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ARTICLE

Thermoregulation in a cold-adapted species (Cyren's Rock Lizard, *Iberolacerta cyreni*): influence of thermal environment and associated costs

S. Aguado and F. Braña

Abstract: Thermal constraints may limit the physiology and behaviour of ectotherms because of the high thermal dependence of metabolic functions. The adaptive mechanisms of thermoregulation and the cost of confronting thermal constraints were studied in the Cyren's Rock Lizard (*Iberolacerta cyreni* (Müller and Hellmich, 1937)), a lacertid lizard endemic to mountain areas of central Spain. Semicontinuous monitoring of body temperature (T_b) in the laboratory indicated that the preferred temperature range for this population (T_{pref}) was lower than those found for most lacertid lizards, and field body temperatures of active animals in summer were even lower than T_{pref}. Overall these results, together with distribution of field operative temperatures (T_e), indicate that *I. cyreni* is an active and relatively accurate thermoregulator, although limited by thermal constraints in their habitat. Laboratory experiments in contrasting thermal environments showed that even under thermally restricted conditions, lizards achieved their T_{pref} by modifying their thermoregulatory behaviour, principally through changes in space use, basking time, and body posture. However, these behavioural adjustments to reach the T_{pref} have associated costs, and lizards spent 80% of their time in thermoregulation when tested under low radiation conditions, which in the wild would limit the scope for other activities and eventually increase predation risk. Our results suggest that thermoregulatory behaviour may play an important role in coping with global climate change, hence predictions of the effects of climate warming on lizards inhabiting cold habitats should take into account the buffering role of behavioural thermoregulation.

Key words: dual-threshold thermoregulation, Cyren's Rock Lizard, *Iberolacerta cyreni*, thermal constraints, thermoregulatory behavioural adjustments.

Résumé : Comme les fonctions métaboliques dépendent fortement de la température, des contraintes thermiques pourraient limiter la physiologie et le comportement des ectothermes. Les mécanismes adaptatifs de thermorégulation et le coût des ajustements en réaction à des contraintes thermiques ont été étudiés chez le lézard montagnard ibérique *Iberolacerta cyreni* (Müller et Hellmich, 1937), un lézard lacertidé endémique des régions montagneuses du centre de l'Espagne. La surveillance semi-continue de la température corporelle (T_b) en laboratoire indique que l'écart de température préférée de cette population (T_{pref}) est moindre que celles de la plupart des lézards lacertidés, et les températures corporelles d'animaux actifs mesurées sur le terrain en été étaient encore moindre que T_{pref}. Globalement, ces résultats, combinés à la distribution des températures opératives (T_e), indiquent que *I. cyreni* présente une thermorégulation active et assez précise, bien que limitée par des contraintes thermiques dans son habitat. Des expériences en laboratoire qui comparent des milieux thermiques ont démontré que, même dans des conditions de restriction thermique normales, les lézards atteignaient leur T_{pref} en modifiant leur comportement de thermorégulation, principalement par des changements d'utilisation de l'espace, du temps passé à lézarder et de la posture du corps. Il y a toutefois des coûts associés à ces ajustements comportementaux permettant d'atteindre la T_{pref}, et les lézards vouaient 80 % de leur temps à la thermorégulation dans le cadre d'essais dans des conditions de faible rayonnement, ce qui, dans la nature, limiterait la possibilité d'autres activités et, à terme, accroîtrait le risque de prédation. Nos résultats portent à croire que le comportement de thermorégulation pourrait jouer un important rôle dans l'adaptation aux changements climatiques planétaires et donc, que les prévisions des effets du réchauffement climatique sur les lézards vivant dans des habitats froids devraient tenir compte du rôle de tampon que joue la thermorégulation comportementale. [Traduit par la Rédaction]

Mots-clés : thermorégulation à deux seuils, lézard montagnard ibérique, *Iberolacerta cyreni*, contraintes thermiques, ajustements des comportements thermorégulateurs.

Introduction

Temperature is one of the most important ecophysiological factors influencing the biology of ectothermic animals because their metabolic functions generally show high thermal dependence (Angilletta 2009), and therefore, thermoregulation is of great importance in coping with the thermal fluctuations of the environment. Many reptiles use physiological and behavioural mechanisms to regulate their temperature in heterogeneous thermal environments, and minimize body temperature fluctuations outside the optimal range to overcome thermal constraints on functional performance (Huey 1982; Stevenson 1985*b*). Behavioural mechanisms include shuttling between sun and shade patches, selection of thermally suitable microhabitats, modification of body postures to maximize heat exchange, and regulation of activity times (Cowles and Bogert 1944; Bauwens et al. 1996). Moreover, body temperature can be modified by physiological adjust-

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ments such as variation in metabolic rate or in cardiovascular rate (Seebacher and Franklin 2005; Brown and Au 2009), and can also be affected by individual characteristics such as body size (Stevenson 1985*a*) or colour (e.g., melanism: Clusella-Trullas et al. 2009).

In mountainous areas, which are typically cold, lizards must confront severe thermal constraints to reach their preferred temperatures and, frequently, meeting their biological requirements has higher costs (Gvoždík 2002; Amat et al. 2003). Consequently, climate imposes restrictions on the spatial distribution of organisms at the edges of their distribution ranges, which are likely to change as a consequence of global warming (Huey et al. 2009; Sinervo et al. 2010). The consequences of the global climate change may be more important for lizards in mountain areas (Shine et al. 2002), and might determine the modification of distribution limits, or even bring about extinction, for species without the behavioural plasticity or evolutionary mechanisms necessary to buffer climate warming at local or global scales (Angilletta 2009). Studying the thermal biology of cold-adapted species near their upper elevational limits will contribute to understanding the implications that global climate change could have on the future distribution of these species. The endemic Iberian genus *Iberolacerta* Arribas, 1997 contains a number of species adapted to cold climates that were preserved in isolated habitats in glacial refugia during the Quaternary climate oscillations (Carranza et al. 2004; Crochet et al. 2004). We used the montane species Cyren's Rock Lizard (*Iberolacerta cyreni* (Müller and Hellmich, 1937)) as a model organism to study thermoregulation in cold environments and to envisage how these organisms might respond to future climate change.

Body temperature of lizards depends on the interaction between the thermal environment and the species' thermoregulatory capacities, thus we combined field data and thermal preferences in the laboratory to study thermoregulation of *I. cyreni*. In contrast to most homeotherms, reptiles do not usually have one single optimal body temperature, but rather a narrow range at which physiological and behavioural processes perform at near maximal capacity (Cowles and Bogert 1944; Angilletta et al. 2002) that usually correspond with their preferred temperatures (Huey 1982; for sprint speed see Van Berkum et al. 1986 and Bauwens et al. 1995). We therefore tested whether *I. cyreni* thermoregulate according to a dual set-point threshold model, which predicts that body temperature should fluctuate between an upper and a lower limit rather than being concentrated around a central value (Barber and Crawford 1977; for lacertid lizards see Tosini et al. 1995). Taylor et al. (2004) showed that under this model, semicontinuous sampling provides a better estimate of the thermal profiles of reptiles than point-sampling and therefore body temperatures of individual lizards in the laboratory were monitored in a semicontinuous manner to evaluate the thermal profiles of *I. cyreni*. In addition, to evaluate the possible thermal constraints imposed by their natural environment, the quality of the thermal habitat and the accuracy of thermoregulation in the field were measured simultaneously, following the protocol proposed by Hertz et al. (1993), and compared with the preferred temperatures determined in the laboratory. Furthermore, we studied the thermoregulatory strategies adopted by lizards in contrasted thermal conditions in the laboratory to test two hypotheses: (1) under unfavourable thermal conditions, lizards should adopt a strategy of thermoconformity that is in line with the predictions of the cost–benefit model of thermoregulation (Huey and Slatkin 1976), and (2) in unfavourable environments, lizards should develop physiological and behavioural adjustments to reach their preferred range by increasing efficiency of thermoregulation as has been described for other species (Blouin-Demers and Nadeau 2005; Besson and Cree 2010). Comparing the behavioural thermoregulatory response in contrasted environments will allow a better understanding of the thermoregulatory strategy and the mechanisms involved.

Materials and methods

Species and study area

Iberolacerta cyreni is a diurnal insectivorous mountain lizard endemic to the Sistema Central (Spain), where the species inhabits high altitudes (between 1700 and 2350 m above sea level) and is strongly linked to large rock outcrops and mixed bush (Martín and Salvador 1997; Monasterio et al. 2009). *Iberolacerta cyreni* is a medium-sized lizard with no sexual size dimorphism; mean (±SD) snout–vent length (SVL) of the individuals in our sample was 67.67 ± 6.18 mm and mean (±SD) body mass was 7.72 ± 1.94 g.

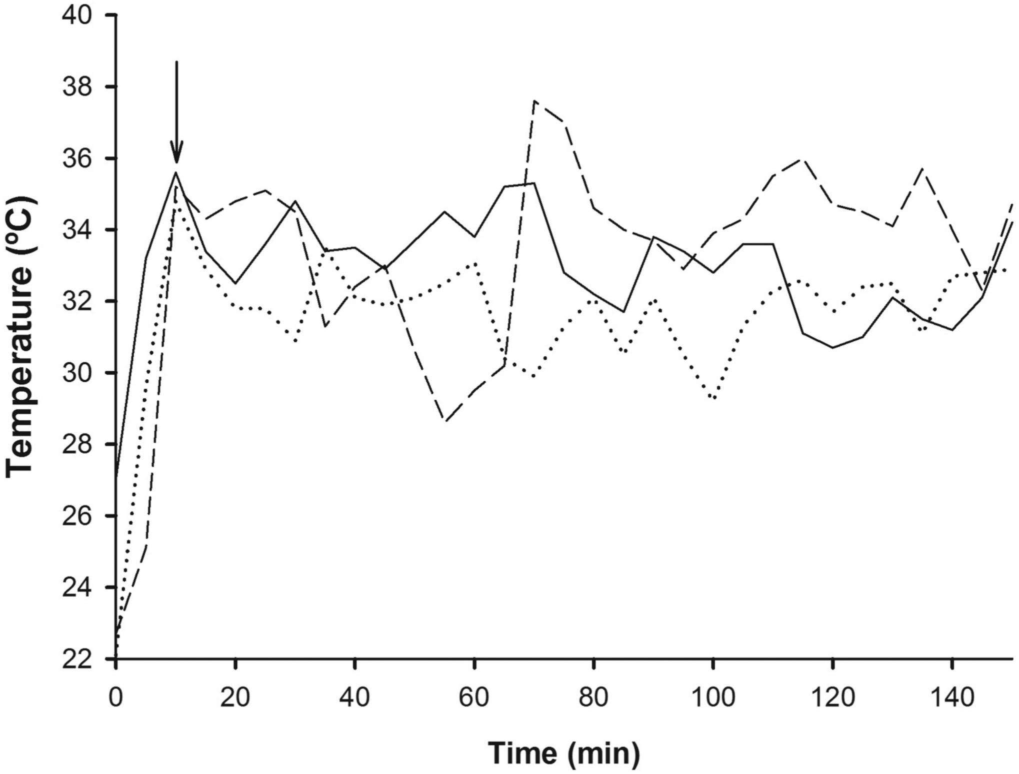
Lizards were captured by noose in the Sierra de Guadarrama (Sistema Central, Spain; between 1800 and 2000 m above sea level), between May and June each year from 2010 to 2012, with permission of the environmental authorities of the Madrid Community (reference Nos. 10/171227.9/10, 10/142717.9/11, 10/188097.9/12), and taken to the Zoology laboratory of Oviedo University. They were housed at room temperature (25.7 ± 1.1 °C during daylight hours) with natural photoperiod in plastic terraria (52.5 cm long × 39 cm wide × 27.5 cm high) with potting soil as substrate and several shelters; food (crickets and mealworms) and water were provided ad libitum. Basking opportunities were given by 50 W halogen bulbs, in a daily cycle from the hours of 0900 to 1900 with a switch off interval from the hours of 1300 to 1500 to simulate the field activity cycle in the natural population. Lizards were sexed, weighed to the nearest 0.001 g, and measured (SVL) with a digital caliper to the nearest 0.01 mm. All individuals were released at the site of capture after the experiments finished.

Preferred body temperatures

To test whether *I. cyreni* followed the "dual set-point threshold model" of thermoregulation and to study the preferred body temperature of the lizards, we established temperature gradients in plastic terraria (65 cm long × 43 cm wide × 26 cm high) in the laboratory using 100 W incandescent bulbs (1340 lm; FBrigth) suspended (8 cm) above the substrate. To consider these measurements to be the preferred body temperatures of lizards, environmental stimuli (food, water, refuges, and predators) were eliminated and the experimental setup was designed to provide environmental temperatures that widely exceed selected temperatures previously reported for various lacertid lizards (Bauwens et al. 1995). The available temperature gradient ranged from 27.0 to 43.5 °C, estimated through the equilibrium temperature of copper models positioned at different points in the terraria (Grant and Dunham 1988; Hertz et al. 1993). Models were made from hollow copper cylinders (7 cm long × 1 cm internal diameter) painted to match the colour of the lizards, the ends of which were sealed with plastic plugs. Body temperatures of lizards ($n = 69$) were monitored individually by a flexible thermocouple probe (type T) inserted approximately 10 mm into the cloaca, fixed with adhesive tape at the tail base, and connected to an electronic thermometer (TESTO 925; TESTO, Lenzkirch, Germany). The body temperature of the lizards (to the nearest 0.1 °C) was recorded every 5 min for 2.5 h.

For each lizard, we computed the mean preferred temperature, the preferred temperature range (defined as that which includes the central 80% of all body temperature measurements for each individual; Bauwens et al. 1995), and the maximal range of temperature (calculated as the difference between the maximal and the minimal temperature measured for each animal). Then the mean value for all lizards was calculated to determine the mean population preferred temperature (T_p) and the mean preferred range for the population (T_{pref}). Lizards were tested in the morning after being in their retreats overnight; they tended to reach almost the maximal temperature of their preferred ranges very

Fig. 1. Thermal profiles of body temperatures of three representative Cyren's Rock Lizards (*Iberolacerta cyreni*) recorded every 5 min in a thermal gradient in the laboratory. The vertical arrow represents the first temperature peak; only data after the arrow were used to compute the thermal variables.



quickly at the beginning of the experiment (see Fig. 1), thus only data from after the first temperature peak were considered in calculating thermal variables to guarantee that the lizards were thermoregulating freely and had available the preferred range.

Field temperatures

Field body temperatures (T_b) of lizards and operative temperatures (T_e) in the field were simultaneously measured over three consecutive sunny days in summer (June 2012). Body temperatures of lizards active on the surface (n = 52) were measured, within 10 s of capture, through a flexible thermocouple probe connected to an electronic thermometer (described above). To obtain a profile of the temperatures expected under a null model of no active temperature regulation (Hertz et al. 1993), we used 26 copper models (as described above) to measure the T_e. Models, with a thermocouple inserted approximately 10 mm, were evenly distributed across the natural habitat, being placed in different microhabitats that might potentially be used by lizards, including different types of substrates (rock, grass, or ground) or areas with different exposure to the sun's radiation (exposed, shaded, or filtered). Operative temperatures were registered hourly from 0800 to 2000 and a mean environmental temperature was calculated for each hour.

Precision of thermoregulation was measured through several indices proposed by Hertz et al. (1993). Thermal quality of the habitat (d_e) was calculated as the mean of the absolute deviations of T_e from the nearest limit of T_{pref}. Values within the preferred interval were computed as 0, such that a lower value of d_e indicates a habitat of higher thermal quality. We calculated accuracy of thermoregulation (d_b) analogously as the mean of absolute deviations of T_b from the nearest limit of T_{pref}, meaning that lower values of d_b indicate higher accuracy of thermoregulation. To evaluate the effectiveness of thermoregulation, we used the index of Blouin-Demers and Weatherhead (2001), computed as $d_e - d_b$: positive values of $d_e - d_b$ representing active thermoregulation; a value of 0 representing thermoconformity; and negative values representing avoidance of favourable thermal environments.

Thermal response and thermoregulatory behaviour in contrasted thermal environments

To evaluate the thermal response and thermoregulatory behaviour in contrasted environments, an incandescent light bulb of a specific power was suspended 8 cm above the substrate in one end of each terrarium to provide three different levels of thermal radiation: high (100 W bulb), medium (60 W bulb), and low (40 W bulb). The T_e associated with each level were measured using 10 copper models in different positions in the terraria for each radiation level. The mean T_e in the three thermal radiation levels relates to the previously calculated limits of preferred temperature range of lizards as follows: the mean T_e in the high radiation level was close to the upper limit of T_{pref}; the mean T_e in the medium radiation level was above the lower limit of T_{pref}; and the mean T_e in the low radiation level was below the lower limit of T_{pref}. Ten lizards were individually tested in each radiation level in a random order and body temperatures were recorded every 5 min. Thermal indices of thermal quality and accuracy were calculated in the same way as in the field to make comparisons between the three thermal levels, while the thermal response of the lizards was calculated as described above for preferred temperatures in the laboratory.

The position in the terrarium and body posture of each lizard were recorded at 5 min intervals. We assessed the position of lizards in the thermal gradient by dividing the terrarium into three equal zones with respect to their proximity to the heat source, namely, hot, warm, and cold zones. Body postures of lizards were roughly divided into thermoregulatory postures, indicating heat acquisition, either by heliothermy (i.e., body flattened and oriented towards the heat source) or thigmothermy (i.e., body prostrated on the substrate) (Carrascal et al. 1992; Bauwens et al.

1996); no explicit thermoregulatory posture (i.e., head up and body not bent or oriented to the heat source) and others (e.g., moving). For each individual lizard, body posture and time spent in each thermal zone were analysed as the number of time intervals where each posture and position were observed, and in addition, for each radiation level (high, medium, and low), the number of time intervals in which body temperature increased or decreased (heating and cooling processes, respectively) was also calculated.

Statistical analyses

Preliminary analyses showed that there were no differences between the sexes in thermal variables in the thermal gradient laboratory trial, hence sex was not considered in subsequent analyses, except for field body temperatures, because of the possibility that males and females might select different basking sites. In this case, sexual differences in field body temperature were tested using a one-factor analysis of variance (ANOVA). The effect of body size on temperature variables and thermal rates in the laboratory was tested by carrying out correlation analyses between thermal variables and SVL. In the experiment of contrasted thermal environments, the differences in mean body temperature between thermal radiation levels were analysed by Friedman's nonparametric ANOVA followed by a posteriori sign test. Differences in the thermal indices between radiation levels were tested using Kruskal–Wallis tests. To examine the effect of radiation level on lizard thermoregulatory behaviour, position was analysed with a repeated-measures ANOVA, with thermal radiation level as within-subject factor (three levels: high, medium, and low), while body posture was analysed by a Friedman's test with an a posteriori sign test because the data did not meet the assumptions for parametric analyses. Time (number of intervals) spent in each thermal process (heating or cooling) at the different levels of thermal radiation was analysed by repeated-measures ANOVA, with thermal process (heating or cooling) and thermal radiation level as within-subject factors.

Thermal variables were checked for normality (Shapiro–Wilk's test) and homoscedasticity and transformed where necessary prior to applying parametric analyses. We also tested the sphericity assumption in repeated-measures ANOVAs using a multivariate test when this assumption was not met. Box–Cox transformation was used with SVL in correlation analyses, while heating and cooling rates were log-transformed. The significance level for all tests was set at $\alpha = 0.05$. All statistical analyses were conducted using STATISTICA software version 8.0 (StatSoft Inc., Tulsa, Oklahoma, USA).

Results

Preferred body temperatures

Body temperatures of lizards tested in the thermal gradient were neither stable nor concentrated in the central values of the range, but rather oscillated continuously (Fig. 1). The mean (±SD) T_p was 32.9 ± 1.1 °C ($n = 69$); T_{pref} in the thermal gradient experiment ranged from 30.6 ± 1.3 to 35.1 ± 1.1 °C (mean ± SD) (Fig. 2A). Semicontinuous monitoring of body temperatures enabled the analysis of the relationship between thermal variables and body size. The maximal range of temperature exhibited a significant negative relationship with SVL ($r = -0.29$, $P = 0.018$), as well as heating rate (°C/min), calculated as the largest increase in temperature in a single 5 min interval ($r = -0.26$, $P = 0.031$). On the other hand, cooling rate (°C/min), calculated as the largest decrease in temperature in a single interval, did not present significant correlation with SVL, although the trend was also negative ($r = -0.18$, $P = 0.15$).

Field temperatures

Body temperature of adult *I. cyreni* in the field was 30.8 ± 2.3 °C (mean ± SD), with no difference between sexes ($F_{[1,50]} = 0.001$, $P = 0.97$). Thermoregulatory accuracy in the field was only moderately high ($d_b = 0.78$), with body temperatures being below the lower limit of T_{pref} in 46.15% of cases (Fig. 2B). Operative temperatures depended on time of day (Kruskal–Wallis ANOVA, $H_{[11,728]} = 213.53$, $P < 0.00001$), with lower values being recorded in the early and final hours of the day and higher values in the central hours; thermal quality of the habitat was low ($d_e = 5.98$), with only 16.21% of T_e within T_{pref} (Fig. 2C, but for distributions of T_b and T_e see Fig. 3). Finally, the effectiveness of the thermoregulation index ($d_e - d_b$) had a positive value (5.2), indicating that *I. cyreni* exhibit active thermoregulation in the field. The number of active lizards was low in the first and final hours of the day, when T_b were below T_{pref}, as well as in the central hours of the day (from 1230 to 1530), when T_e exceeded T_{pref} (Fig. 3).

Thermoregulatory response and thermoregulatory behaviour in contrasted thermal environments

Thermoregulatory response

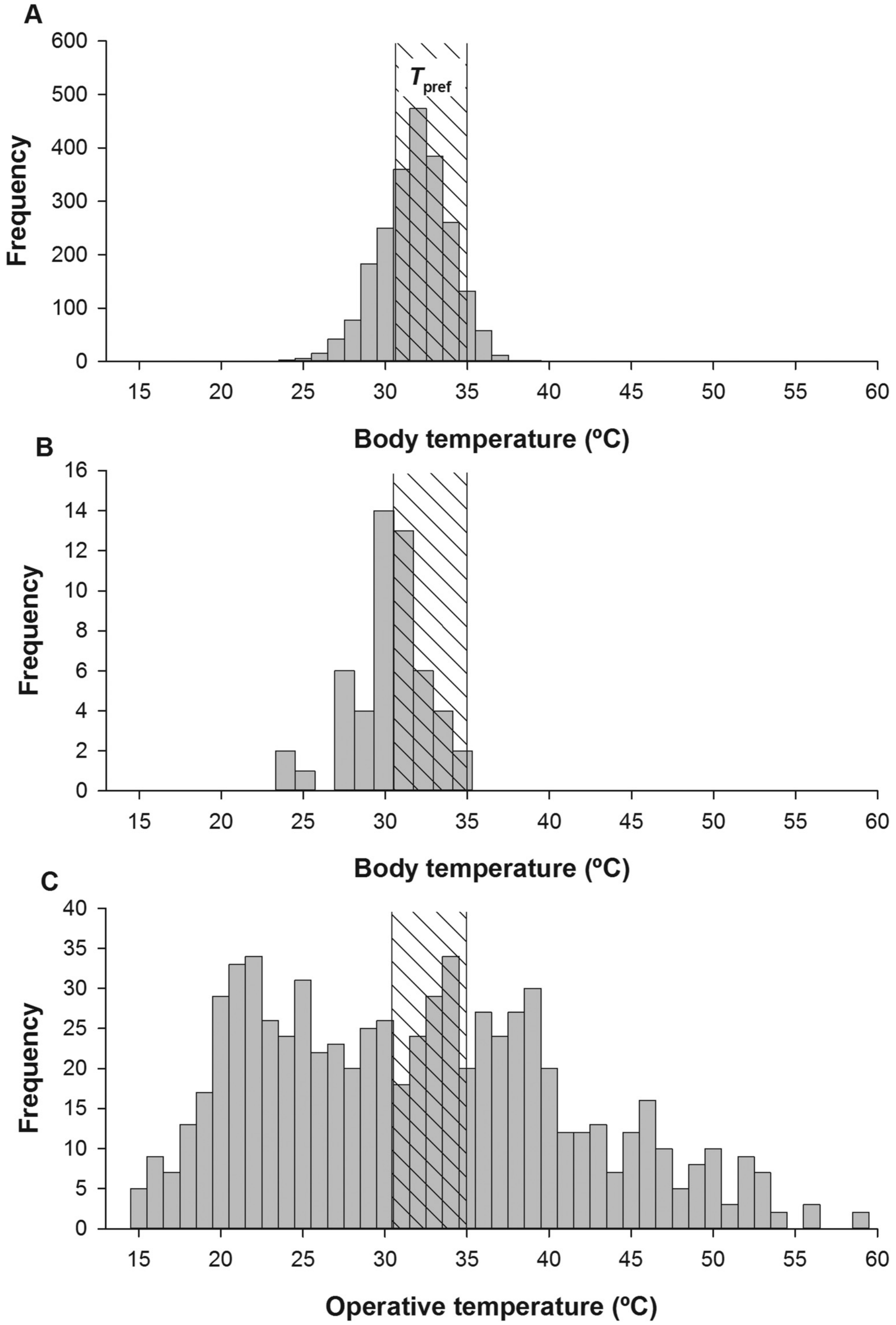
Mean body temperature of lizards in the laboratory thermal gradients presented significant differences between thermal radiation levels (Friedman's test, $Z = 13.50$, $P = 0.001$), being significantly lower for the low radiation level than for the medium radiation level (sign test, $Z = 3.25$, $P = 0.0010$) or the high radiation level (sign test, $Z = 2.25$, $P = 0.024$), and the mean in the low level was always in the lower half of T_{pref} (Fig. 4). Maximal range of temperature did not show significant differences between thermal radiation levels ($F_{[2,18]} = 1.35$, $P = 0.28$), and neither did heating rate ($F_{[2,18]} = 1.78$, $P = 0.20$) nor cooling rate ($F_{[2,18]} = 0.74$, $P = 0.50$).

Lizards had active thermoregulation at all levels of radiation ($d_e - d_b$: high = 3.66, medium = 2.49, low = 2.43). Radiation levels presented significant differences in thermal quality (Kruskal–Wallis test, $H_{[2,808]} = 48.60$, $P < 0.0001$) whereby the high level of radiation exhibited significantly lower thermal quality compared with the other levels (Mann–Whitney *U* test, $P < 0.0001$ in both cases) (d_e: high = 3.99, medium = 2.73, low = 2.62), mainly because T_e in the high level were above the upper limit of the preferred range of lizards more often than in the other levels. Accuracy of thermoregulation also differed between radiation levels ($H_{[2,1082]} = 13.13$, $P < 0.01$), with higher accuracy being found in the low radiation level (d_b: high = 0.33, medium = 0.23, low = 0.19). Effectiveness of thermoregulation presented significant differences between levels of radiation ($H_{[2,1082]} = 41.21$; $P < 0.0001$), with thermoregulation being more effective in the high level with respect to the other levels (Mann–Whitney *U* test, $P < 0.0001$ in both cases).

Thermoregulatory behaviour

Lizards showed significant differences between radiation levels in the time spent (number of intervals) in the hot zone ($F_{[2,18]} = 35.00$, $P < 0.0001$). Under the low level of radiation, lizards spent significantly more time thermoregulating in the hot zone than at the high level of radiation (80% vs. 15%; $P < 0.01$), and marginal differences were also found between the low and the medium levels ($P = 0.059$) (Fig. 5). There were also significant differences in the time lizards remained in each body posture (Friedman's test, $Z = 37.84$, $P < 0.0001$), specifically at the low level of thermal radiation where they spent significantly more time in thermoregulatory postures than in non-thermoregulatory postures (62% vs. 25%; $P = 0.045$). Additionally, time spent cooling and heating at each radiation level was analysed over the whole experimental period and a significant effect of the interaction between thermal radiation level and thermal process was found (Wilks' $\lambda = 2.27$, $F_{[2,8]} = 10.66$, $P = 0.006$), as well as a marginal effect of thermal process (Wilks' $\lambda = 2.70$, $F_{[1,8]} = 3.77$, $P = 0.084$). Lizards spent more time in cooling processes in the medium and high levels of radiation, while lizards under low levels of radiation spent more time in heating processes.

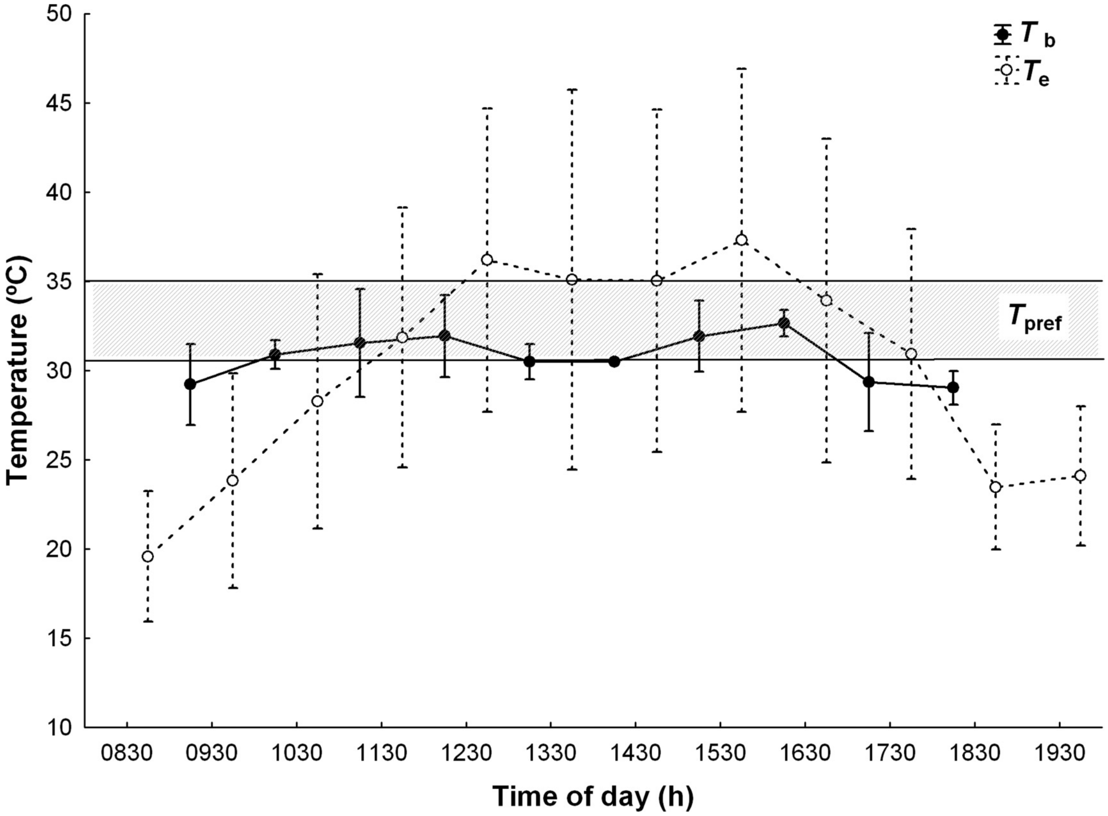
Fig. 2. Body temperatures of the Cyren's Rock Lizard (*Iberolacerta cyreni*). (A) Frequency of body temperatures in a thermal gradient in the laboratory for all lizards tested. (B) Frequency of field body temperatures (T_b). (C) Frequency of operative temperatures (T_e) in the field. In all cases, T_{pref} (shaded, hatched zone) represents the mean preferred temperature range for this population in the thermal gradient, defined as the range that includes the central 80% of all T_b values.



Discussion

Our experimental study indicates that the T_b of *I. cyreni* is not concentrated around one particular central value but continuously oscillates between two limits of a relatively wide range, as expected from the dual set-point threshold model of lizard thermoregulation (Barber and Crawford 1977; Kingsbury 1993). Furthermore, body size influences temperature oscillation such that small individuals, even with the same mean temperature, present a wider maximal range of T_b and faster heating rates than bigger lizards, as expected from the fact that heat loss and gain are negatively related with body size (Stevenson 1985*a*; Seebacher and Shine 2004). This implies that small lizards should have more frequent but

Fig. 3. Mean operative temperatures (T_e, open circles) and field body temperatures (T_b, solid circles) in the natural habitat of the Cyren's Rock Lizard (*Iberolacerta cyreni*) throughout the day. T_{pref} (shaded, hatched zone) represents the population mean preferred temperature range determined in the thermal gradient in the laboratory. Bars denote SD values.



shorter basking pulses to maintain their temperature within the same preferred range as larger lizards.

Field data indicate that *I. cyreni* is an active thermoregulator living in a low thermal quality habitat, and has moderate thermoregulatory accuracy probably because of the considerable fluctuation in T_e throughout the day in the study area. *Iberolacerta cyreni* showed a bimodal activity pattern, which has been reported for other diurnal heliothermic lizards (Huey et al. 1977; Braña 1991; Castilla and Bauwens 1991): during the central hours of the day, most lizards hid in rock crevices or bushes, thereby avoiding predation risk, where the high environmental temperatures probably allowed them to maintain near optimal temperatures (Bauwens et al. 1996). *Iberolacerta cyreni* is able to maintain T_b in the field that are close to its preferred range during most daylight hours in summer, even in the challenging weather conditions characteristic of mountain environments, with T_e surpassing both the upper and the lower limits of T_{pref} within a single day. The mean temperature selected in the laboratory thermal gradient (32.9 °C) was, along with the Viviparous Lizard (*Zootoca vivipara* (Lichtenstein, 1823)), the lowest of all those lacertid lizards species that have been examined (see Bauwens et al. 1995). Also, mean field T_b of *I. cyreni* (30.8 °C) were comparatively low, being situated at the coldest end of the field T_b reported for 53 species of lacertid lizards (range from 27 to 40 °C, $T_{mean} = 33.8$ °C, with 50% of values between 31.9 and 35.5 °C; Castilla et al. 1999), and close to the other species of *Iberolacerta*, all inhabiting mountain environments (Arribas 2013). The strong similarities between the species of the genus *Iberolacerta* in presenting low field T_b together with the low T_{pref} exhibited by the few species in which this feature is known (Bauwens et al. 1996; *I. cyreni*: this paper; Iberian Mountain Lizard (*Iberolacerta monticola* (Boulenger, 1905)): S. Aguado and F. Braña, unpublished data) suggest that the thermal preferendum is a conserved trait in the *Iberolacerta* clade and is related to the adaptation of this species group to mountain environments and their isolation in fragmented habitats during cold periods of the Pleistocene (Carranza et al. 2004; Crochet et al. 2004; Remón et al. 2013).

Although the T_{pref} of *I. cyreni* was comparatively low, mean field T_b in summer was even lower than T_{pref}, which has been found in other cold-adapted species (e.g., *Z. vivipara*: Rodríguez-Díaz et al. 2010), and in contrast to warm-adapted species, which present field T_b similar to T_{pref} (e.g., Common Wall Lizard (*Podarcis muralis* (Laurenti, 1768)): Braña 1993; Columbretes Rock Lizard (*Podarcis atrata* Boscá, 1916): Castilla and Bauwens 1991). These data indicate that even during the most favourable time of the year, there are thermal restrictions in the species' natural habitat which impose constraints on them reaching their T_{pref}, and thus we can expect increased thermoregulatory costs in spring and autumn as has been reported for other species in temperate climates (Díaz and Cabezas-Díaz 2004; Zamora-Camacho et al. 2013).

As an alternative to the thermal constraint hypothesis, low field T_b could be due to lizards adopting a thermoconformist strategy in a low-quality habitat, according to the predictions of the cost–benefit model of lizard thermoregulation (Huey and Slatkin 1976). However, our results in contrasted thermal environments, even taking into account the limitations of a laboratory experiment that simplifies the conditions of the natural environment, evidenced that under the most unfavourable conditions *I. cyreni* actively modified their thermoregulatory behaviour to approach their T_{pref}. This even occurred when the temperatures reached are probably suboptimal because maximal performance of different physiological processes frequently occurs close to the upper limit of the preferred range (e.g., locomotor performance: Bauwens et al. 1995; digestive performance: Angilletta 2001; predatory

Fig. 4. Body temperatures (T_b) of the Cyren's Rock Lizard (*Iberolacerta cyreni*) and operative (T_e) temperatures in three contrasted thermal environments defined by three radiation levels (high, medium, and low). Shaded and hatched zone represents the population mean preferred temperature range (T_{pref}). Bars denote SE values.

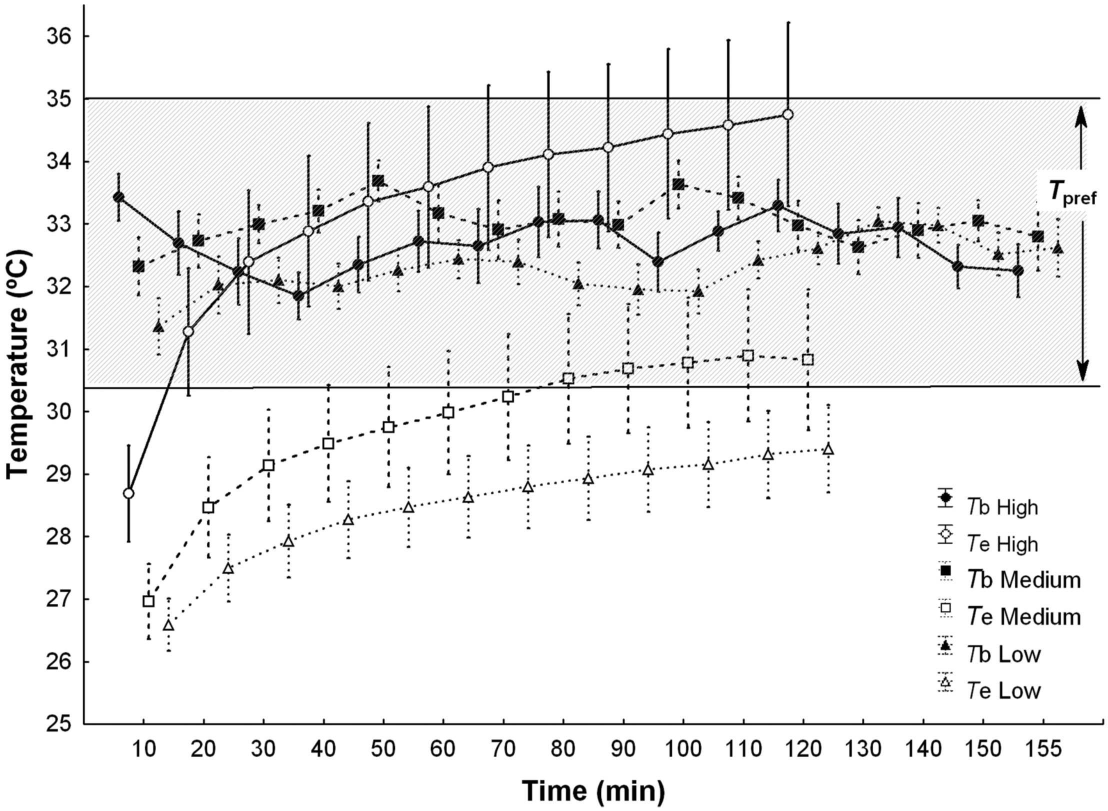
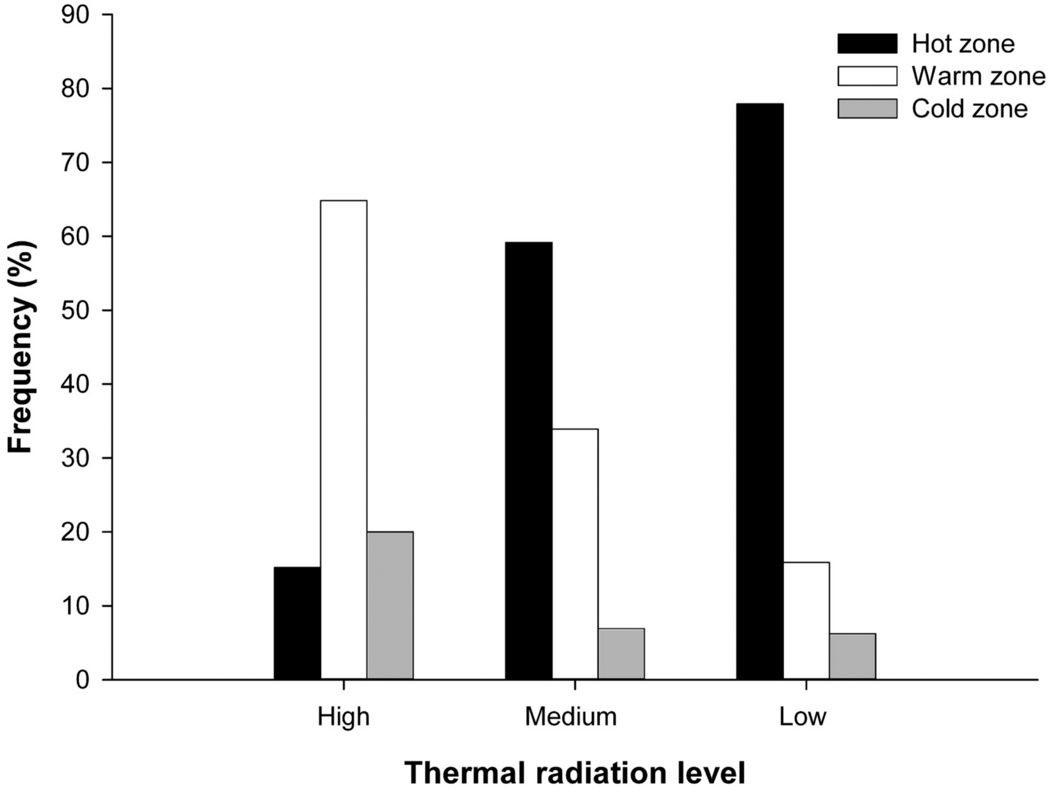


Fig. 5. Position of the Cyren's Rock Lizard (*Iberolacerta cyreni*) in the terrarium in three zones defined by the proximity to the heat source (hot zone, warm zone, and cold zone) and under three radiation levels. Frequencies were calculated as the percentage of time intervals in which each position was recorded.



efficiency: Avery et al. 1982). According to conventional indices, thermoregulatory accuracy should be higher in the low radiation treatment, but the interpretation of these indices requires caution considering, for instance, that they do not differentiate between deviations which are above the lizards' T_{pref} and those that are below it, even though these would have different ecophysiological implications. In our experiment, the lower accuracy in the high radiation treatment is mainly due to the fact that lizards attained T_{b} above the preferred range more frequently than they did in the other thermal treatments. In the same way, the high radiation treatment would have the lowest thermal quality according to these indices in spite of T_{e} being probably closer to the physiological optima.

Iberolacerta cyreni exhibited behavioural adjustments at different temporal and spatial scales, evidenced by the differences in their daily activity patterns, selection of microsites, orientation to the sun, and postural modifications according to variations in the thermal environment, as previously described for other diurnal lizards (Carrascal et al. 1992; Martín et al. 1995; Bauwens et al. 1996; Herczeg et al. 2006). These behavioural adjustments, although they are important thermoregulatory mechanisms in reptiles (Cowles and Bogert 1944; Huey 1982; Stevenson 1985*b*), also have associated costs. Our results showed higher costs associated with unfavourable thermal conditions (i.e., low radiation level) in which lizards spend most of their time thermoregulating at warmer sites, and consequently, they would devote less time to other activities, increasing their predation risk. Some studies have suggested that cold-adapted species reduce the priority of thermoregulating accurately when faced with situations having strong and immediate fitness consequences (e.g., mate acquisition: Shine et al. 2000; predation avoidance: Herczeg et al. 2008), while other activities such as foraging usually do not prevail over thermoregulatory activity (Herczeg et al. 2008). Other studies have found evidence of a trade-off between basking and antipredator behaviour in *I. cyreni* in the field, mainly due to the rapid loss of temperature inside the refuges (Martín and López 2003; Amo et al. 2007; Polo et al. 2005, 2011). Thus, results in our study species support the idea that even with its high-associated cost, thermoregulation should have higher benefits than thermoconformity in cold environments, which is contrary to the predictions of the cost–benefit model of Huey and Slatkin (1976; for a theoretical discussion see Blouin-Demers and Nadeau 2005) but is similar to findings for certain other species living in challenging environments (van Damme et al. 1987; Herczeg et al. 2003; Row and Blouin-Demers 2006; Besson and Cree 2010).

Global climate change is likely to strongly affect the geographic distribution and conservation of many species, particularly those adapted to cool climates such as montane organisms (Bernardo and Spotila 2006; Lourdais et al. 2013). Models of climate evolution in the Iberian Peninsula predict an increase in temperature (Brunet et al. 2009) that could affect the distribution range of some mountain species, particularly those of the genus *Iberolacerta* (Araújo et al. 2011). Warmer temperatures could be detrimental for cold-adapted species, for example, by restricting activity time to avoid overheating (Sinervo et al. 2010) or by lowering hatchling success (Monasterio et al. 2011). Furthermore, there is increasing evidence for a substantial impact of indirect effects associated with climate-driven changes on interacting species, thereby modifying niche partitioning (e.g., Tylianakis et al. 2008; Buckley 2013). In our study system, climate warming is likely to favour the expansion of warm-adapted species such as *P. muralis* (which inhabits elevations immediately below those of *I. cyreni*), allowing competitive displacement (Arnold 1973, 1987; Carranza et al. 2004; but see Monasterio et al. 2010) and increasing extinction risk (Cahill et al. 2013). However, global warming could also contribute to reducing thermal constraints in cold habitats (Kearney et al. 2009), which might be beneficial for *I. cyreni*. In this sense, our results show that under high levels of radiation, with T_{e} close to the upper limit of T_{pref}, *I. cyreni* thermoregulates efficiently with low costs in terms of time; on the other hand, field T_{b} were far below T_{pref}, thus these results support the idea that a moderate increase in temperature could favour this species by mitigating thermal constraints in its natural environment. Warmer temperatures could even raise reproductive investment by enlargement of body size (Chamaillé-Jammes et al. 2006), or by extending the activity season, thereby facilitating an increase in the number of clutches reared in the same season, which occurs in lowland vs. highland populations of the closely related species *I. monticola* (Braña et al. 1990). Therefore, although further experiments are necessary to ascertain the possible effects of climate change on *I. cyreni*, our study reveals that a species capacity to make behavioural adjustments is important to predict how different species might cope with challenging thermal environments (Muñoz et al. 2014), and as such, thermoregulatory abilities should be taken into consideration along with environmental variables in predictive models on a population's response to climate change (Huey et al. 2009; Kearney et al. 2009; Yagi and Litzgus 2013).

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