

Thermoregulation in the lizard *Psammodromus algirus* along a 2200-m elevational gradient in Sierra Nevada (Spain)

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Abstract Achieving optimal body temperature maximizes animal fitness. Since ambient temperature may limit ectotherm thermal performance, it can be constrained in too cold or hot environments. In this sense, elevational gradients encompass contrasting thermal environments. In thermally pauperized elevations, ectotherms may either show adaptations or suboptimal body temperatures. Also, reproductive condition may affect thermal needs. Herein, we examined different thermal ecology and physiology capabilities of the lizard *Psammodromus algirus* along a 2200-m elevational gradient. We measured field (T_b) and laboratory-preferred (T_{pref}) body temperatures of lizards with different reproductive conditions, as well as ambient (T_a) and copper-model operative temperature (T_e), which we used to determine thermal quality of the habitat (d_e), accuracy (d_b), and effectiveness of thermoregulation (d_e-d_b) indexes. We detected no T_b trend in elevation, while T_a constrained T_b only at high elevations. Moreover, while T_a decreased more than 7 °C with elevation, T_{pref} dropped only 0.6 °C, although significantly. Notably, low-elevation lizards faced excess temperature ($T_e > T_{pref}$). Notably, d_e was best at middle elevations, followed by high elevations, and poorest at low elevations. Nonetheless, regarding microhabitat, high-elevation d_e was more suitable in sun-exposed microhabitats, which may increase exposition to predators, and at midday, which may limit daily activity. As

for gender, d_b and d_e-d_b were better in females than in males. In conclusion, *P. algirus* seems capable to face a wide thermal range, which probably contributes to its extensive corology and makes it adaptable to climate changes.

Keywords Elevation · Ambient temperature · Field body temperature · *Psammodromus algirus* · Selected body temperature

Introduction

Attaining optimal body temperature maximizes animal fitness since physiological and biochemical processes such as digestion (McConnachie and Alexander 2004), locomotion (Xiang et al. 1996), growth (Brewster et al. 2013), and reproduction (Du et al. 2005; Sun et al. 2012) strongly depend upon temperature. Ectotherms do not generate enough metabolic heat nor have adequate thermal isolation for efficient body-temperature upkeep (Brown and Au 2009). Thus, ectotherms depend mainly upon external heat sources to attain body temperatures within preferred temperature ranges (PTR), at which physiological processes are optimized (Hertz et al. 1993). Most ectotherms rely on behavioral thermoregulation, mainly by means of two complementary pathways: heliothermy, which consists of heat gain by solar radiation, and thigmothermy, where heat exchange by conduction and convection dominates (Belluire and Carrascal 2002). However, despite benefits of heat acquisition and maintenance, these pathways are particularly costly for ectotherms (Alford and Lutterschmidt 2012). Active surface thermoregulation makes diurnal ectotherms highly conspicuous to predators, thereby increasing predation risk (Herczeg et al. 2006). Moreover, thermoregulating ectotherms spend much time adjusting body temperature, which reduces the time available for foraging

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(Verwajen and Van Damme 2007), mating, reproducing, or defending a territory (Huey and Slatkin 1976). Costs are especially pronounced in thermally challenging habitats, where temperatures ectotherms can passively reach in the field do not match preferred temperatures. In that situation, ectotherms should thermoregulate, frequently being exposed to predators, or otherwise maintain suboptimal temperatures, with the concomitant physiological costs.

Ectotherm PTR is mostly considered as an evolutionarily conservative trait (Truter et al. 2014). Therefore, thermal environment can greatly constrain reaching PTR, especially in thermally challenging habitats (Fei et al. 2012). The extent to which ambient temperature matches a given ectotherm thermal preference varies geographically: temperature becomes usually gradually colder as latitude (Sunday et al. 2010) and elevation (Stevens 1992) increase. Classically, two opposite hypotheses address the issue of ectotherm thermal-environment adaptation across ectotherm distribution range: the labile and the static hypotheses. The labile hypothesis states that ectotherm thermal preferences can evolve according to thermal environment, so that optimum temperatures are easier to achieve in spite of geographic variation in thermal environment (Hertz et al. 1983; Rodríguez-Serrano et al. 2009). On the contrary, the static hypothesis applies when ectotherm thermal preferences are evolutionarily conservative and remain fairly constant despite thermal-environment variation (Hertz et al. 1983; Crowley 1985). In this sense, the current ongoing climate change is provoking alterations in the thermal environment ectotherms are facing (e.g., Moreno-Rueda et al. 2009). How ectotherms respond to these thermal changes is key to predict their capacity to maintain their populations, otherwise, they will be prone to extinction (Sinervo et al. 2010). Probably, the capacity of response of ectotherms depends upon whether they follow the static or the labile hypothesis.

One way or another, ectotherm thermoregulation is subject to a cost/benefit balance (Huey and Slatkin 1976). In thermally challenging habitats, the costs of no-thermoregulation often outweigh those of thermoregulation, so that thermoregulation may be a priority when the chances to reach optimal temperature are constrained (Blouin-Demers and Nadeau 2005). Accordingly, the extended model of thermoregulation cost/benefit balance predicts that ectotherms will thermoregulate in thermally challenging habitats, where ambient temperature deviates from PTR (Vickers et al. 2011). Reflecting the importance of thermal upkeep in cold habitats, alpine lizards spend more time basking (Díaz 1997). Accordingly, lower thermal-tolerance limits decrease as latitude increases in many terrestrial ectotherms, while upper thermal-tolerance limits remain unaltered (Sunday et al. 2010). Thus, cold-habitat ectotherms have greater thermal widths (Valdecantos et al. 2013).

Besides habitat thermal quality (*sensu* index in Hertz et al. 1993; see further description in “Materials and methods” section), physiological and metabolic conditions can also affect

ectotherm body-temperature performance. For instance, thermal requirements of reproductive processes can shift ectotherm thermal preferences. For example, male adders *Vipera berus* show lower body temperatures imposed by spermiogenesis (Herczeg et al. 2007). Pregnant females of the viviparous lizard *Eulamprus tympanum* attain temperatures similar to those of males and non-gravid females, but they require more basking time to reach optimal body temperature (Schwarzkopf and Shine 1991). Nevertheless, female lizards often show a trend to temporally prefer lower temperatures when gravid than after parturition both in oviparous (Mathies and Andrews 1997) and viviparous species (Le Galliard et al. 2003). In fact, embryos developed at temperatures slightly below female PTR result in neonates with better body conditions and escape speed in those species (Mathies and Andrews 1997; Le Galliard et al. 2003). While the lower body temperature preferred by gravid females seems adaptive in the aforementioned species, in the oviparous lizard *Podarcis muralis*, field body temperatures of gravid females were lower than in non-gravid females; however, gravid and non-gravid females preferred similar temperatures when allowed to thermoregulate in a thermal gradient, suggesting that environmental constraints limit thermoregulation accuracy in gravid females in the field (Braña 1993).

In this study, we examine whether the temperate lizard *Psammodromus algirus* thermoregulates along a 2200-m elevational gradient in six populations from 300 to 2500 m asl in Sierra Nevada (SE Spain). We addressed the following issues: (1) We examined whether this lizard thermoregulates according to the static hypothesis or the labile hypothesis. The static hypothesis posits that lizards will not shift their thermal preferences with elevation, despite thermal-environment constraints, while the labile hypothesis predicts that lizards will prefer lower body temperatures in high-elevation, low-thermal-quality (cold) habitats. To do so, we collected data on field body temperature (T_b), ambient temperature (T_a), substrate temperature (T_s), hollow copper-model operative temperature (T_e), and laboratory-determined preferred body temperature (T_{pref}), and calculated accuracy (d_b), and effectiveness of thermoregulation ($d_e - d_b$) indexes, regarding reproductive condition. (2) We also assessed elevational trends in thermal quality of the habitat (d_e). And (3) we tested whether gravid females choose lower body temperatures for better embryo development, as other species do (Mathies and Andrews 1997; Le Galliard et al. 2003).

Materials and methods

Experimental species

P. algirus is an abundant, oviparous, euryoic, medium-sized lacertid lizard (53–95 mm of minimum and maximum adult

snout-vent length [SVL] of males and females in this study area) which inhabits shrubby zones in Mediterranean climates of Western Europe and Africa, from the sea level to more than 2600 m asl (meters above the sea level) (Salvador 2011). It is an opportunistic arthropod predator, which can either use a “sit-and-wait” strategy or (more often) search for prey actively (Salvador 2011). Lizards heat up mainly heliothermally (Díaz and Cabezas-Díaz 2004), by sunbathing near the shrubbery they use as a shelter from potential predators (Martín and López 2000). In other populations, these lizards shift slightly their thermal preference seasonally, but preferred body temperature fluctuates around 32–34 °C (Díaz et al. 2006).

Lizards were captured by hand within their mating season (April–June) in 2010–2013. Males and females were collected, and females were classed according to reproductive condition (gravid and non-gravid). We recognized males because they have proportionally wider heads, orange spots in the corners of their mouths, and more numerous and conspicuous external pores of femoral epidermal glands. Gravid females were recognized by manual palpation of developing eggs. As males hold females during copulation by firmly biting their neck or side, a bite mark in those areas allowed us to distinguish postpartum females from those that had not mated. Plus, females in this system only produce one clutch per year (unpublished data).

Field measurements

Lizards were captured on the southern face of Sierra Nevada (SE Spain) in six populations at 300, 700, 1200, 1700, 2200, and 2500 m asl. We chose places as similar as possible regarding habitat structure (see Appendix A in Zamora-Camacho et al. 2013) since habitat structure may have an effect on habitat thermal quality (Lara-Reséndiz et al. 2014). We measured T_b of lizards at whichever time they were caught fully active, during reproductive season (April–June) from 2010 to 2012. Measurements were taken within 30 s after capture, putting a 1-mm-diameter thermocouple, assembled to a thermometer (model Hibok 14, accuracy 0.1 °C), 8 mm into the cloaca. Next, we recorded T_a , 1 m above the ground, under shade. Also, when available, we measured T_s at the exact point where a captured lizard was first detected (whether it was rocky, grassy, or bare soil).

Furthermore, on a clear day, halfway through the reproductive season of 2012 (July 13–17), we ascertained T_e , i.e., the predicted body temperature that lizards would attain in the field if they did not thermoregulate actively, thus providing a null hypothesis of no thermoregulation, by using hollow copper models. Hollow copper models heat up like lizards with similar length, width, and volume (Hertz 1992; Díaz 1997). Models need to be calibrated against living animals (Dzialowski 2005; Bakken and Angilletta 2014), so we used models identical to those successfully calibrated by Díaz

(1997) in this species: copper models were unpainted, measured 5 × 1 cm, and had both ends sealed with artificial cork, but a small hole in one end allowed us to insert the thermocouple. In each sampling plot, 31 copper models were distributed 1 m from each other, putting a “ventral” part in contact with the substrate. We measured T_e once an hour throughout the morning, from 10:00 to 14:00 (local time). Also, we considered three microhabitats regarding the exposure of the copper models to the sun: fully exposed to sunlight, partially exposed, or under shade.

Laboratory measurements

In 2012 and 2013, lizards were taken to the laboratory the day of capture, and placed 1 day in individual terrariums (100 × 20 × 40 cm) built in 5-mm-thick methacrylate, with a 150-W red-light bulb at one end, 15 cm over the pine-cork substrate (Díaz et al. 2006). The bulb was switched on during daytime, generating a thermal gradient of approximately 20–55 °C, and a window let natural daylight in, permitting circadian rhythm upkeep. The following day, lizards stayed in those conditions, free to choose the preferred temperature, and we recorded their body temperature five times, as described above, once an hour, from 10:00 to 14:00 (local time). Then we calculated each lizard’s T_{pref} as the mean of those five measurements, as well as its variance. As we kept gravid females in the laboratory until egg-laying, as a part of a long-term reproduction study, we recorded clutch size (number of eggs), egg burden (female investment in clutch), and days from T_b and T_{pref} measurements until oviposition. We calculated egg burden as the difference in body mass between the moment of temperature measurement (T_b in the field and T_{pref} in the laboratory) and right after egg laying. Throughout the process, all lizards had water (in form of aqueous nutritious gel) and food (*Tenebrio molitor* larvae) *ad libitum*. Lizards suffered no pain as a consequence of this study and were set free at their provenance population as soon as the experiment finished.

Also, we calculated set-point ranges (T_{set}) as the central distribution of T_{pref} values. Some debate exists on the use of 50 or 80 % central boundaries of these values (Blouin-Demers and Nadeau 2005), so we calculated both. Since the results were rather similar, and 50 % is more restrictive and mostly preferred (Blouin-Demers and Nadeau 2005), we opted for showing findings with this value, results calculated with the central 80 % being available as Supplementary Material.

Indexes

The information collected on T_e , T_b , and T_{set} allowed us to calculate some thermoregulation indexes widely used in ectotherm thermal ecology (Hertz et al. 1993; Díaz 1997; Blouin-Demers and Nadeau 2005),

(A) Thermal quality of the habitat (d_e): describes the extent to which T_e matches T_{set} and is defined as the average of the absolute values of deviations of T_e relative to the nearest T_{set} boundary. Thermal quality of the habitat is higher as d_e index approaches 0, as $d_e=0$ represents a complete match between T_e and T_{set} . A larger deviation between T_{set} and T_e implicates a lower thermal quality and higher effort of thermoregulation to reach T_{pref} . This index was calculated for every microhabitat in each elevation, as well as hourly.

(B) Accuracy of body temperature (d_b): describes the extent to which T_b matches T_{set} and is defined as the average of the absolute values of deviations of T_b relative to the nearest T_{set} boundary. Accuracy of body temperature is higher as d_b index approaches 0, as $d_b=0$ represents a complete match between T_b and T_{set} .

(C) Effectiveness of thermoregulation (d_e-d_b ; Blouin-Demers and Weatherhead 2001): This index provides an intuitive and straightforward proxy of the extent to which ectotherms effort to thermoregulate (Blouin-Demers and Weatherhead 2001; Blouin-Demers and Nadeau 2005). Values close to 0 indicate thermoconformity, values close to 1 indicate thermoregulation, and values below 0 indicate avoidance of preferred temperatures.

Statistical analyses

Since all models fulfilled the criteria of residual normality (assessed with Lilliefors tests) and homoscedasticity, we conducted parametric statistics (Quinn and Keough 2002). We analyzed most data with Linear Models by Ordinary Least Squares, according to our aims. Statistical tests were performed with the software R version 3.1.1 (R Development Core Team 2012).

1. In order to ascertain whether lizards respond to the static or the labile hypothesis of thermoregulation, we first used a one-way ANOVA to assess elevational variation in T_a , T_s , and T_e , determining environmental thermal constrains. Then, we performed a two-way ANOVA to assess T_b variation depending on elevation and reproductive condition, and a one-way ANOVA to assess the effect of elevation on T_{pref} . In addition, multiple regression tests were used to assess the effect of T_s and T_a on T_b . We also analyzed the elevational trends of the relationship between difference between T_b and T_a , and between T_b and T_s , with T_a and T_s , respectively, to ascertain the relative contribution of T_a and T_s on lizard T_b , and trends of the difference between T_b and T_a , and between T_b and T_s with increasing T_a and T_s , respectively. Furthermore, Spearman rank tests were performed to assess elevational trends in T_a , T_s , T_b , and T_{pref} , using the average values in each of the six populations. Also, we assessed differences between T_b and T_{pref} with a t test for dependent samples,

and we used a two-way ANOVA to detect possible effects of elevation and reproductive condition on the difference between T_{pref} and T_b . Also, we assessed the effects of elevation and reproductive condition on T_{pref} variance with a two-way ANOVA. Lastly, we performed Spearman rank tests to check elevational trends in d_b and d_e-d_b , using the average values in each of the six populations. In all cases, we performed Bonferroni post hoc analyses to assess differences among levels of factors of significant or marginally non-significant ANOVAs (Table S1).

2. We used a three-way ANOVA to assess the effects of reproductive condition, microclimate, and elevation on d_e , and a two-way ANOVA to assess the effects of reproductive condition and elevation on d_b .
3. The effect of reproductive condition on T_{pref} was assessed with a one-way ANOVA. Moreover, for gravid females, we conducted correlation tests of both T_b and T_{pref} with clutch size, egg burden, and days until oviposition, by using Pearson's product-moment correlations.

Results

Thermal ecology trends

Thermal gradient

We confirmed elevational differences in T_a ($F_{5, 311}=37.134$; $P<0.001$; Fig. 1; Table S2a), the three highest populations showing lower T_a . Spearman rank test showed a significant trend of T_a to diminish with rising elevation ($n=6$ populations; $r_s=-0.83$; $P=0.042$). In turn, although T_s when lizards were active varied among populations ($F_{5, 163}=10.315$; $P<0.001$), it showed no elevational pattern (Fig. 1). Spearman rank test was not significant ($r_s=-0.66$; $P=0.16$). Operative temperature (T_e) showed significant differences among elevations ($F_{5, 925}=74.88$; $P<0.001$; Fig. 1). Spearman rank test proved a marginally non-significant trend of T_e to diminish with increasing elevation ($r_s=-0.77$; $P=0.07$).

Field body temperature (T_b)

Although lizards from different elevations had different T_b s ($F_{5, 311}=3.94$; $P=0.002$), we detected no clear elevational pattern (Fig. 1). Accordingly, Spearman rank correlation between population-average T_b and elevation was non-significant ($r_s=-0.49$; $P=0.33$).

Consequently, the difference between T_b and T_a (ΔT_{ba}) tended to decrease with increasing elevation ($F_{5, 350}=18.36$, $P<0.001$). As a whole, ΔT_{ba} followed a non-linear relationship

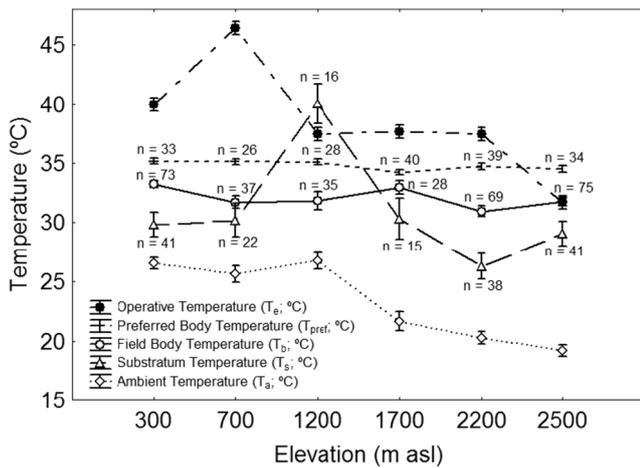


Fig. 1 Operative (T_o), lizard selected (T_{pref}), and field body temperatures (T_b) as well as substratum (T_s) and ambient temperature (T_a) in each sampling plot. Although we detected population differences in all the five variables, only T_{pref} and T_a showed a significant elevational trend. Sample size of ambient and field body temperatures were the same at each elevation since both measurements were made at once. Operative temperature calculations were based on 31 copper models at each elevation, measured five times, so sample size is 155 at each sampling plot. Vertical bars represent standard errors

with T_a (linear effect— $F_{1, 353}=12.38, P<0.001$; quadratic effect— $F_{1, 353}=69.68, P<0.001$; $R^2=0.69$; Fig. 2a). For high T_a , T_b was smaller than T_a (negative ΔT_{ba}). As T_a decreased, T_b was relatively higher following a linear trend. When T_a was below 30 °C (approximately), T_b was higher than T_a (positive ΔT_{ba}). However, for low T_a (between 20 and 25 °C), when the difference ΔT_{ba} was 9.07 °C (breakpoint), the slope strongly decreased, from -0.82 to -0.46 (piecewise linear regression; $R^2=0.73$), the relationship between T_a and ΔT_{ba} approaching to an asymptote (Fig. 2a). The non-linear relationship between T_a and ΔT_{ba} was general across populations (Table 1—note that β values were consistently negative for the quadratic effect). As a consequence of this non-linear relationship, T_b was not correlated with T_a in the three lowest elevations ($P>0.16$ in all cases), but it showed a positive correlation in populations at 1700 ($r=0.52$; $P=0.005$), 2200 ($r=0.45$; $P<0.001$), and 2500 m asl ($r=0.31$; $P=0.007$).

Regarding the relationship between T_b and T_s , the difference between T_b and T_s (ΔT_{bs}) followed a linear relationship with T_s (Fig. 2b). That is, T_b did not seem to be constrained by T_s : when T_s was relatively high, ΔT_{bs} was negative, and when T_s was relatively low, ΔT_{bs} was positive. Note that this finding contrasts with that found for T_a , given that for low values of T_a , lizards showed difficulties to thermoregulate adequately (see Fig. 2a). The relationships between T_s and T_b were not consistent across elevations. T_s showed a positive correlation with T_b at 700 m and 2200 m populations ($r>0.4$; $P<0.05$ in both cases), while no correlation was found in the remaining elevations ($P>0.05$). We assessed the effect of T_s and T_a on T_b by using multiple regressions

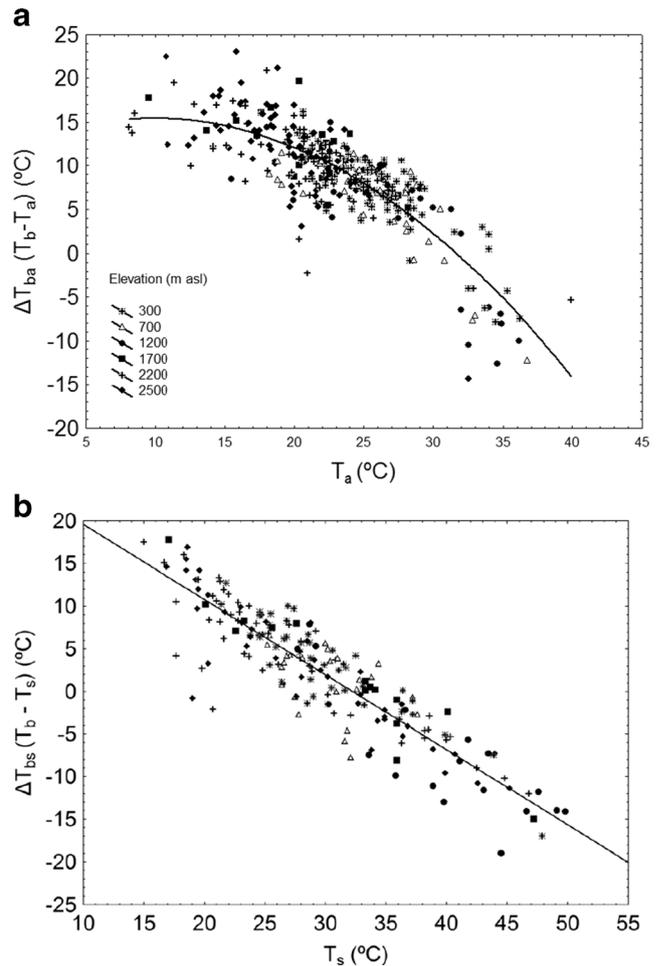


Fig. 2 ΔT_{ba} , calculated as body temperature (T_b) minus ambient temperature (T_a) followed a non-linear relationship with T_a (Fig. 2a). The asymptote at low T_a suggests that T_b is constrained by T_a at low T_a . Meanwhile, ΔT_{bs} , calculated as body temperature (T_b) minus substratum temperature (T_s), followed a linear relationship with T_s (Fig. 2b). The linear relationship suggests no constraint of T_s on T_b

for each elevation. In general, T_a influenced T_b more than T_s , except at 2200 m population (Table 2).

Table 1 Linear and quadratic relationships between T_a and ΔT_{ba} in all populations

Elevation	df	Linear effect		Quadratic effect	
		F	β	F	β
300	1, 78	1.76	0.93	6.23*	-1.76
700	1, 36	19.55***	3.05	31.49***	-3.87
1200	1, 35	20.15***	2.81	33.96***	-3.65
1700	1, 27	0.04	0.16	1.24	-0.91
2200	1, 81	0.12	0.11	6.78*	-0.80
2500	1, 81	6.20*	1.13	16.99***	-1.86
Total	1, 353	12.38***	0.59	69.68***	-1.41

F statistics and β values are shown. In bold, significant results

* $P<0.05$; *** $P<0.001$

Table 2 Multiple regressions testing the effects of T_s , T_a , and T_a^2 on T_b for each elevation

Elevation	df	T_s	T_a	T_a^2
300	1, 41	3.12	5.15*	5.28*
700	1, 20	12.89**	47.10***	50.37***
1200	1, 14	0.05	1.17***	19.79***
1700	1, 11	0.26	0.26	0.27
2200	1, 46	8.86**	1.52	0.93
2500	1, 45	2.53	6.36*	8.83**

In bold, significant results

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Selected temperature (T_{pref})

Elevational variation in T_{pref} was marginally non-significant, with a trend to diminish with rising elevation ($F_{5, 193} = 2.24$; $P = 0.052$; Fig. 1 and Table S2b and Table S2c). Hence, Spearman rank test between population average T_{pref} and elevation was significant ($r_s = -0.83$; $P = 0.042$), confirming that lizards tended to prefer lower T_{pref} as their provenance elevation rose. However, the difference in T_{pref} between the lowest and the highest populations was only of 0.6 °C. Interestingly, T_{pref} variance showed a marginally non-significant trend ($F_{5, 193} = 2.12$; $P = 0.065$) to be greater in the three highest elevations (average variance \pm SE [°C]; 1700 m asl, 7.47 ± 1.17 ; 2200 m asl, 5.11 ± 1.16 ; 2500 m asl, 5.34 ± 1.34) than in the three lowest elevations (300 m asl, 3.78 ± 1.30 ; 700 m asl, 2.79 ± 1.45 ; 1200 m asl, 2.63 ± 1.40).

Lizard T_{pref} was significantly higher than field T_b (paired t test, $t_{78} = 6.65$; $P < 0.001$; Fig. 1). Nevertheless, neither elevation ($F_{5, 71} = 0.58$; $P = 0.72$) nor reproductive condition ($F_{2, 71} = 0.38$; $P = 0.69$) significantly affected the difference between T_b and T_{pref} .

Accuracy (d_b) and effectiveness of thermoregulation ($d_e - d_b$)

Although we found differences among populations ($F_{5, 290} = 3.28$; $P = 0.007$), d_b showed no clear elevational pattern (Fig. 3). In fact, Spearman rank test between d_b and elevation was not significant ($r_s = 0.26$; $P = 0.62$). However, females thermoregulated more accurately than males ($F_{2, 290} = 3.72$; $P = 0.025$; Fig. 4). Results proved similar after using 80 % of the T_{pref} values to estimate the accuracy of body temperature (Figs. S1 and S2).

Regarding effectiveness of thermoregulation, lizards from low elevations (300 and 700 m asl) thermoregulated more effectively than those from mid (1200 and 1700 m asl) and high elevations (2200 and 2500 m asl; Tables S3 and S4). Spearman correlations between $d_e - d_b$ and elevation were negative for lizards in all reproductive conditions, although they were marginally non-significant only for gravid ($r_s = -0.77$;

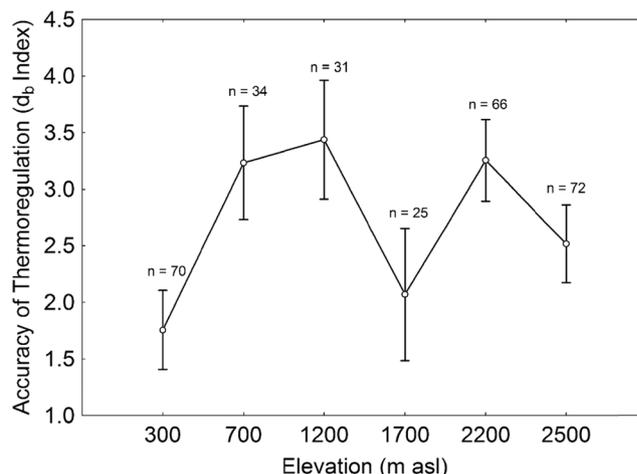


Fig. 3 Accuracy of thermoregulation (measured as d_b index) showed no clear elevational pattern. Accuracy of thermoregulation increases as d_b value approaches 0. Vertical bars represent standard errors. These results were calculated from T_{set} considered as 50 % central values of T_{pref} . Results from T_{set} considered as 80 % central values of T_{pref} were very similar and are available as Supplementary Material (Fig. S1)

$P = 0.07$) and non-gravid females ($r_s = -0.77$; $P = 0.07$), but not for males ($r_s = -0.49$; $P = 0.33$). This result agrees with females having higher thermoregulation accuracy.

Thermal quality of the habitat (d_e)

Thermal quality of the habitat varied with elevation, microhabitat, and hour in a complex way, as reflected by the multiple interactions between the three factors (Table 3; Fig. 5). In general, thermal quality was worse for lizards in exposed microhabitats than in the shade—except at high elevations—and

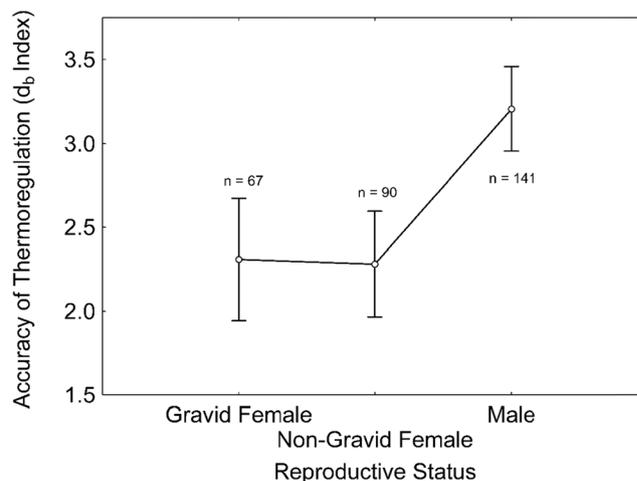


Fig. 4 Accuracy of thermoregulation (measured as d_b index) according to reproductive condition. Accuracy of thermoregulation increases as d_b value approaches 0. Both gravid and non-gravid females thermoregulated more accurately than did males. Vertical bars represent standard errors. These results were calculated from T_{set} considered as 50 % central values of T_{pref} . Results from T_{set} considered as 80 % central values of T_{pref} are available as Supplementary Material (Fig. S2)

Table 3 Results of three-way factorial ANOVA testing the effect of elevation, hour, microhabitat, and their interactions on thermal quality of the habitat (d_e)

	<i>df</i>	<i>F</i>
Elevation	5, 881	82.51***
Hour	4, 881	28.40***
Microhabitat	2, 881	118.32***
Elevation×hour	20, 881	33.86***
Elevation×microhabitat	10, 881	48.38***
Hour×microhabitat	8, 881	41.13***

Results of d_e from T_{set} calculated as 80 % central values of T_{pref} were very similar and are available in Table S5 in Supplementary Material

*** $P < 0.001$

at low elevations than in middle and high elevations (Fig. 5a–c). We found similar results when using 80 % of the values of T_{pref} to estimate thermal quality of the habitat (Table S5; Fig. S3).

Gravity

Reproductive condition had no effect on T_b ($F_{2, 338} = 0.36$; $P = 0.70$). Neither clutch size ($r = -0.013$; $P = 0.92$), egg burden ($r = -0.078$; $P = 0.56$), nor days until oviposition correlated significantly with gravid female T_b ($r = -0.094$; $P = 0.70$; Fig. 6). Similarly, reproductive condition had no significant effect on T_{pref} ($F_{2, 198} = 13.5$; $P = 0.34$), and neither clutch size ($r = -0.18$; $P = 0.21$) nor egg burden ($r = -0.24$; $P = 0.12$) were correlated with gravid female T_{pref} . Nevertheless, we found a positive correlation between days until oviposition and gravid female T_{pref} ($r = 0.55$; $P < 0.001$; Fig. 6). Similarly, reproductive condition had no effect on T_{pref} variance ($F_{2, 183} = 0.319$; $P = 0.73$).

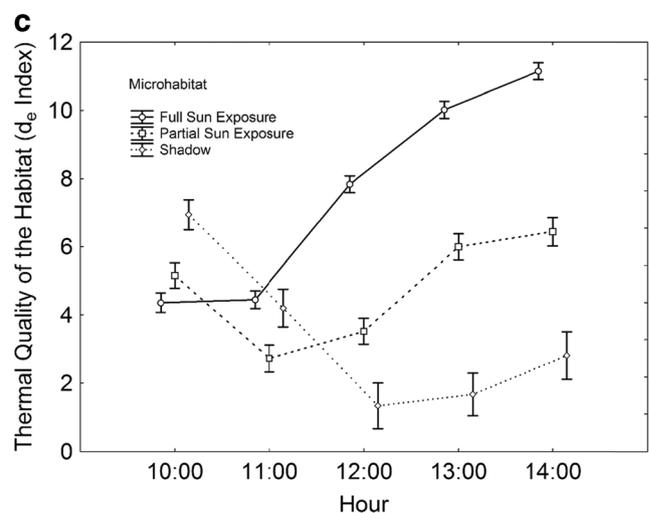
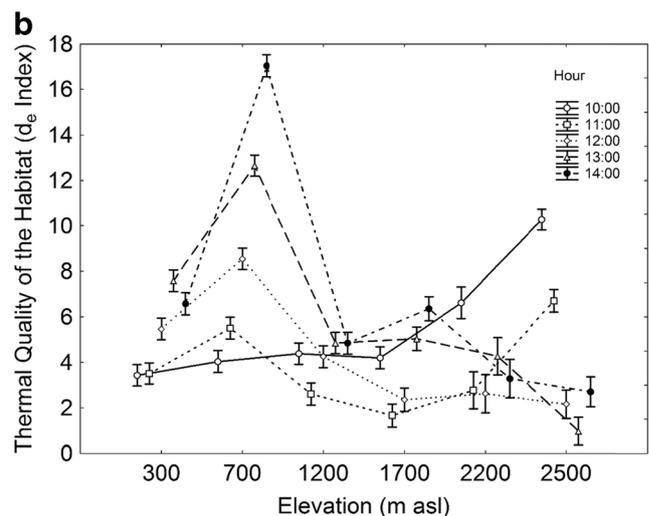
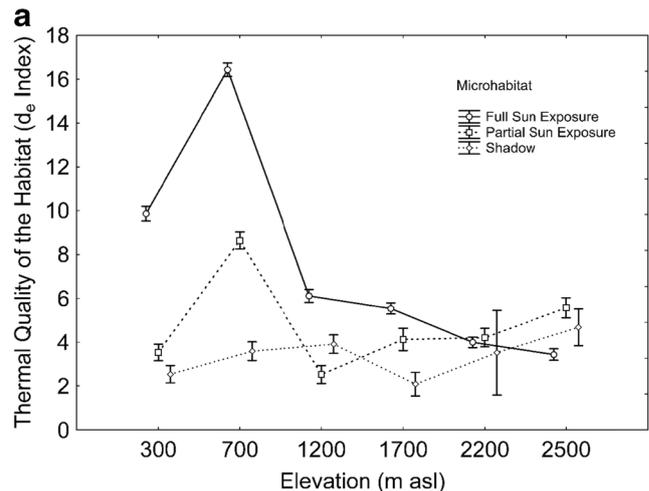
Discussion

Elevational trends in thermal ecology

Ectotherm thermal ecology is closely related to temperature in their environment (Angilletta 2009), which decreases with

Fig. 5 Thermal quality of the habitat (measured as d_e index) increases as d_e value approaches 0. In low elevations, thermal quality of the habitat is maximal under shade, but at high elevations full sun exposure is more suitable (Fig. 5a). At low elevations, habitat thermal quality is maximal at the beginning of the day, while at high elevations the central day hours are best (Fig. 5b). Maximal thermal quality of the habitat occurred in fully sun-exposed microhabitats at the beginning of the day, shifting gradually to partially exposed and finally to shaded microhabitats (Fig. 5c). Vertical bars represent standard errors. These results were calculated from T_{set} considered as 50 % central values of T_{pref} . Results from T_{set} considered as 80 % central values of T_{pref} were very similar and are available as Supplementary Material (Fig. S3)

elevation and with latitude (Hertz and Huey 1981; Aguado and Braña 2014). Thus, lizard thermal performance could be gradually constrained along this 2200-m elevational gradient, where T_a diminished with rising elevation (see Grant and Dunham 1990). However, T_b followed no detectable



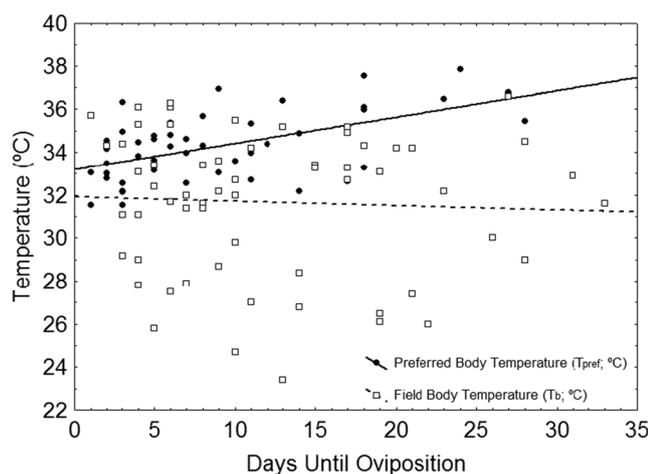


Fig. 6 Correlations between both gravid female selected (T_{pref}) and field body temperature (T_{b}) and days until oviposition. Gravid females preferred lower T_{pref} as oviposition approached. However, we found no significant correlation between T_{b} and days until oviposition. Sample sizes were 46 gravid females for T_{pref} and 61 for T_{b}

elevational pattern. For instance, the T_{b} of lizards at 2500 m asl (31.6 °C in average), where T_{a} was the lowest, was very similar to that of lizards at high T_{a} populations such as 700 and 1200 m asl (31.5 and 32.0 °C, respectively). Moreover, T_{pref} attained in the laboratory without environmental constraints, diminished gradually for 0.6 °C as elevation rose, while T_{a} decreased more than 7.3 °C with rising elevation. Similarly, Diaz et al. (2006) found no differences in T_{pref} in two populations of *P. algirus* separated 700 m in elevation. Interestingly, we found a marginally non-significant trend of T_{pref} variance to be greater at the three highest elevations, supporting wider thermal niches in cold-habitat ectotherms (Sunday et al. 2010; Valdecantos et al. 2013).

The mismatch between T_{pref} and T_{e} , and the concomitant low habitat thermal quality, involves a high thermoregulation effort in the long term. Also, the fact that T_{b} was consistently lower than T_{pref} suggests that thermoregulation capability is constrained in the wild, which may determine the temperature that lizards can actually attain in the field. Accordingly, Aguado and Braña (2014) found that T_{pref} was higher than T_{b} in the high-elevation lizard *Iberolacerta cyreni*. In thermally challenging situations, one of the main constraints on ectotherm thermoregulation is ambient temperature (Grant and Dunham 1990; Adolph and Porter 1993). However, we only found a correlation between T_{a} and T_{b} in the highest populations, suggesting that ambient temperature is limiting only at high elevations. Our findings suggest that thermoregulation is constrained below 20–25 °C: when T_{a} is lower, the relationship between the difference in $T_{\text{b}}-T_{\text{a}}$ and T_{a} seems to approach an asymptote. A number of abiotic factors, with predictable geographical patterns, such as solar radiation, long-wave radiation, or conductive and convective heat flow, can affect lizard thermoregulation (Fei et al. 2012). In addition, other biotic

factors may be constraining lizard ability to thermoregulate in the field, such as predation pressure (Carter et al. 2010), food availability (Yu et al. 2008), or reproduction opportunities (Shine et al. 2000). Those factors are presumably relevant also in this study system; however, in our study, T_{a} explained around 70 % of variation in T_{b} . The relationship between T_{s} and T_{b} in this species, and thus the role of thigmothermy, remains obscure, but it does not seem preponderant.

These data suggest that T_{a} is limiting at high elevations. However, surprisingly, thermal quality (d_{e}) improved at high elevations with respect to low elevations, the best being at mid-elevation populations. This result indicates that lizards at low elevations face excess T_{e} . Accordingly, d_{e} at low elevations was more suitable for lizards at the beginning of the day and in shaded microhabitats. The excessively hot thermal environment in low elevations might explain why these populations harbor the lowest population densities, while densities are highest at mid-elevation and medium at high elevation (Zamora-Camacho et al. 2013). Plus, in high elevations, d_{e} was more suitable at sun-exposed patches, mainly at the beginning of the day, being more appropriate in shaded microhabitat at midday. Hence, to some extent, lizards can behaviorally compensate too high or too low ambient temperatures, driven either by elevation or daily thermal cycles, by shifting between shaded and sunny microhabitats (Huey et al. 2003). Our findings have important consequences in a scenario of climate warming, as they suggest that low-elevation populations could be in risk of extinction if environmental temperature rises beyond the possibilities of behavioral buffering (Huey et al. 2003; Kearney et al. 2009; Sinervo et al. 2010). Also, climate warming could induce lizard migration towards higher elevations (Chen et al. 2011).

On the contrary, thermal environment in high elevations was more appropriate at midday and in sunny microhabitats. This finding implies that, although overall d_{e} is better at high than at low elevations, high-elevation lizards still have to bask actively in order to reach optimal T_{b} , which increases thermoregulation costs, especially predation risk (Alford and Lutterschmidt 2012). Moreover, daily optimal temperature at high elevations appeared to be constrained to the central hours, when thermal quality of the habitat is more suitable. This temporal constraint is also a major limitation to lizard circadian activity. In fact, thermoregulation was more effective at low than at high elevations, suggesting that lizards can more easily attain appropriate T_{b} by avoiding heat when it is excessive than by acquiring it when temperature is below the optimum. Furthermore, habitat thermal quality was measured halfway through the reproductive season, when lizard activity peaks in all populations (see Zamora-Camacho et al. 2013). Thus, habitat thermal quality could be worse at high and better at low elevations in spring or autumn, when ambient temperature is lower (Zamora-Camacho et al. 2013).

Hence, our results support the static hypothesis of ectotherm thermal-environment adaptation (Crowley 1985; Gilchrist 1995), which posits that ectotherm capability to modify thermal physiology, and thus thermal preferences (Hertz et al. 1983), can be evolutionarily constrained. Moreover, our findings match the extended model of thermoregulation cost/benefit balance (Vickers et al. 2011), which predicts that ectotherms will thermoregulate appropriately in thermally challenging habitats because the costs of no-thermoregulation outweigh those of thermoregulation. In fact, high-elevation lizards attained T_b values as high as those of low and mid-elevation lizards, despite the ecological and thermal constraints. Similarly, several species of *Liolaemus* and *Phymaturus* lizards thermoregulate suitably at high elevations (Ibargüengoytia et al. 2008; Moreno Azócar et al. 2013; Valdecantos et al. 2013). Lizards can display several mechanisms for accurate thermoregulation in thermally challenging habitats. For instance, montane *Iberolacerta monticola* uses long basking periods to gain heat (Carrascal et al. 1992), and *Zootoca vivipara* spends more time basking at 1450 than at 250 m asl (Gvoždík 2002). Furthermore, *P. algirus* is darker at higher elevations in our study system (Reguera et al. 2014), which could help them heat up faster (Clusella-Trullas et al. 2007). Moreover, *P. algirus* cools down more slowly at higher elevations as a consequence of their size increasing with elevation (Zamora-Camacho et al. 2014a). In addition, although copper-model temperature decreased at higher elevations (figure 3 in Zamora-Camacho et al. 2013), this trend reversed when controlling for ambient temperature, suggesting that heat sources besides ambient temperature (presumably radiation) can boost high-elevation lizard thermoregulation (Zamora-Camacho et al. 2013). In conclusion, *P. algirus* seems to have developed adaptations in order to maintain thermoregulation performance in high elevations in Sierra Nevada: darker dorsal color (Reguera et al. 2014) and larger body size (Zamora-Camacho et al. 2014a).

Reproductive condition

We found that T_b was similar in lizards of all reproductive conditions. However, male accuracy and effectiveness of thermoregulation were lower than those of gravid and non-gravid females. This result may be a consequence of males spending more time searching for mates (Shine et al. 2000) or defending their territories (Marler et al. 1995) to the detriment of thermoregulation.

Regarding gravid females, they might be facing a trade-off between their own PTR and optimum embryo-development temperature, which has proven to be lower in several oviparous (Mathies and Andrews 1997) and viviparous (Beuchat 1986; Shine and Harlow 1993) lizards. Actually, we found that gravid female T_{pref} was lower as egg laying approached. This finding suggests that embryo need for lower temperatures

increases at more advanced developmental stages. However, T_{pref} of gravid females was similar to that of non-gravid females and males. Other lizards show impaired escape speed when gravid (Shine 2003), and thus avoid exposure to predators by reducing basking time, leading to reduced body temperatures (Lin et al. 2008). Nevertheless, we can discard this explanation since escape speed is not impaired in gravid *P. algirus* in this system (Zamora-Camacho et al. 2014b). In fact, gravid females in this system show impaired escape capacity only at suboptimal body temperature (Zamora-Camacho et al. 2015), which probably encourages them to achieve higher body temperature.

Conclusions

In short, T_a , T_{pref} and d_e index tended to diminish with rising elevation, while T_b showed no elevational tendency. This result suggests that, in the field, other factors than thermal availability constrain lizard thermoregulation capacity. In fact, T_b seems to be constrained by T_a at the highest elevations. Nevertheless, d_e is more suitable at high elevations, suggesting that low-elevation lizards face excess ambient temperature. However, d_e at high elevations is better in fully sun-exposed microhabitats and at midday. This finding indicates that high-elevation lizards still have to bask actively to attain appropriate T_b , thus increasing thermoregulation costs, and their optimal daily activity period is limited to midday.

For reproductive status, the accuracy and effectiveness of thermoregulation was better in gravid and non-gravid females than in males, probably because males spend more time defending their territories and searching for mates. Furthermore, gravid females chose lower T_{pref} as egg laying approached, consistent with lower optimum embryo-development temperatures.

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All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. This article does not contain any studies with human participants performed by any of the authors. The authors declare that they have no conflict of interest.

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