thermal preferred range (T_{sel}), defined as the central 80% of all T_b values selected in a laboratory thermogradient, has been previously reported for both species by Bauwens *et al.* (1995). We used the ranges obtained in that study (*I. cyreni*: 31.4–35.7°C; *P. muralis*: 31.9–36.5°C) assuming that geographic variation in thermal preferences and thermal physiology is negligible, as it is in the case of all lacertid species that have been examined to date (Van Damme *et al.*, 1989, 1990; Díaz *et al.*, 2006b).

Data analyses and evaluation of mechanisms of temperature regulation

The following indices were used to evaluate the thermal quality of each habitat, the accuracy of thermoregulation (i.e. the extent to which T_b values overlap T_{sel}) and the effectiveness of thermoregulation (i.e. the improvement of accuracy with respect to non-thermoregulating models) at the three study areas (see Hertz *et al.*, 1993, for a detailed discussion).

1. Thermal quality of the habitat ($\overline{d_e}$), computed as the mean of the absolute deviations of T_e values from the nearest limit of T_{sel}. Given that $d_e = 0$ when T_e values fall within T_{sel}, the lower $\overline{d_e}$, the higher the thermal quality.

2. Accuracy of thermoregulation ($\overline{d_b}$), which is the same as above but for T_b values. Analogously, the lower $\overline{d_b}$, the higher the accuracy.

3. Effectiveness of thermoregulation: $E = 1 - (\overline{d_b}/\overline{d_e})$. This value will approach one when $\overline{d_b} << \overline{d_e}$, indicating that lizards thermoregulate carefully. Conversely, when lizards do not thermoregulate, $\overline{d_b}$ will be similar to $\overline{d_e}$, and E will approach zero.

Data were analysed using standard parametric techniques, maximum likelihood chi-square tests and log-linear analyses. The significance level for all tests was set as $\alpha = 0.05$. To compare the effectiveness of thermoregulation among the three study sites and between the two species, we used the bootstrap process suggested by Hertz *et al.* (1993). Random samples (with replacement, and with the same sample size as the original ones) were obtained from the distributions of T_e and T_b at each study site area, and $\overline{d_e}$, $\overline{d_b}$ and E were calculated, using the above procedures. This process was repeated 1000 times per site (or species), and the resulting paired bootstrap estimates of E were compared. The effectiveness of thermoregulation was assumed to differ significantly between the two samples (i.e. species or localities) when one value of E was higher than the other in fewer than 50 of the 1000 paired comparisons ($P = 0.05$).

RESULTS

Operative temperatures and availability of sunlit patches

Controlling for variation between times of day and sun-exposure categories (which were highly significant in a three-way ANOVA with the data shown in Fig. 1: time of day: $F_{7,\,836} = 85.2$, $P < 0.001$; sun exposure: $F_{2,\,836} = 365.2$, $P < 0.001$), operative temperatures differed significantly between sites ($F_{2,\,836} = 41.5$, $P < 0.001$), being higher at the lower-elevation shrub site than at the higher-elevation shrub site and the pine forest site, especially during the morning. Patterns of hourly variation differed between sites and between sun-exposure categories (site × time of day interaction: $F_{14,\,836} = 2.6$, $P = 0.001$; sun exposure × time of day interaction: $F_{14,\,836} = 7.0$, $P < 0.001$), with a more pronounced rise through the day at the two cooler sites than at the warmer one, and with a stronger response for models in full sun than for models in partial or full shade. The rise of T_e values for sunlit models with time of day was highest in the pine forest (sun exposure × site interaction: $F_{4,\,836} = 6.3$, $P < 0.001$), increasing drastically after 13:00 h (exposure × time of day × site interaction: $F_{28,\,836} = 2.61$, $P < 0.001$). However, overall temperatures remained lower at the pine forest site than at the shrub sites owing to the lower proportion of models in full sun in the former (Fig. 2). In fact, a log-linear analysis of the contingency table of model observations classified according to

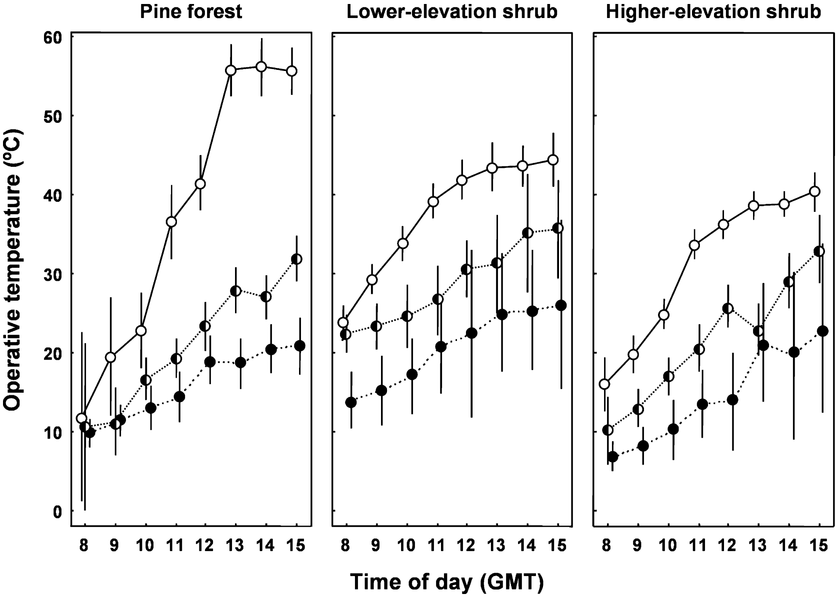

Figure 1 Variation (mean ± 1 SE) in environmental operative temperatures available (T_e values) at the three study sites as a function of time of day (GMT) and sun exposure (open circles, full sun; half-shaded circles, filtered sun, black circles: full shade).

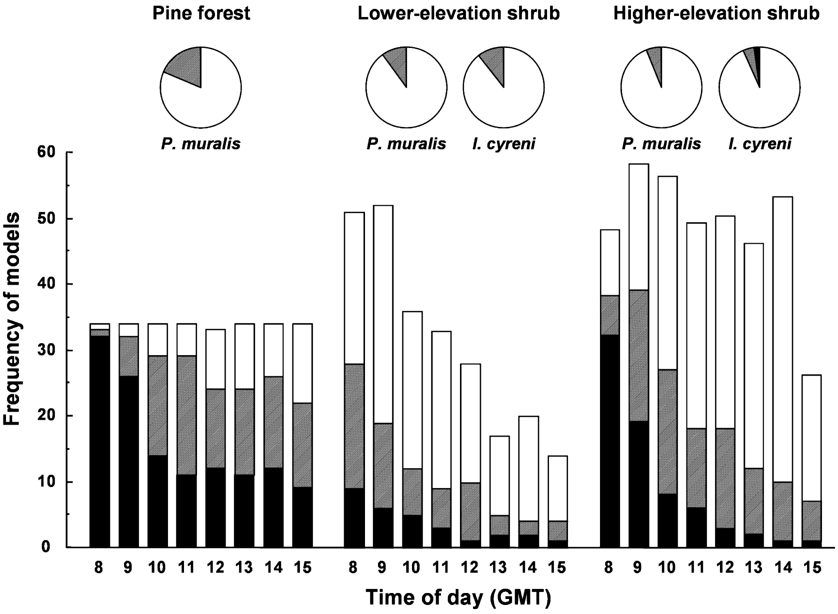

Figure 2 Hourly variation in the frequency of models in full sun, filtered sun and full shade (histograms) and of lizards (*Iberolacerta cyreni* and *Podarcis muralis*) in full or filtered sun (circles) at each of the three study sites. Open areas, full sun; striped areas, filtered sun; filled areas, full shade. The frequency of models changes throughout the day owing to weather conditions, because temperature and sun exposure were measured only in sunny weather and storms were frequent in the afternoon.

site, sun exposure and time of day produced a final model that included the three-way interaction between all factors ($\chi^2_{28} = 46.9$, $P = 0.014$ for the null hypothesis that the three-way interaction is zero), meaning that the daily pattern of hourly variation in the availability of sunlit and shaded patches differed significantly between sites. The two-way interactions were also significant, meaning that: (1) the availability of sunlit patches, as measured by the proportion of models in full or filtered sun, was higher at the mixed-shrub sites (88.45% at the lower-elevation shrub site and 81.68% at the higher-elevation shrub site) than at the pine forest site (53.14%; partial association for the site × sun exposure interaction: $\chi^2_4 = 198.3$, $P < 0.001$); (2) as it could be expected, the availability of sunlit patches increased more or less consistently throughout the day (partial association for the sun exposure × time of day interaction: $\chi^2_{14} = 146.1$, $P < 0.001$); and (3) the distribution of data into hourly periods was not homogeneous between sites owing to differences in sample sizes ($\chi^2_{14} = 82.6$, $P = 0.005$).

Thermal habitat quality

Study site, time of day, and the interaction between these two factors had a significant effect on the deviations of T_e values from the selected ranges of *I. cyreni* (two-way ANOVA with the data shown in Fig. 3; site: $F_{2,\,981} = 146.7$, $P < 0.001$; time of day: $F_{7,\,981} = 62.9$, $P < 0.001$; interaction: $F_{14,\,981} = 11.6$, $P < 0.001$) and *P. muralis* (two-way ANOVA; site: $F_{2,\,981} = 145.7$, $P < 0.001$; time of day: $F_{7,\,981} = 61.6$, $P < 0.001$; interaction: $F_{14,\,981} = 11.4$, $P < 0.001$). These results indicate that, for both species (results for *P. muralis* are nearly identical to those shown in Fig. 3 for *I. cyreni*), habitat thermal quality was highest at the lower-elevation shrub site and lowest at the pine forest site, showing a pronounced increase during the morning hours especially at the higher-elevation shrub site (Fig. 3). Thus, whereas at the two mixed-shrub sites deviations from T_{sel} were low and similar in the afternoon, the pine forest site exhibited low thermal quality all day long, owing to the overall paucity of sunlit patches and also to the excessively high T_e values (far above T_{sel}) in sunlit patches after midday (Fig. 1). Thus, the percentage of T_e values that fell below, within or above T_{sel} differed significantly between sites ($\chi^2_4 = 38.3$, $P < 0.001$); the percentage of T_e values within T_{sel} was lower at the pine forest area (2%), confirming its inferior thermal quality, than at the shrub sites (13.9% and 12.3% at the lower-elevation and higher-elevation shrub sites, respectively), and the pine forest site had the greatest proportion of T_e values below T_{sel} (79.8% vs. 59.3% and 64.4% at the lower-elevation and higher-elevation shrub sites, respectively).

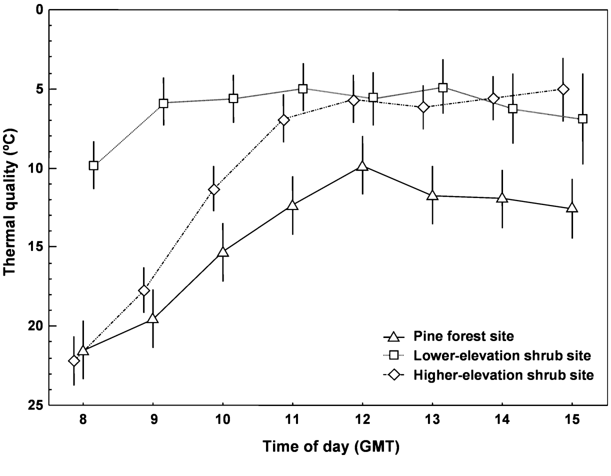

Figure 3 Hourly variation in the thermal quality of the environment (mean ± 1 SE for the absolute values of the deviations of operative temperatures from the preferred temperature range of *Iberolacerta cyreni*) at each of the three study sites.

Lizard thermoregulation

Both species actively selected sunlit patches in the three study sites (Fig. 2), as deduced from the fact that almost all lizards were in full or filtered sun when first observed (*I. cyreni*: 93%, 5% and 2% lizards in full sun, filtered sun and full shade, respectively, at the higher-elevation shrub site; and 89%, 11% and 0%, at the lower-elevation shrub site; *P. muralis*: 94% and 6% lizards in full and filtered sun at the higher-elevation shrub site; 90% and 10% at the lower-elevation shrub site; and 81% and 19% at the pine forest site), thereby showing a much higher proportion of observations in sunlit patches than non-thermoregulating models (log-linear analyses of the contingency tables of observations classified according to site, sun exposure and models vs. lizards; *I. cyreni*, partial association for the model–lizard × sun exposure interaction: $\chi^2_2 = 69.1$, $P < 0.001$; *P. muralis*: $\chi^2_4 = 39.5$, $P < 0.001$).

Females had lower temperatures than males in both species, and *P. muralis* had higher field temperatures than *I. cyreni* (two-way ANOVA with the data in Table 1; species: $F_{1,\,103} = 16.6$, $P < 0.001$; gender: $F_{1,\,103} = 13.0$, $P < 0.001$; interaction: $F_{1,\,103} = 0.14$, $P = 0.713$). Body temperatures did not vary between study sites in *I. cyreni* (two-way ANOVA; gender: $F_{1,\,61} = 8.61$, $P < 0.005$; site: $F_{1,\,61} < 0.1$, $P > 0.99$; interaction: $F_{1,\,61} = 0.06$, $P = 0.801$) but they did vary in *P. muralis* (two-way ANOVA; gender: $F_{1,\,36} = 3.61$, $P = 0.065$; site: $F_{2,\,36} = 4.78$, $P = 0.014$; interaction: $F_{2,\,36} = 0.10$, $P = 0.904$). Thus, whereas rock lizards did not translate between-site differences in the thermal environment into significant differences in T_b values, wall lizards had significantly lower temperatures at the higher-elevation shrub site (Table 1).

For both species, $\overline{d_b}$ values were significantly smaller than $\overline{d_e}$ values in all the populations examined (Table 1), indicating that T_b values were closer to T_{sel} than were T_e values, and thus providing unequivocal evidence of active thermoregulation. For *I. cyreni* the difference between $\overline{d_b}$ values and $\overline{d_e}$ values was greater at the higher-elevation than at the lower-elevation shrub site (two-way ANOVA with the deviations from T_{sel} as the dependent variable and study site and model vs. lizard as factors; model–lizard: $F_{1,\,803} = 30.69$, $P < 0.001$; site: $F_{1,\,803} = 4.60$, $P = 0.032$; interaction: $F_{1,\,803} = 4.29$, $P = 0.038$), suggesting more effective thermoregulation *sensu* Hertz *et al.*

Table 1 Mean values (± 1 SE, in °C) for environmental operative temperatures available, thermal quality of the habitat (deviations of operative temperatures from the preferred thermal range of *Iberolacerta cyreni*), body temperatures of both lizard species, and accuracy of thermoregulation (deviations of body temperatures from the preferred thermal range of each species).

	Pine forest site			Lower-elevation shrub site			Higher-elevation shrub site		
	Temperature (°C)	Deviation (°C)	*n*	Temperature (°C)	Deviation (°C)	*n*	Temperature (°C)	Deviation (°C)	*n*
Environment (models)	23.3 ± 0.9	14.4 ± 0.4	272	30.3 ± 0.5	6.2 ± 0.3	324	25.6 ± 0.6	10.1 ± 0.4	416
Iberolacerta cyreni									
Males	–	–	–	29.3 ± 0.7	2.1 ± 0.7	12	29.1 ± 0.4	2.5 ± 0.4	31
Females	–	–	–	27.1 ± 0.8	4.3 ± 0.8	9	27.2 ± 0.8	4.2 ± 0.8	13
Podarcis muralis									
Males	31.6 ± 0.6	0.8 ± 0.4	9	32.1 ± 0.9	0.8 ± 0.5	6	29.3 ± 0.8	2.6 ± 0.8	7
Females	30.4 ± 1.0	1.7 ± 1.0	7	30.2 ± 1.8	2.2 ± 1.6	4	28.3 ± 0.7	3.6 ± 0.7	9

(1993). In fact, the effectiveness of thermoregulation was higher at the higher-elevation ($E = 0.70$) than that at the lower-elevation ($E = 0.52$) site; to test for differences in E, we generated 1000 bootstrap resampling estimates per site, showing that the lower-elevation data had a greater E value only in 21 of the paired comparisons ($P = 0.021$). Because deviations from T_{sel} were similar in both populations (one-way ANOVA comparing mean d_b values: $F_{1, 65} = 0.01$, $P = 0.916$), that is, the accuracy of thermoregulation was similar, differences in the extent to which T_b values were closer to T_{sel} than were T_e values should be attributed to lower thermal quality at the higher site: lizards thermoregulated more effectively at the site where the thermal environment was less suitable.

Podarcis muralis showed significant differences between d_b values and d_e values in the three study sites (two-way ANOVA; model–lizard: $F_{1, 1048} = 56.1$, $P < 0.001$; site: $F_{2, 1048} = 4.04$, $P = 0.018$; interaction: $F_{2, 1048} = 5.15$, $P = 0.006$). Individuals of this species thermoregulated more efficiently at the site with the lowest thermal quality (i.e. the pine forest) than at the thermally more suitable mixed-shrub sites (E values of 0.92, 0.79 and 0.69 at the pine forest, lower-elevation shrub site and higher-elevation shrub site, respectively), although only the difference between the two extreme values (i.e. the pine forest and the higher-elevation shrub site) was significant in the bootstrap resampling test (higher-elevation data had a greater E value in only one of the paired comparisons: $P = 0.001$). In contrast to the case for *I. cyreni*, in *P. muralis* the accuracy of thermoregulation ($\overline{d_b}$) differed significantly between sites ($F_{2, 39} = 4.56$, $P = 0.017$), being lower at the higher-elevation shrub site.

Although both species thermoregulated with comparable efficiency at the higher-elevation shrub site (bootstrap resampling test: $P = 0.454$), *P. muralis* showed higher effectiveness than *I. cyreni* at the lower-elevation shrub site ($P = 0.029$). There were no overall differences between the two species in the extent of thermoregulation, as estimated by the difference between d_b values and d_e values pooling together all localities (interaction term in the two-way ANOVA with the deviations from T_{sel} as the dependent variable and model vs. lizard and species as factors: $F_{1, 2129} = 0.63$, $P = 0.426$), but, interestingly, they showed opposite altitudinal trends: whereas *I. cyreni* thermoregulated more efficiently at higher elevation, the opposite was true for *P. muralis*.

Distance to refuges

The three study sites differed significantly in the proximity of refuges available to lizards; mean distance to nearest refuge was greatest at the pine forest site, intermediate at the lower-elevation shrub site, and shortest at the higher-elevation shrub site (Table 2; ANOVA with the distances between randomly distributed models and nearest refuges: $F_{2, 580} = 98.04$, $P < 0.001$).

Iberolacerta cyreni actively chose microhabitats with much shorter distances to the nearest refuge than expected at random, and this selection was significantly more intense at the lower-elevation shrub site, where retreat sites were further apart, than at the higher-elevation shrub site (two-way ANOVA; model–lizard: $F_{1, 450} = 29.25$, $P < 0.001$; site: $F_{1, 450} = 16.22$, $P < 0.001$; interaction: $F_{1, 450} = 14.27$, $P < 0.001$). Although shrubs were more readily available than rocks as nearest refuges (76% and 67% of model observations were closer to shrubs than to rocks at the lower- and higher-elevation shrub sites, respectively), lizards preferred rocks as their closest retreat (68% and 70% of lizard observations were closer to rocks than to shrubs at the lower- and higher-elevation shrub sites; $\chi^2_1 = 17.3$ and 19.9, respectively, $P < 0.001$ in both cases).

Similarly, remaining close to refuges was also important for *P. muralis*. However, the intensity of selection (as measured by the difference between models and lizards in the mean distance to nearest refuge) was somewhat smaller and more variable between sites (two-way ANOVA; model–lizard: $F_{2, 625} = 13.03$; $P < 0.001$; site: $F_{2, 625} = 12.18$, $P < 0.001$; interaction: $F_{2, 625} = 8.86$, $P < 0.001$). This was a result of the fact that, whereas in the pine forest individuals of *P. muralis* were observed much closer to retreat sites than expected by chance (Table 2), at the lower-elevation shrub site they were found mainly around a road bank where refuges were scarce and sparsely distributed. In fact, both species were observed close to refuges at the higher-elevation shrub site, but at the

Table 2 Mean distance (± 1 SE, in cm) to the nearest rock, to the nearest shrub, and to the nearest refuge (which is the shorter of the two former distances) of randomly distributed copper models and of lizards of our two study species.

	Nearest rock (cm)	Nearest shrub (cm)	Nearest refuge (cm)	*n*
Pine forest site				
Refuge availability (models)	308 ± 15	288 ± 18	183 ± 9	202
Iberolacerta cyreni	–	–	–	
Podarcis muralis	100 ± 23	91 ± 32	23 ± 9	16
Lower-elevation shrub site				
Refuge availability (models)	249 ± 13	142 ± 9	126 ± 9	219
Iberolacerta cyreni	75 ± 39	37 ± 12	6 ± 2	22
Podarcis muralis	369 ± 209	162 ± 49	103 ± 35	10
Higher-elevation shrub site				
Refuge availability (models)	117 ± 10	50 ± 5	24 ± 2	168
Iberolacerta cyreni	52 ± 20	73 ± 17	3 ± 1	45
Podarcis muralis	38 ± 14	40 ± 7	18 ± 6	16

lower-elevation shrub site the mean distance to nearest refuge was much shorter for *I. cyreni* than for *P. muralis* (two-way ANOVA; species: $F_{1,\ 89} = 39.95$, $P < 0.001$; site: $F_{1,\ 89} = 24.95$, $P < 0.001$; interaction: $F_{1,\ 89} = 21.42$, $P < 0.001$). Overall, *P. muralis* also preferred rocks rather than shrubs as nearest refuges (54% of lizard observations vs. 35% of model observations were closer to rocks than to shrubs in the pooled sample of the three sites; $\chi^2_1 = 5.6$, $P = 0.017$), although the proportion of observations closer to shrubs than to rocks was somewhat higher for *P. muralis* (46%) than for *I. cyreni* (30%).

DISCUSSION

Our results yield three main conclusions. First, both thermal habitat quality and refuge availability were lowest within the pine forest, suggesting that this vegetation belt might function as a barrier for the expansion of rock lizards towards lower elevations. Second, rock lizards seemed to thermoregulate relatively well in harsh alpine environments, their thermoregulatory effectiveness being more dependent on the availability of appropriate refuges than on the thermal quality of the habitat. Third, our observations suggest that competition with wall lizards was unlikely to explain either the distribution of rock lizards or their thermoregulatory effectiveness, although we did not directly test this hypothesis. In the light of these results, we discuss the possible roles of local adaptation and interspecific competition in the restricted distribution pattern of *I. cyreni*.

Between-site variations in habitat thermal quality

Although alpine environments are challenging for small ectotherms, because of their harsh thermal conditions, some species across different taxa have managed to survive at high elevations across different latitudes (Bauwens *et al.*, 1990; Melville & Swain, 2003), including most European rock lizards within the genus *Iberolacerta*, which have restricted distributions in southern Mediterranean mountains (Carranza *et al.*, 2004). In the Sierra de Guadarrama, opportunities for lizard thermoregulation above the alpine tree line are mainly constrained by two conditions: the remarkably low temperatures experienced during the morning hours, when lizards tend to be more active, and the presence of clouds that can lead to storms in the late afternoon, especially in the warmer areas (cloudy weather was much more frequent, for instance, at our lower-elevation than at our higher-elevation shrub site). At lower altitudes, conditions become milder, providing more suitable thermal environments for lizards. In fact, *Psammodromus algirus* lizards inhabiting deciduous forests at lower elevations in the same range, 7 km away as the crow flies, thermoregulate better than the rock lizard populations reported herein (Díaz, 1997; Díaz & Cabezas-Díaz, 2004), showing higher proportions of T_b values that fall within T_{sel}, and higher thermoregulatory accuracy ($\overline{d_b}$ values <1ºC) and effectiveness ($E \geq 0.9$) than those exhibited by *I. cyreni* in the present study ($\overline{d_b}$ = 3.0 °C and $E \leq 0.7$; see Table 1). Remarkably, only one of 109 lizard observations corresponded to an individual in full shade, evidencing the importance of sunlit patches in alpine, cool environments. Increased basking activity and/or selectivity for sunlit patches has been observed in other lizards inhabiting high elevations (Hertz, 1981; Bauwens *et al.*, 1990; Díaz, 1997; Gvoždík, 2002) or latitudes (Van Damme *et al.*, 1990), and it can be interpreted as an indication of the amount of time that rock lizards invest in behavioural thermoregulation to compensate for the low thermal suitability of the Sierra de Guadarrama.

Among the alpine habitats studied, the pine forest offered the poorest thermal quality for lizards, which was mainly as a result of the great amount of shade produced by the tree canopy. Provided that body temperature is crucial for the physiological performance of ectotherms (Van Damme *et al.*, 1991; Bauwens *et al.*, 1995; Herczeg *et al.*, 2008), and given that the habitat colonization success of reptiles can be negatively affected by the scarcity of sunlit patches, the Scots pine vegetation belt cannot be ruled out as a possible factor preventing rock lizards from thriving below the tree line. In fact, the poor microhabitat quality of these forests is associated with a low diversity of Mediterranean lizard species (Amo *et al.*, 2007a), but this is the first demonstration of their low thermal suitability. Nevertheless, it should also be noted that the area with the best thermal quality (i.e. the lower-elevation shrub site) was not the most densely occupied by either of the two lizards species studied, suggesting that other factors such as predation or competition may also be influencing lizard colonization success (see below).

Thermoregulatory effectiveness and refuge availability

The two species showed opposite trends in thermoregulatory effectiveness with elevation: whereas thermoregulation by *I. cyreni* was more effective, that by *P. muralis* seemed to be worse at the higher-elevation shrub site than at the two lower-elevation localities. It is important to note that for *I. cyreni*, higher effectiveness was not the result of higher T_b values or T_b values closer to T_{sel}, but of changes in habitat quality (d_e). This raises the question of why rock lizards did not attain higher T_b values at the lower-elevation site, where thermal quality was higher. We suggest that this may be a consequence, at least in part, of habitat requirements that are more related to predator avoidance and refuge availability than to thermal constraints. In fact, *I. cyreni* is typically associated with large scree rocks and *Cytisus* shrubs (Martín & Salvador, 1997), whereas *P. muralis* is more opportunistic and it appears more linked to anthropogenic habitats (Diego-Rasilla, 2004). Thus, at the lower-elevation shrub site *I. cyreni* may not be able to attain higher T_b values and take full advantage of its higher thermal quality, because the scarcity of refuges can affect the thermoregulatory behaviour of these lizards by restricting their movements to areas close to rocks and limiting their opportunities to use a wider range of sunlit patches. Previous studies suggest that rocks are essential to fulfil the combined requirements of basking and refuge (Carrascal *et al.*, 1992; Martín & Salvador, 1997; Amo *et al.*, 2007a,b). Moreover, increased perception risk can force lizards to remain longer within refuges, thus lowering their T_b values (Martín *et al.*, 2003). In fact, remaining close to refuges was more important at the lower-elevation site, which suggests that risk perception was higher where retreat sites were less available. By contrast, at the higher-elevation site rocks were more readily available and the movements of *I. cyreni* were not impaired by refuge availability; thermoregulation could therefore be optimized without compromising predation risk. Thus, the higher refuge availability at the higher-elevation shrub site seemed to override its lower thermal quality, allowing lizards to thermoregulate more effectively. Similar results, where more effective thermoregulation evolves in areas of lower thermal quality, have also been found for other lizards (Herczeg *et al.*, 2003; Blouin-Demers & Nadeau, 2005).

It could be argued that, because population density is higher at higher elevation (C. Monasterio, A. Salvador & J.A. Díaz, unpublished data), territoriality might influence the ability of lizards to move freely, thus reducing the number of available refuges. However, this species shows extensive home-range overlap between individuals of both sexes (Salvador *et al.*, 2008), and at the higher-elevation site scree slopes and formations of mixed shrubs offer a continuum of available refuges (Table 2). In fact, although males form a dominance hierarchy to access females in the reproductive season (Martín & Salvador, 1993), we have never observed an active defence of basking sites. Moreover, in the hypothetical case that lower population density allowed lower levels of intraspecific competition, this would reinforce the importance of refuge availability as a factor determining thermoregulatory effectiveness, because lizards would not be able to achieve higher T_b values at the lower-elevation shrub site despite its higher thermal quality and lower population density.

Our results confirm the ubiquity of the wall lizard *P. muralis*, and its ability to thrive locally even in the pine forest, in which it manages to thermoregulate effectively around the canopy clearings. Similarly, at the lower-elevation site, the species was practically confined to the margins of the shrub area, but showed a better thermoregulation effectiveness than that exhibited at the higher-elevation shrub site – and, in fact, a higher thermoregulation effectiveness than the sympatric population of *I. cyreni*. This, together with the lower temperatures and lower adjustment to preferred thermal range registered at the higher-elevation shrub site, corroborates the increasing dependence of *P. muralis* on environmental temperatures with elevation (Braña, 1991), suggesting a limited ability to cope with the low thermal quality of the alpine environment in spite of its opportunistic use of habitat.

Local adaptation vs. competitive exclusion

The overall picture of thermoregulation suggests that local adaptation, instead of competitive exclusion, is a more plausible explanation for the restricted distribution of Iberian rock lizards. When both species occurred in sympatry, *I. cyreni* was much more abundant than *P. muralis*, which seemed to exploit habitat patches unoccupied by the other species. Thus, our results do not support the hypothesis that wall lizards are contributing to the restriction of *I. cyreni*, and preliminary analyses of an experiment designed to test competition for preferred habitat patches in an outdoor enclosure suggest that large rock lizard males are dominant over all other individuals of both species (C. Monasterio, A. Salvador & J.A. Díaz, unpublished data).

In summary, the rock lizard *I. cyreni* seemed to be adapted to the thermal conditions of alpine shrub areas, although its ability to thermoregulate successfully was apparently constrained by refuge availability. Thus, it was probably the compromise between thermal quality and refuge abundance, and not the presence of *P. muralis*, that explained the altitudinal distribution and associated variation in thermoregulatory effectiveness of *I. cyreni*. Nevertheless, other factors, which should be the focus of future studies, may also influence the alpine confinement of *I. cyreni*, including physiological and life-history traits such as incubation temperature or egg retention by pregnant females. Our results also suggest that the Scots pine vegetation belt may prevent the species from expanding its range, given that these forests combine a very low availability of refuges with environments of poor thermal quality, thus yielding a barrier of unsuitable habitat that cannot be traversed because of low vagility (Salvador *et al.*, 2008). From here we can deduce that, although the expected rise of temperature resulting from global climate change (Nogués-Bravo *et al.*, 2007) will presumably ameliorate thermal conditions for lizards, *I. cyreni* may have thermoregulatory difficulties if refuges are not readily available, and the species could also be negatively affected by the advance of the tree line, which is one of the predicted effects of global climate change (Grace *et al.*, 2002). However, although there is evidence suggesting that warmer temperatures favour *P. sylvestris* expansion in northern latitudes (Grace & Norton, 1990; James *et al.*, 1994), some studies have suggested that the southernmost populations are very sensitive to global climate change as a result of an expected increase in populations of their pathogens (Hódar *et al.*, 2003). We conclude that neither thermoregulation nor probably competition seems to be confining the distribution of rock lizards to alpine environments, as long as there is enough suitable habitat (such as mixed shrub and rock screes) that combines basking opportunities with plenty of antipredator refuges.

ACKNOWLEDGEMENTS

This paper is a contribution to the project CGL2007-02744/BOS, funded by the Spanish Ministry of Education and Science. C.M. was funded by a CSIC-El Ventorrillo grant and P.I. was funded by a PhD studentship from the Universidad Complutense de Madrid. Permission to capture lizards was provided by the Dirección General del Medio Natural of the Madrid region.

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BIOSKETCH

Our research team focuses on evolutionary biology, reptile ecophysiology and the evolution of life histories along biogeographical gradients. To deal with the interesting questions that often arise in evolutionary ecology, we use lizards as study systems, bringing together biogeography, behavioural ecology, physiology, evolutionary ecology, population genetics and conservation biology in an integrative approach. All authors (C.M., A.S., P.I. and J.A.D.) contributed to conceiving the ideas, collecting and analysing the data, and writing the paper.

Editor: Nicholas J. Gotelli