

Ecological correlates of the thermal quality of an ectotherm's habitat: a comparison between two temperate lizard populations

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Summary

1. Although thermal factors are of paramount importance to the quality of the habitats occupied by small ectotherms (e.g. lizards), the hypothesis that the relative abundance of squamate populations is related to the thermal quality of their habitats remains untested. If differences in the availability of thermally suitable microhabitats was the primary determinant of the overall quality of a lizard's habitat, population density in a habitat should be proportional to its thermal quality.

2. The influence of the thermal quality of a habitat on thermoregulatory behaviour, body temperatures, expected physiological performance and relative abundance was compared in two populations of the temperate lizard *Psammotromus algirus* separated by 700 m altitude in central Spain. Habitat thermal quality was estimated with an index of how closely the available operative temperatures in a habitat match the range of body temperatures that lizards attempt to maintain in a laboratory thermogradient (Hertz, Huey & Stevenson 1993).

3. Operative temperatures, measured using copper models, were higher at the lowland site, where a large proportion of readings fell within or above the preferred range, especially in the early morning. Thermal habitat quality was also higher at the low altitude site, with smaller absolute deviations from the preferred range throughout most of the morning hours. Moreover, lizard body temperatures, the accuracy of thermoregulation and the predicted running performance of lizards were somewhat higher at the lowland site, although differences were smaller than expected on the basis of operative temperatures. A log-linear analysis showed that lizard selectivity for basking sites was more pronounced at the thermally inferior montane site. Thus, the observed differences in the thermal quality of habitats appeared to influence the behaviour of lizards.

4. Nevertheless, the relative abundance of lizards, as estimated by repeated transect counts, was higher at the montane site. This unexpected result suggests that thermal constraints may not be the most important factor determining lizard population densities on a regional scale. Alternatively, food availability and/or predation pressure might have a greater impact on the overall quality of a habitat for temperate lizards.

Key-words: Habitat quality, lizard thermoregulation, operative temperatures, *Psammotromus*, relative abundance

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Introduction

The evaluation of habitat quality is a central topic in contemporary ecological studies (Huey 1991). This requires the integration of a large number of factors (e.g. limitation by physical constraints, predation risk, mating opportunities, resource availability) and their interactions. Thermal factors are of paramount importance to the quality of the habitats occupied by small ectotherms (Heatwole 1977; Dunham, Grant & Overall 1989; Huey

1991). All else being equal, differences in the thermal quality of habitats produce variations in demographic parameters of small terrestrial ectotherms, particularly those with limited dispersal capacities. Several studies have explored how the necessity of temperature regulation influences the time available to find food or mates or to avoid predators (Dunham *et al.* 1989; Grant & Dunham 1990; Adolph & Porter 1993). These have provided useful insights into the mechanisms that link life-history phenotypes of lizards to the thermal environment.

However, no study has yet addressed the simple question of whether the relative abundance of squamate populations is related to the thermal quality of their habitats. Here, it is proposed that thermal conditions and body temperatures vary geographically (i.e. between habitats) in ways that affect short-term physiological capacities (Huey & Stevenson 1979; Bennett 1980; Huey 1983; Waldschmidt & Tracy 1983; Stevenson, Peterson & Tsuji 1985). These, in turn, partially determine demographic parameters (Huey 1982, 1991; Kingsolver 1989; Dunham *et al.* 1989; Grant & Dunham 1990) and, ultimately, population density. Thus, if differences in the availability of thermally suitable microclimates was the primary determinant of the quality of an ectotherm's habitat, population density in a habitat should be proportional to its thermal quality (but see van Horne 1983). This hypothesis can be tested with data on the relative or absolute abundance of ectotherm populations and data on the thermal quality of the habitats they occupy.

The effect of habitat thermal quality is evaluated on thermoregulatory behaviour, body temperatures and (ultimately) relative abundance in two populations of a common Iberian lacertid lizard, the Large Psammodromus, *Psammodromus algirus* (L.) 1758. These populations inhabit areas separated by *c.* 700 m along an altitudinal gradient in central Spain. More specifically, the hypothesis is tested that the effects of habitat structure on the abundance of *P. algirus* (Díaz & Carrascal 1991) are mediated by the positive influence of low shrub cover on the thermal environment experienced by lizards. Dense vegetation cover near the ground produces a thermal mosaic (Strijbosch 1988; Díaz & Carrascal 1991) that minimizes the shuttling distance between sun and shade. The thermal mosaic thus reduces the costs of thermoregulation (Huey 1974; Huey & Slatkin 1976), allowing lizards to invest more time and energy in growth and reproduction.

The distribution of operative temperatures in space and time is used to evaluate the thermal quality of habitats. Operative temperatures, which integrate all factors that influence heat exchange between the organism and its environment, can be measured using copper models whose physical properties simulate the thermal responses of non-thermoregulating animals (Bakken & Gates 1975; Bakken 1992). More specifically, the protocol developed by Hertz *et al.* (1993) is followed, whereby the correspondence of available operative temperatures to body temperatures selected in the laboratory is used as an index of a habitat's thermal quality. This is easier to measure and more straightforward than previous estimates of habitat thermal quality (Huey & Slatkin 1976; Tracy & Christian 1986; see Huey 1991 for a detailed discussion), and it provides an objective yardstick for evaluating inter- or intraspecific differences in thermoregulatory behaviour and relative abundance. The accuracy of behavioural thermoregulation is esti-

mated by the correspondence of field body temperatures to body temperatures selected in the laboratory (Hertz *et al.* 1993). The effects of habitat thermal quality on lizard performance are also evaluated by integrating field data on body temperatures in each habitat with published laboratory data (Bauwens *et al.* 1995) on the effect of body temperature on relative sprint speed (Huey 1983; Waldschmidt & Tracy 1983; Hertz *et al.* 1993).

Materials and methods

ANIMALS

Psammodromus algirus is a medium-sized lacertid lizard (adult snout-vent length 60–85 mm; mass 6–14 g) inhabiting shrub and woodland habitats of the Iberian peninsula, southeastern coastal region of France and northwest Africa (Arnold 1987; Díaz & Carrascal 1991). It is a ground-dwelling, shuttling heliotherm (Díaz 1991), whose microhabitat selection is strongly influenced by thermoregulatory constraints and, apparently, by the need to minimize predation risk (Díaz 1992).

STUDY AREAS

Lizards were sampled at two localities in the Sierra de Guadarrama region, Madrid, central Spain. The lower elevation site (El Pardo; 40°31'N, 03°47'W; 650–700 m elevation) is a holm oak (*Quercus rotundifolia*) broad-leaved, perennial forest in which *Q. rotundifolia* also dominates the shrub layer, together with *Cistus ladanifer*, *Lavandula* and *Thymus*. This site has a mean annual temperature of 12.5 °C and a mean July temperature of 23.4 °C; mean annual precipitation is 686 mm. The higher elevation site (Morcuera; 40°54'N, 03°53'W; 1400–1500 m elevation) is a *Quercus pyrenaica* deciduous broad-leaved forest, in which the shrub layer is formed by patches of *Q. pyrenaica* offshoots interspersed with dense, spiny shrubs of *Rosa*, *Crataegus*, *Rubus* and *Genista*. This site is cooler and wetter than the low altitude one: mean annual and July temperatures are 10.0 and 18.8 °C, respectively, and mean annual precipitation is 971 mm.

Psammodromus algirus is the most abundant lizard species at both locations, sharing its habitat with other lacertids such as *Psammodromus hispanicus*, *Lacerta lepida*, *Podarcis hispanica* (at both El Pardo and Morcuera), *Acanthodactylus erythurus* (at El Pardo) and *Lacerta schreiberi* (at Morcuera). Lizards were studied on sunny days between 20 June and 8 July 1994, the season with the largest daily fluctuations of environmental temperatures. Data were collected between 0700 and 1300 hours (Mean European Time, MET), when lizard detectability reaches its peak during the summer months (Carrascal & Díaz 1989) and when the thermal environment exerts a pronounced

effect on the behaviour (Díaz 1991) and microhabitat selection of lizards (Díaz 1992). At each study area, data on operative temperatures, body temperatures and lizard abundance were simultaneously collected.

FIELD SAMPLING

The relative abundance at each site along four transects was estimated, each sampled on a different day. Each transect was walked twice per hour, and the mean of the two hourly replicates was used as a single data point to test for the effects of site and time of day on the number of lizards seen. To control for potential differences in visibility between sites, only lizards within 2.5 m of the transect were considered. Each lizard was placed in one of three categories of sun exposure (full sun, sun filtered by vegetation, or shade) when it was first sighted.

Lizards were captured by hand or with a noose ($n = 91$ at El Pardo; $n = 61$ at Morcuera), and the following data were recorded: time, sun exposure (as defined above), sex, size (adult or subadult; juveniles absent at this time of year) and body temperature (cloacal, $= T_b$), measured to the nearest 0.1°C with a Miller–Weber quick-reading mercury thermometer using standard precautions (Avery 1982). Because previous analyses (Díaz 1988) show that neither thermoregulatory behaviour nor T_b varies significantly with the size or sex of the lizards, all subsequent analyses are based upon pooled samples for each site. The high population densities and wariness of *P. algirus* at both sites, combined with the effort made to visit a different area each sampling day, reduced the probability of resampling individuals.

Data on operative temperatures ($=T_e$) were obtained using hollow copper models. Models were unpainted copper cylinders (length = 5 cm, diameter = 1 cm) closed at both ends except for a small fissure that allowed the sensing tip of an electronic digital thermometer to be inserted (digi-thermo[®]; $\pm 0.1^\circ\text{C}$ precision). The thermal responses of models and lizards were compared by measuring equilibrium temperatures of two models and two restrained live lizards, under identical radiant heat loads (100-W incandescent bulb at different heights above experimental subjects; range of equilibrium T_b s = $29\text{--}40^\circ\text{C}$). The equilibrium temperatures for lizards and models were highly correlated ($r^2 = 0.98$), and a regression equation ($T_{e\text{ adj}} = 4.36 + 0.875 T_e$; $n = 10$, $P < 0.001$) was used to correct T_e s measured in the field.

Thirty copper cylinders were used at each site to estimate T_e s. Models were placed at randomly selected intervals (1–9 m; $x \pm \text{SD} = 5.6 \pm 2.3$ m) along a transect. Each was dropped on the ground at its random location and positioned so that part of its ‘ventral’ surface contacted the substrate. Each day models were installed along a different sampling line at each study site. Whenever possible, temperatures from all models were recorded at hourly intervals; when time

limitations prevented all models being sampled, every other model in a line was sampled. In addition to T_e , the time of day and exposure to sun (full sun, filtered sun or shade) were also recorded for each model. The distribution of models in sun–shade patches provides a null hypothesis (Grant & Dunham 1988; Adolph 1990; Hertz 1992a,b; Díaz 1994a) against which lizards’ selectivity for sunlit or shaded patches can be evaluated.

PREFERRED TEMPERATURES AND THERMAL SENSITIVITY OF SPRINT SPEED

Data on the target T_b s that lizards attempt to maintain in the laboratory (selected temperature range) were obtained using 13 animals captured at the lowland site and transported to the Estación Biogeológica El Ventorrillo (Navacerrada, Madrid), where they were allowed to acclimatize for one week in terraria ($100 \times 50 \times 40 \text{ cm}^3$) with a light–dark cycle of 12–12 h and a temperature gradient identical to the one used to estimate thermal preferences. Food (crickets and mealworms) and water were supplied *ad libitum*.

Lizards thermoregulate between lower and upper threshold temperatures rather than around a single T_b (Barber & Crawford 1977). The selected temperature range was estimated indirectly by measuring the T_b s selected by individual lizards in a laboratory thermal gradient. A 150-W light bulb was suspended 11 cm above one end of a terrarium to create a thermal gradient with operative temperatures ranging between 18 and 58°C . A second 60-W bulb outside the cage illuminated the cool end of the gradient. Food and water were provided *ad libitum* during the trials. A Miller–Weber quick-reading mercury thermometer was used to measure the T_b s of active lizards after 1 h in the thermogradient. These readings estimate the temperatures that lizards would attempt to achieve in the field in the absence of physical and biotic constraints (Licht *et al.* 1966). Two measurements per individual were obtained, always on different days, and subsequently joined all data. The selected temperature range was then calculated ($= T_{\text{sel}}$) as the central 80% of all T_b s selected in the thermogradient (Bauwens *et al.* 1995).

Because T_{sel} was estimated for the low altitude population only, it was assumed that lizards from both populations have similar thermal preferences. This assumption is supported by two lines of evidence. First, the absence of intraspecific variation in thermal preferences has been demonstrated in two species of lacertid lizards living along altitudinal gradients that are more pronounced than the one studied here (Van Damme *et al.* 1989; Van Damme, Bauwens & Verheyen 1990). Second, preliminary data (J. A. Díaz, unpublished observations) suggest that the selected temperature range of the montane lizards may be narrower than, and contained within, that of their lowland conspecifics. Consequently, the thermal

quality of the montane habitat and the thermoregulatory accuracy of the montane lizards may have been overestimated (see Data analyses). This would make this approach a conservative one.

Data on the thermal sensitivity of running performance (temperature performance breadth, or TPB, defined as the range of T_b s over which speed is equal to or higher than 80% of its maximum; see Huey & Stevenson 1979) were obtained from Bauwens *et al.* (1995). Sprint capacities of lizards at the observed field-active T_b s were estimated by interpolation between maximal speed vs T_b data points available in the literature (Spellerberg 1976; Bauwens *et al.* 1995).

DATA ANALYSES

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

1. Thermal quality of a habitat: d_e , computed as the mean of the absolute values of the deviations of T_e s from T_{sel} ($d_e = [T_e - \text{upper limit of } T_{sel}]$ for T_e s above T_{sel} , $d_e = [\text{lower limit of } T_{sel} - T_e]$ for T_e s below T_{sel} , and $d_e = 0$ for T_e s within T_{sel}).
2. Accuracy of thermoregulation: \bar{d}_b (same as above but for T_b s).
3. Effectiveness of thermoregulation: $E = 1 - (\bar{d}_e/\bar{d}_b)$. The value of E will generally range between 0, when lizards do not thermoregulate and their deviations from preferred range are similar to those of models, and 1, when lizards thermoregulate carefully and their deviations from preferred range are much smaller than those of models (Hertz *et al.* 1993).

Data were analysed using standard parametric techniques, maximum-likelihood χ^2 -tests and log-linear analysis. To compare the effectiveness of thermoregulation at both localities, the bootstrap process suggested by Hertz *et al.* (1993) was used. Random

samples (with replacement) were obtained from the distributions of T_e s and T_b s at each study area, and d_e , \bar{d}_b and E were calculated, using the above procedures. This process was repeated 1000 times per study site and the resulting paired bootstrap estimates of E at both sites were compared. The significance level for all statistical tests was set at $\alpha = 0.05$.

Results

LIZARD RELATIVE ABUNDANCE

Counts of lizards at the montane site (Table 1) were about 60% higher than those at the lowland site, even though hourly variation in the numbers observed were similar at both areas (two-way ANOVA; site: $F_{1, 36} = 17.2$, $P < 0.001$; time of day: $F_{5, 36} = 3.8$, $P < 0.01$; interaction: $F_{5, 36} = 0.5$, $P > 0.7$). At both study sites, lizards showed activity patterns typical of Mediterranean lacertids, with a pronounced peak 2–3 h after sunrise and decreased levels at midday hours. Peak activity occurred a little later in the morning at high elevation (Table 1).

EXPOSURE TO SUN AND OPERATIVE TEMPERATURES

The availability of sunlit sites was somewhat higher at the lowland than at the montane site (72% vs 66% of models in full or filtered sun; $G = 4.6$, $df = 1$, $P = 0.032$). Similarly, overall operative temperatures were higher at low elevation ($\bar{x} = 36.3^\circ\text{C}$, $SD = 11.8$, $n = 448$) than at high elevation ($\bar{x} = 33.3^\circ\text{C}$, $SD = 13.1$, $n = 538$), and varied significantly with time of day (Fig. 1; two-way ANOVA; site: $F_{1, 974} = 28.4$, $P < 0.001$; time of day: $F_{5, 974} = 211.9$, $P < 0.001$; interaction: $F_{5, 974} = 1.1$, $P > 0.3$). However, the higher T_e s registered at low elevation did not merely result from greater exposure to sunlight, since T_e s were higher within all sun–shade categories (two-way ANOVA; site: $F_{1, 980} = 22.3$, $P < 0.001$; insolation: $F_{2, 980} = 434.0$, $P < 0.001$; interaction: $F_{2, 980} = 0.9$, $P > 0.3$).

SELECTED TEMPERATURES AND THERMAL HABITAT QUALITY

Lower and upper limits of T_{sel} , computed from the central 80% of all T_b s selected in the thermogradient, were 32.4 and 37.4°C , respectively. The median-selected T_b was 35.6°C and the interquartile range was 2.3°C ($n = 26$). In the field, elevation, time of day and an interaction between the two factors had a significant effect on the deviations of available T_e s from the selected range (Table 2: two-way ANOVA; site: $F_{1, 974} = 13.9$, $P < 0.001$; time of day: $F_{5, 974} = 26.7$, $P < 0.001$; interaction: $F_{5, 974} = 4.3$, $P < 0.001$). This result indicates that overall thermal quality was lower at the high altitude site, but that the lower morning T_e s at the montane site were partially compensated by smaller departures from T_{sel} at midday. The two sites

Table 1. Abundance of lizards (in number of individuals) at each study area: hourly mean, standard deviation (computed on the basis of four data points per hourly period and site, each one corresponding to the average of two replicated censuses), and maximum number of lizards seen during a 20-min survey of a 5-m wide transect

Hour (MET)	El Pardo (650 m)			Morcuera (1500 m)		
	\bar{x}	SD	Max.	\bar{x}	SD	Max.
700–800	2.50	1.83	6	3.38	2.29	8
800–900	5.50	2.04	9	7.13	1.97	11
900–1000	4.38	1.93	8	8.00	2.68	14
1000–1100	3.50	1.47	5	6.25	1.71	10
1100–1200	3.00	0.71	4	5.00	2.27	8
1200–1300	2.88	1.49	7	5.63	1.65	9
Overall	3.63	1.79		5.90	2.42	

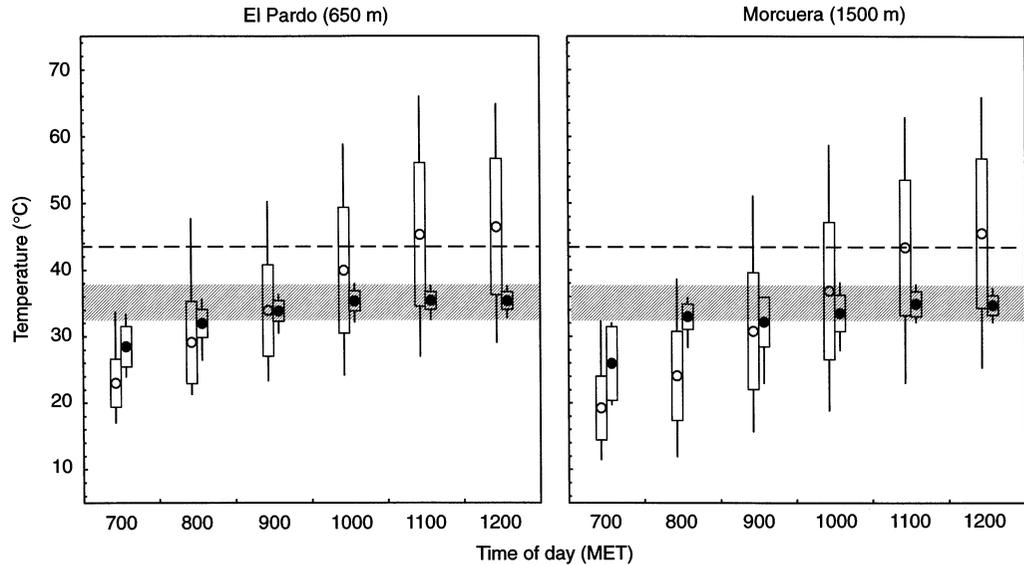


Fig. 1. Hourly variation (mean, standard deviation, range) of operative temperatures (T_e ; open symbols) and lizard body temperatures (T_b ; closed symbols) at low (left) and high elevation (right). The hatched area indicates the central 80% of all T_b s selected in a thermogradient (T_{sel}), the presumed target range for behavioural thermoregulation, and the dashed horizontal line shows the position of the critical thermal maximum (CT_{Max}). Sample sizes in Tables 2 and 3.

Table 2. Thermal quality of the habitat (\bar{d}_e , in °C: n , mean, SD) at the two study areas. See text for explanation

Hour	El Pardo (650 m)			Morcuera (1500 m)		
	n	\bar{d}_e	SD	n	\bar{d}_e	SD
700–800	73	9.4	3.59	90	13.2	4.80
800–900	75	5.3	3.40	90	8.7	6.13
900–1000	75	3.6	3.32	90	6.0	4.66
1000–1100	75	6.2	6.26	90	6.9	4.72
1100–1200	75	9.9	8.38	88	8.6	7.27
1200–1300	75	10.3	8.66	90	10.3	8.65
Overall	448	7.5	6.55	538	8.9	6.62

also differed in the percentages of T_e readings that fell below, within, and above T_{sel} (Fig. 2; $G = 6.3$, $df = 2$, $P < 0.05$). Although the proportion of readings within T_{sel} was similar at both sites ($G = 1.0$, $df = 1$, $P > 0.05$), a larger proportion of T_e s fell below T_{sel} at the montane site, and a higher proportion of T_e s fell above T_{sel} at the lowland site. Thus, the major thermal differences between the sites were: (1) a larger proportion of T_e s below the preferred range especially in the early morning at the high-altitude site, and (2) overall smaller absolute deviations from the preferred range throughout most of the morning hours at the low-altitude site.

The proportion of T_e readings that fell within the 80% thermal performance breadth for burst running speed (28.3–39.1 °C; see Bauwens *et al.* 1995; Fig. 2), a measure of the impact of the thermal environment on the predicted performance of lizards in an ecologically relevant task, differed between the sites (33.3% at low elevation vs 24.5% at high elevation; $G = 9.1$,

$df = 1$, $P < 0.005$). Thus, a slightly smaller fraction of hypothetical non-thermoregulating lizards would be able to run at 80% or more of their maximal speed at the montane site.

LIZARD BODY TEMPERATURES AND EXTENT OF THERMOREGULATION

Overall, body temperatures varied markedly with time of day at both sites and were lower at the high-altitude site (two-way ANOVA on data in Fig. 1: site: $F_{1, 140} = 7.0$, $P < 0.01$; time of day: $F_{5, 140} = 28.9$, $P < 0.001$; interaction: $F_{5, 140} = 1.9$, $P > 0.05$). Although this difference was maintained during five of the six morning hours, it was on average only 1.0 °C. The dispersion of T_b s around their mean was similar in both populations (Levene's test for homogeneity of variances: $F_{1, 150} = 0.02$, $P > 0.8$). However, T_b s were less variable than T_e s at both sites (Levene's test: $P < 0.001$ in both cases).

The accuracy of thermoregulation, or the correspondence of field-measured T_b s to T_{sel} (\bar{d}_b), increased through the day at both localities, and was marginally lower at high elevation (Table 3; two-way ANOVA; site: $F_{1, 140} = 4.6$, $P = 0.034$; time of day: $F_{5, 140} = 23.0$, $P < 0.001$; interaction: $F_{5, 140} = 1.8$, $P > 0.05$). Nevertheless, the proportions of T_b s that fell below, within, and above the preferred range were similar at both sites (Fig. 3; $G = 0.2$, $df = 2$, $P > 0.9$). Thus, similar fractions of the lizards had T_b s within the selected range at both sites; however, among those that did not, \bar{d}_b s were somewhat larger at the montane site (Table 3). The observation that \bar{d}_b s were smaller than \bar{d}_e s at both sites (El Pardo: $t = 9.7$, $df = 537$, $P < 0.001$; Morcuera: $t = 9.4$, $df = 597$, $P < 0.001$)

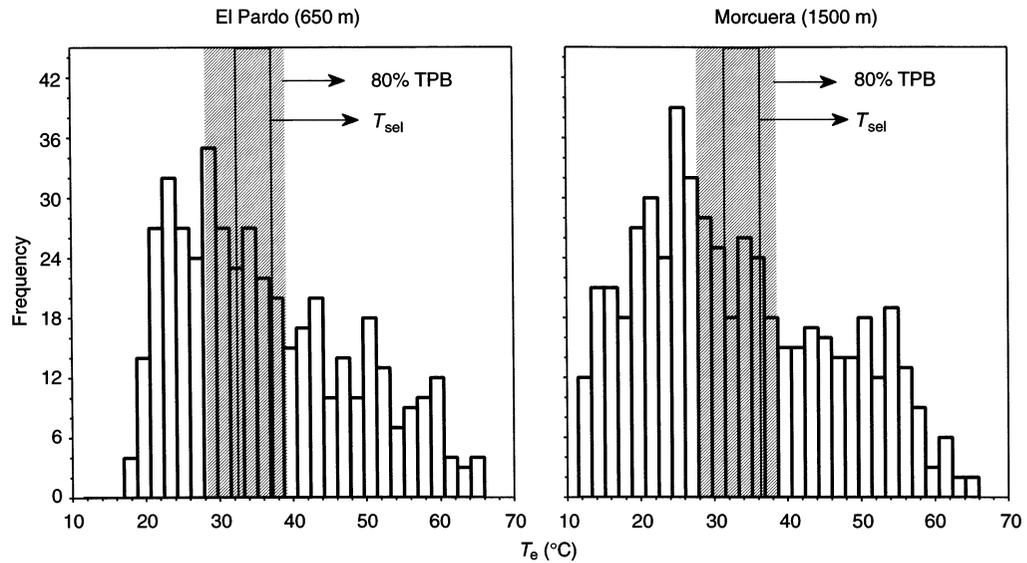


Fig. 2. Frequency distribution of operative temperatures (T_e) at low (left) and high elevation (right). Hatched area and vertical lines indicate the 80% thermal performance breadth for burst running speed and the central 80% of all T_b s selected in a thermogradient (T_{sel}), respectively.

Table 3. Accuracy of lizard thermoregulation (\bar{d}_b , in °C: n , mean, SD) at the two study sites. See text for explanation

Hour	El Pardo (650 m)			Morcuera (1500 m)		
	n	\bar{d}_b	SD	n	\bar{d}_b	SD
700–800	10	4.01	2.87	5	6.46	5.57
800–900	21	1.00	1.56	13	0.52	1.21
900–1000	13	0.17	0.53	8	1.17	3.32
1000–1100	17	0.06	0.15	11	0.63	1.37
1100–1200	14	0.01	0.05	8	0.08	0.15
1200–1300	16	0.01	0.03	16	0.03	0.07
Overall	91	0.71	1.71	61	0.92	2.63

provides unequivocal evidence of thermoregulation in the two populations.

The T_b measurements (Fig. 3) indicate that the vast majority of lizards would be able to run at 80% or more of their maximal capacity at both the low (85 of 91) and the high elevation sites (56 of 61; $G = 0.1$, $df = 1$, $P > 0.7$); no animal achieved a T_b exceeding 80% TPB at either site. Nevertheless, quantitative estimates of predicted sprint speeds (Table 4) were marginally higher at low elevation than at the montane site (two-way ANOVA: site: $F_{1, 140} = 4.0$, $P = 0.048$; time of day: $F_{5, 140} = 21.4$, $P < 0.001$; interaction: $F_{5, 140} = 1.8$, $P > 0.1$), largely because lizards captured at low elevation during the early warm-up period had higher, and less impairing, T_b s (Fig. 3).

In summary, geographic differences in body temperatures, accuracy of thermoregulation and running performance were much smaller than predicted on the basis of habitat thermal qualities. One would therefore predict that lizards at the montane site used thermoregulatory behaviours (e.g. the selection of sun–shade

patches) more explicitly. A log-linear model on the complete data set of lizard and model observations, classified according to study site, time of day and exposure to sun (Table 5; $G = 11.2$, $df = 20$, $P = 0.94$) included both a model-lizard \times hour \times sun–shade interaction (partial association: $G = 173.4$, $df = 5$, $P < 0.001$) and, more importantly, a model-lizard \times site \times sun–shade interaction (partial association: $G = 8.5$, $df = 1$, $P < 0.005$). The first interaction merely implies that the proportion of lizards in full or partial sun decreased with time of day, whereas the proportion of ‘basking’ models increased, so that at both sites the distribution of lizards was more selective early in the morning and in the heat of midday (Table 5). The second interaction suggests that the active selection of basking sites was, in fact, more pronounced at the montane site, where 71% of the lizards (vs 66% of the models) were in full or partial sun when first sighted. At the low altitude site, in contrast, 64% of the lizards (vs 72% of the models) were in a sunlit spot when first sighted (Table 5).

However, differences between sites in T_b , accuracy of thermoregulation and expected running performance, though smaller than expected by chance, were significant. As a consequence, no clear predictions could be made concerning the effectiveness of temperature regulation (extent to which T_b s are closer to preferred range than T_{es} : $E = 1 - (\bar{d}_b/\bar{d}_b)$). Estimated values of E were 0.905 and 0.897 for the lowland and montane sites, respectively. To test for differences in thermoregulatory effectiveness, the bootstrap procedure suggested by Hertz *et al.* (1993) was used, obtaining 1000 bootstrap resampling estimates per study area. The lowland site had a greater E -value only in 53.9% of the paired comparisons. Thus, the effectiveness of thermoregulation was similar at both sites.

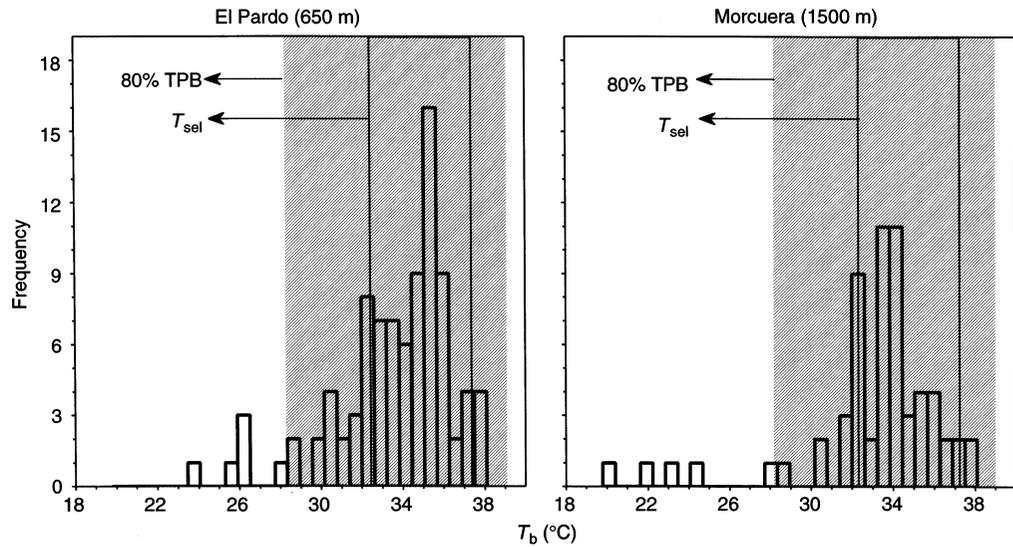


Fig. 3. Frequency distribution of lizard body temperatures (T_b) at low (left) and high elevation (right). See caption to Fig. 2 for details.

Table 4. Predicted maximal speed of lizards (cm s^{-1} ; n , mean, SD) at different hours at two sites. Maximal sprint speeds estimated with data on the thermal sensitivity of sprint speed (Spellerberg 1976; Bauwens *et al.* 1995) and T_b measurements (Fig. 3)

Hour (MET)	El Pardo (650 m)			Morcuera (1500 m)		
	n	\bar{x}	SD	n	\bar{x}	SD
700–800	10	192.7	28.3	5	169.2	52.3
800–900	21	222.8	15.8	13	228.6	12.9
900–1000	13	232.2	6.4	8	222.4	33.1
1000–1100	17	231.3	6.2	11	226.0	14.6
1100–1200	14	231.7	4.9	8	230.6	6.2
1200–1300	16	232.2	5.3	16	231.9	4.9
Overall	91	225.4	17.4	61	223.6	25.8

Table 5. Percentage of models and lizards in full or filtered sun

Hour (MET)	El Pardo (650 m)				Morcuera (1500 m)			
	Models		Lizards		Models		Lizards	
	%	n	%	n	%	n	%	n
700–800	45.2	73	96.5	29	36.7	90	90.0	30
800–900	58.7	75	85.3	61	58.9	90	90.8	65
900–1000	77.3	75	68.2	44	67.8	90	77.8	63
1000–1100	82.7	75	63.4	41	71.1	90	65.4	52
1100–1200	84.0	75	36.8	38	81.8	88	60.9	46
1200–1300	85.3	75	30.8	39	80.0	90	42.1	57
Overall	72.3	448	64.3	252	66.0	538	70.6	313

Discussion

The results indicate that lizards from the montane population did not entirely compensate for the limitations dictated by the lower thermal quality of their habitat. Nevertheless, lizards were more abundant at the montane site. The relevance of the observed altitudinal changes in the thermal environment to lizard thermoregulation is first evaluated, considering both

the behavioural aspects of temperature regulation (activity times, selection of sun–shade patches) and the resultant T_b s (Huey 1982). The focus is then placed on the unexpected result that thermal quality of the habitat was unrelated to lizard abundance, and some alternative hypotheses are discussed.

THERMAL QUALITY OF HABITATS AND LIZARD THERMOREGULATION

On average, operative temperatures deviated from lizards' selected range by absolute values ranging from 3.6 to 10.3 °C at low elevation, and from 6.0 to 13.2 °C at high elevation (hourly means for d_e). Tropical anoles compensate for similar altitudinal changes in the thermal environment by behavioural means (Huey & Webster 1976; Hertz 1981, 1992a; Hertz & Huey 1981; Hertz *et al.* 1993), shifting to more open habitats and increasing basking frequency at high elevations. Similarly, lizards in the montane population used sunlit patches more frequently than did low-altitude conspecifics, despite a lower availability of sunlit perches at the high-altitude site. This contrasts with other species of Lacertidae (*Podarcis tiliguerta* and *Lacerta vivipara*; Van Damme *et al.* 1989, 1990), that did not seem to compensate for thermal changes associated with altitude either behaviourally or physiologically. The data also show that the number of lizards seen per hourly period (Table 1) was weakly correlated with temporal variations in the thermal quality of their habitats (hourly averages for d_e : Table 2) at both low ($r = -0.800$, $P = 0.056$) and high elevation ($r = -0.831$, $P = 0.04$), suggesting that lizards from both populations were using patterns of daily activity as a behavioural device for temperature regulation (Heath 1964; Hertz 1981; Hertz & Huey 1981; Peterson 1987; Grant & Dunham 1988). Thus, lizards adjusted activity times

to take advantage of within-habitat changes in their thermal environment, whereas altitudinal differences were counterbalanced by different patterns of sun–shade use.

Altitudinal differences in habitat thermal quality also arise because deviations of T_e above and below T_{sel} may differ in their impact on physiological performance (Hertz *et al.* 1993). The $T_{b,s}$ selected by most lizards (and the associated plateau of physiologically ‘optimal’ temperatures) are generally located near the CT_{Max} or upper critical temperature (Huey 1982 & references therein; Huey & Kingsolver 1993). In *P. algirus*, for instance, the median preferred temperature (about 35.5 °C; Bauwens *et al.* 1995 and results of present study) is much closer to the critical thermal maximum (43.5 °C; Bauwens *et al.* 1995) than to the critical thermal minimum (7 °C; Spellerberg 1976). Accordingly, in this study there were fewer lizards with $T_{b,s}$ exceeding T_{sel} than with $T_{b,s}$ below T_{sel} . If deviations above or below the preferred range were weighted by their expected physiological effect, then the thermal quality of the habitat would be lower at the low-altitude site, where a larger fraction of models had temperatures above T_{sel} . However, positive departures from the preferred range (T_e in full sun > T_{sel}) may be compensated behaviourally (e.g. by seeking shelter in the shade) whereas negative differences (T_e in full sun < T_{sel}) cannot. Lizards from the montane population, for instance, could hardly compensate for thermal shortcomings in the early morning (0800–0900 h), when there were few perches in full sun (14.4%) and their temperature was low (mean $T_e = 22.8$ °C). Conversely, lizards in the low-altitude forest could maintain their temperatures within their preferred range, by shade seeking, even in the heat of midday (1200–1300 h; 14.4% of models in full shade, mean $T_e = 32.3$ °C). Thus, the apparent similarity in the proportion of T_e s within T_{sel} at the two sites may be misleading.

On the other hand, information on the thermal sensitivity of physiological performance may be more appropriate than T_{sel} to evaluate the thermal quality of a habitat (Huey 1991; Hertz *et al.* 1993). This is especially so because some lizards may have evolved negative correlations between thermal performance breadth and the width of the selected temperature range which is, in fact, the target of regulatory behaviours. For example, Bauwens *et al.* (1995) have shown that lacertid species with high sprint abilities (including *P. algirus*) combine reduced thermal sensitivity (i.e. a wide TPB) with fairly precise temperature regulation (i.e. a narrow selected range). It seems therefore inappropriate to base estimates of environmental thermal quality only on selected ranges, without considering thermal performance curves (Huey & Stevenson 1979; Huey & Kingsolver 1989, 1993; Hertz *et al.* 1993). For the populations studied herein, the proportions of T_e s within preferred ranges were similar at the two sites, whereas the proportion of T_e s

within 80% TPB for running performance was larger at the lowland site. Thus, strictly physiological issues are relevant to a quantitative estimate of the thermal quality of an ectotherm’s habitat (see also Huey 1991).

To what extent did behavioural adjustments compensate for altitudinal changes in the thermal quality of habitats? According to the data on $T_{b,s}$, lizards had lower temperatures at the montane site, though differences were small and had only a minor (but significant) effect on both the accuracy of thermoregulation (Table 3) and the expected running performance of active animals (Table 4). Hence, the overall effectiveness of temperature regulation was similar at the two study areas. In both cases the E -values were higher than those reported for six *Anolis* populations in Puerto Rico (see Table 3 in Hertz *et al.* 1993), confirming that temperate lacertids are more effective thermoregulators than tropical anoles (although $d_{e,s}$ were also greater for the anoles). Thus, changes in the thermal quality of habitats seemed to be relevant to lizards because (1) they were associated with a behavioural shift towards a more selective use of sunlit patches, in spite of which (2) body temperatures and the extent to which they corresponded to T_{sel} decreased significantly with increasing altitude.

LIZARD ABUNDANCE AND THERMAL QUALITY OF HABITATS

The number of lizards observed during the transect counts was highest at the montane site. It is assumed that this disparity reflects a difference in lizard abundance rather than in lizard visibility. This is supported by two lines of evidence. First, detectability of lizards was similar at the two study areas, as judged by mean approach distances, that were measured during preliminary transects (El Pardo: $\bar{x} \pm SD = 110 \pm 47$ cm, $n = 22$; Morcuera: 96 ± 36 cm, $n = 31$; Mann–Whitney’s $U = 279$, $P > 0.2$). Second, lizards at the montane site tended to hide in the leaf litter layer (see below), where they could hardly be seen. This might have reduced their visibility and, if anything, produced an underestimate of the actual between-sites difference in abundance. Therefore, it is certain that lizards attained higher densities at the montane site. The observed abundances were, in fact, very similar to those recorded in a previous survey of the same areas (Díaz & Carrascal 1991), thus confirming the temporal constancy of the between-sites difference in lizard population densities.

However, the thermal quality of the habitat was higher at the low-altitude site. This implies that the thermal properties of the environment are not the only determinants of regional-scale variations in lizard abundance. Moreover, the measures of thermal quality are for the warmest season of year. Hence, the thermal quality of the montane site, measured over a full year, should be substantially less than that of the lowland site. If so, this would reinforce the finding that

habitat thermal quality does not readily predict abundance in this species. Of course, thermal constraints may determine reptilian distribution patterns on larger spatial scales; several authors (e.g. Morris 1987; Wiens 1989) have noted that different determinants of habitat preferences may operate at different spatial scales. Thus, the thermal properties of the montane site were not bad enough to have a big effect on overall habitat quality; however, thermal effects perhaps may be more important at higher elevations and at the northern limit of the species' range.

What alternative hypotheses might explain the higher population densities reached by *P. algirus* at the high-altitude site? First, altitudinal changes in the thermal environment may be associated with opposite selection pressures, such as reduced predation or increased food availability. Prey were actually more abundant at the highland forest ($\bar{x} = 2.1$ arthropods larger than 3 mm per 625 cm² of ground surface vs $\bar{x} = 0.8$ at the lowland site; Mann-Whitney's $U = 620.5$, $n = 50$ in both cases, $P < 0.001$), according to counts done in the context of a larger scale study (Díaz & Carrascal 1991) which showed that prey availability has a significant effect on the abundance of *P. algirus*. Because high T_b s promote foraging success (Avery, Bedford & Newcombe 1982; Van Damme, Bauwens & Verheyen 1991; Díaz 1994b), an increase in the abundance of food will raise the benefits of careful thermoregulation (Huey & Slatkin 1976) by enhancing the opportunities for growth (Brett 1971; Crowder & Magnuson 1983; Avery 1984). Thus, lizards at high elevations could profit more from abundant food resources and, at the same time, try to regulate their T_b with the same effectiveness as their lowland conspecifics.

Although there are no data about predation intensity under field conditions at either site, different escape behaviours were observed at the two study areas. When pursued, lizards in the montane site sought shelter in the leaf litter layer, where they could immediately run out of view. In the lowland forest, however, lizards could not hide into the thin layer of hard, spiny holm-oak leaves. Instead, they sought refuge in holm-oak shrubs (Díaz 1992) where they were easy to capture by humans, and perhaps other predators. In fact, the number of lizards captured for this study was larger at the lowland area, despite its less dense lizard population and the larger amount of time invested in chasing animals at the high-elevation site. The observed shift in escape tactics is similar to those documented by previous researchers who found compensatory behaviours associated with changes in ecological pressures and/or the physiological condition of individuals (Bauwens & Thoen 1981; Hertz, Huey & Nevo 1982; Crowley & Pietruszka 1983; Snell *et al.* 1988).

An extension of the above argument suggests that lizards might actually reach higher densities at high altitude and/or northern areas where, despite cooler thermal conditions, predators are rarer or less diverse.

Thus, *Podarcis tiliguerta* in Corsica occurs at higher densities at a cold montane site, apparently with fewer predators, than at a thermally more favourable lowland site (Van Damme *et al.* 1989). Similarly, *Lacerta vivipara* in northern Europe seems to reach population densities (Bauwens, Heulin & Pilorge 1986) that are unsurpassed by those of other ground-dwelling lacertids from the more diversified saurian faunas in the southern Mediterranean peninsulas (D. Bauwens, personal communication). Although further research is clearly needed, results of this study challenge the uncritical view that ectotherms, with their 'low energy approach' to life (Pough 1980), should always achieve higher densities in thermally more suitable environments.

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