



Original article

Seasonal patterns of body temperature and microhabitat selection in a lacertid lizard

Zaida Ortega^{*}, Valentín Pérez-Mellado

Department of Animal Biology, University of Salamanca, Campus Miguel de Unamuno, 37007, Salamanca, Spain

ARTICLE INFO

Article history:

Received 12 May 2016

Received in revised form

8 August 2016

Accepted 13 August 2016

Available online 21 August 2016

Keywords:

Thermal biology

Microhabitat selection

Lacertidae

Lizard

Seasonality

ABSTRACT

In temperate areas, seasonal changes entail a source of environmental variation potentially important for organisms. Temperate ectotherms may be adapted to the seasonal fluctuations in environmental traits. For lizards, behavioural adaptations regarding microhabitat selection could arise to improve thermoregulation during the different seasons. However, little is still known about which traits influence microhabitat selection of lizards and their adaptation to seasonality. Here we used *Podarcis guadarramae* to study the role of potential intrinsic (body size, sex, age) and environmental traits (air and substrate temperatures, wind speed, and sunlight) in the seasonal changes of body temperatures and microhabitat selection of lizards. We measured body temperatures of lizards in the same habitat during the four seasons and compared the climatic variables of the microhabitats selected by lizards with the mean climatic conditions available in their habitat. Body temperatures were similar for adult males, adult females, and juveniles within each season, being significantly higher in summer than in the other seasons, and in spring than in winter. The same pattern was found regarding substrate and air temperatures of the selected microhabitats. Wind speed and air temperature did not affect body temperatures, while body length was marginally significant and substrate temperatures and season did affect the body temperatures of lizards. Our results during the whole year support the idea that the seasonality could be the most important factor affecting body temperatures of these temperate species. Regarding microhabitat selection, environmental constraints, as environmental temperatures and wind speed, affected the seasonal changes on behavioural thermoregulation of lizards. This effect was similar between sexes and age classes, and was independent of body size. In addition, importance of sunlight exposure of the selected microhabitats (full sun, filtered sun, or shade) also changed between seasons. Hence, environmental constraints were the main forces driving seasonal changes in microhabitat selection.

© 2016 Elsevier Masson SAS. All rights reserved.

1. Introduction

Environmental temperatures available for organisms vary mainly with latitude, altitude, habitat structure, seasonality and climate change (Díaz et al., 2006; Solomon et al., 2007; Deutsch et al., 2008; Sears et al., 2011; Graae et al., 2012). All biological functions are thermo-dependent in ectotherms, so they must deal with environmental variations in order to achieve suitable body temperatures for physiological performance (Angilletta, 2009). Thus, thermoregulation is a key aspect of the biology of ectotherms, and determines many facets of their life history, physiology,

ecology and evolution (Cowles and Bogert, 1944; Huey, 1974; Adolph and Porter, 1993; Angilletta, 2009). Seasonal thermal fluctuations may lead ectotherms to adapt their physiology and behaviour (Huey, 1982; Christian and Bedford, 1995; Angilletta, 2009; Basson and Clusella-Trullas, 2015). Despite the supposed important role of seasonal changes in the thermal biology of ectotherms, few studies have specifically addressed the effect of seasonality in lizards (e.g. Díaz and Cabezas-Díaz, 2004; Díaz et al., 2006; Ortega et al., 2014; Basson and Clusella-Trullas, 2015).

Lacertids are effective thermoregulators (Avery, 1976; Van Damme et al., 1990; Ortega et al., 2016b). Their main mechanisms of thermoregulation are the adjustment of their activity periods (Hertz, 1992; Adolph and Porter, 1993), the selection of microhabitats with different climatic traits (Heath, 1970; Bauwens et al., 1996), and the postural adjustments (Bauwens et al., 1996). The combination of these strategies depends on the balance between

^{*} Corresponding author. Department of Animal Biology, University of Salamanca, Campus Miguel de Unamuno, s/n, 37007, Salamanca, Spain.

E-mail address: zaidaortega@usal.es (Z. Ortega).

their costs and benefits (Huey and Slatkin, 1976; Sears and Angilletta, 2015). Here we used *Podarcis guadarramae* to study the relation between potential intrinsic and environmental constraints in the effect of seasonality in body temperatures and microhabitat selection of lizards. The main aims of our study are: (1) to address the effect of intrinsic (body size, sex and age) and environmental (air and substrate temperatures, wind speed, and sunlight) constraints in the body temperature exhibited by lizards across their annual cycle, (2) to test if microhabitat selection changes between seasons, and (3) to study how the environmental variables affect the microhabitat selection of lizards on each season.

2. Materials and methods

2.1. Study species and area

The Lusitanian wall lizard, *Podarcis guadarramae* (Boscá, 1916), the former *P. hispanicus* 'type I' (Pinho et al., 2007; Kaliontzopoulou et al., 2011), has been recently proposed as a species (Geniez et al., 2014). *Podarcis guadarramae* lizards inhabit the central and north-western Iberian Peninsula (Salvador and Carretero, 2014). They are rupicolous lizards, living mainly in granite rocks and artificial walls (Diego-Rasilla and Pérez-Mellado, 2003). They are effective thermoregulators, which rely on selection of microhabitat for their daily patterns of temperature regulation (Díaz et al., 1996; Gabirot et al., 2013). As a model of study, we used a population of *P. guadarramae* of the western end of the Sistema Central of the Iberian Peninsula (Nava de Francia, Salamanca, Spain) at 1050 m a.s.l. The study area is a granite outcrop, mixed with oaks (*Quercus pyrenaica*) and scrub vegetation (mainly *Calluna vulgaris* and *Erica* sp.).

2.2. Body temperatures and environmental variables

We studied lizards in 50 sunny days of fieldwork distributed across the whole annual activity period: spring (7th–8th April, 3rd–10th May and 4th–9th June 2011), summer (27th June, 4th–31st July, and 7th–30th August 2010, and 9th July and 27th August 2011), autumn (20th–27th October and 5th November 2010), and winter (5th–26th February and 20th March 2011). We captured active lizards by noose, during their daily activity period: 07:00–17:00 GMT in spring, 06:00–19:00 GMT in summer, and 10:00–16:00 GMT in autumn and winter. Immediately after capture, we measured the cloacal body temperature (T_b), air temperature (T_a) 1 cm above the capture point, and substrate temperature of the capture point (T_s), as well as wind speed. Temperatures were measured with a Testo® 925 digital thermometer, shadowing the probe, and wind speed was measured with a Kestrel® 3000 anemometer. We also recorded the type of substrate (rock, soil, or grass), the orientation of the

substrate (flat, North, South, East, or West), the altitude of the perch, and the sunlight exposure (full sun, filtered sun, or full shade). Finally, we recorded sex and age class (adult or juvenile), and we measured snout-went length (SLV) and weight of lizards.

2.3. Microhabitat selection

In order to study the influence of the climatic variables on the selection of microhabitat, we compared the climatic conditions of each capture point with the mean values of four points that represent mean availability of each variable. To establish an objective rule, we chose these points as the ones 1 m away from the capture point on each compass direction (North, South, East and West; see Ortega et al., 2016a). Thus, we measured T_a , T_s , and wind speed of these four points, similarly as we did with the capture point of the lizard. We used the mean values of the four points, associated to each capture point, to represent the mean availability of climatic conditions in the surroundings of each particular lizard in a certain moment. We will refer to these measurements as 'mean availability'. Then, for each lizard, we calculated the deviation between the T_s of the selected point and the mean T_s of the four points, which we refer as d_s , and would represent the degree of selection for the T_s . Similarly, we calculated the deviation between the T_a of the selected point and the mean T_a of the four points, referred as d_a , which would represent the degree of selection regarding T_a . Finally, we calculated the deviation between the wind speed of the selected point and the mean wind speed of the four points, d_{wind} , which would represent the degree of selection regarding the speed of the wind.

2.4. Data analysis

We performed parametric statistics when data followed the assumptions of normality and variance homogeneity. When data did not fulfill these assumptions, even after log-transformations, we carried out non-parametric equivalent tests (Crawley, 2012; Sokal and Rohlf, 1995). To assess the effect of the season, body size, and environmental conditions on body temperatures of lizards, we fitted a generalized linear model (GLM) with normal errors (Crawley, 2012). We considered the season, wind speed, substrate temperature, air temperature, and body size of lizards (SVL) as potential explanatory variables, and body temperature as the response variable. First, we considered a saturated model with all explanatory variables and their interactions. Then, following the Akaike Information Criterion (AIC, see Burnham and Anderson, 2004), we removed, in a stepwise procedure, no significant variables and interactions ($p > 0.05$). In this way, we obtained the simplest significant model to explain body temperatures exhibited by *P. guadarramae* lizards along their annual activity. For each

Table 1

The first part of the table show the mean \pm SE (N) values of body temperatures (T_b) of *Podarcis guadarramae* lizards, as well as substrate temperatures (T_s), air temperatures (T_a) and wind speed of their capture places. The second part of the table shows the p-values of the Kruskal-Wallis post-hoc paired comparisons for these variables between seasons. Significant differences are marked in bold.

	Seasons	T_b (°C)	T_s (°C)	T_a (°C)	Wind speed (ms ⁻¹)
Mean values	Spring	23.57 \pm 0.50 (66)	24.24 \pm 0.57 (66)	23.04 \pm 0.54 (68)	0.25 \pm 0.05 (68)
	Summer	28.66 \pm 0.30 (134)	29.11 \pm 0.33 (136)	28.13 \pm 0.35 (137)	0.17 \pm 0.05 (137)
	Autumn	22.18 \pm 0.32 (46)	21.38 \pm 0.35 (46)	20.63 \pm 0.30 (46)	0.10 \pm 0.03 (46)
	Winter	20.68 \pm 0.22 (73)	19.96 \pm 0.27 (73)	18.83 \pm 0.22 (73)	0.32 \pm 0.06 (73)
Paired comparisons	Spring – Summer	<0.0001	<0.0001	<0.0001	<0.0001
	Spring – Autumn	1.000	0.021	0.090	0.080
	Spring – Winter	0.001	<0.0001	<0.0001	1.000
	Summer – Autumn	<0.0001	<0.0001	<0.0001	1.000
	Summer – Winter	<0.0001	<0.0001	<0.0001	<0.0001
	Autumn – Winter	0.133	0.411	0.059	0.031

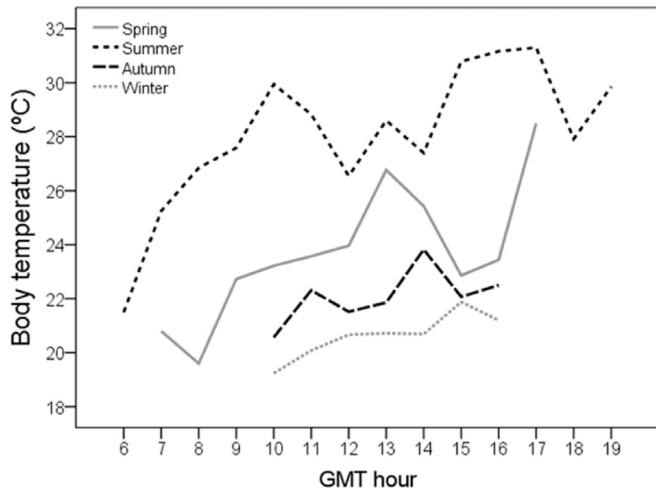


Fig. 1. Daily evolution of body temperatures of *Podarcis guadarramae* lizards regarding season.

Table 2
GLM of the effect of the intrinsic and environmental constraints on body temperatures (T_b) of *Podarcis guadarramae* ($N = 320$).

	Coefficient	SE	t	P
Intercept	5.95225	0.91077	6.535	2.62e⁻¹⁰
Season spring	-0.71124	0.36575	-1.945	0.0527
Season summer	0.84117	0.39163	2.148	0.0325
Season winter	-0.58224	0.34630	-1.681	0.0937
Substrate temperature (T_s)	0.70546	0.02876	24.530	<2e⁻¹⁶
Body size (SVL)	0.02803	0.01623	1.727	0.0852

Deviance residual: 1010.6, with 309 degrees of freedom. AIC = 1275.1, lower than the AIC of more complex models.
Significant results are marked in bold.

model, we evaluated data dispersion and the distribution of residual values (Crawley, 2012). We conducted all analyses on R, version 3.1.3 (R Core Team, 2015). We report mean values of variables accompanied by standard errors. Significance level was $\alpha = 0.05$.

3. Results

The studied population of *P. guadarramae* exhibited sexual size dimorphism, with larger males than females (mean SVL males: 49.40 ± 0.35 mm, $N = 142$; mean SVL females: 45.58 ± 0.42 mm, $N = 101$; one-way ANOVA, $F_{1, 241} = 49.317$, $P < 0.0001$). Males were also significantly heavier than females (mean weight males: 2.69 ± 0.06 g, $N = 142$; mean weight females: 1.82 ± 0.05 g, $N = 102$;

one-way ANOVA, $F_{1, 242} = 100.264$, $P < 0.0001$). In addition, mean SVL of juveniles was 35.95 ± 0.40 mm, and mean weigh 1.02 ± 0.04 g ($N = 77$). However, body temperatures of adults were similar between sexes in all seasons (two-way ANOVA, interaction: $F_{3, 234} = 0.177$, $P = 0.912$, sex: $F_{1, 234} = 0.007$, $P = 0.935$, season: $F_{3, 234} = 71.760$, $P < 0.0001$). Similar results were found for the age classes (two-way ANOVA, interaction: $F_{3, 311} = 0.579$, $P = 0.629$, age: $F_{1, 311} = 0.331$, $P = 0.565$, season: $F_{3, 311} = 76.310$, $P < 0.0001$). Thus, we pooled body temperatures of adult males and females and juveniles for subsequent analyses (Table 1).

Body temperatures were significantly higher in summer than in spring, autumn and winter, and in spring than in winter (Fig. 1, Table 1). Substrate temperatures of the capture points were significantly higher in summer than in other seasons, and significantly higher in spring than autumn and winter, while they were similar during autumn and winter (Table 1). Air temperatures of the capture points were significantly higher in summer than in spring, autumn and winter, and in spring than winter (Table 1). Finally, wind speed was higher for spring and winter than for summer and autumn (Table 1). The GLM reveals that wind speed and air temperature had not a significant effect on body temperatures of lizards, while the substrate temperature and the season significantly affected the body temperatures of lizards (Table 2). In addition, the effect of body size was marginally significant (Table 2).

Mean values of the deviations between the capture points of lizards and the mean availability for substrate temperatures (d_s), air temperatures (d_a) and wind speed (d_{wind}) are reported in Table 3. Neither sex nor age of lizards affected the degree of selection of T_s (two-way ANOVA, $F_{2, 281} = 1.273$, $P = 0.282$). However, the season showed a significant effect on degree of selection of T_s by lizards (two-way ANOVA, $F_{3, 281} = 8.138$, $P < 0.0001$), and this effect was similar for males, females and juveniles (two-way ANOVA interaction term, $F_{6, 281} = 0.899$, $P = 0.496$). Seasonal differences were found between spring and summer with winter, and summer with autumn (Table 3; Fig. 2). The selection for higher T_s was significantly larger (that is, higher d_s) in winter than in spring and summer, and in autumn than in summer (Fig. 2). Sex and age did not affect the degree of selection of T_a either (two-way ANOVA, $F_{2, 281} = 1.689$, $P = 0.187$). Season significantly affected the degree of selection of T_a (two-way ANOVA, $F_{3, 281} = 7.505$, $P < 0.0001$), and the effect was similar for males, females and juveniles (two-way ANOVA interaction term, $F_{6, 281} = 1.940$, $P = 0.074$). Seasonal differences were found between spring and summer with autumn and winter (Table 3). Thus, the extent to which lizards selected T_a higher than the mean available T_a was larger in autumn and winter than in spring and summer (Fig. 2). In fact, lizards did not appear to select their microhabitats regarding T_a during spring and summer (Fig. 2). The selection of microhabitat regarding wind speed was similar for males, females and juveniles within each season (Kruskal-Wallis

Table 3
The first part of the table reports the mean \pm SE values of the deviations between the substrate temperature (d_s), air temperature (d_a), and wind speed (d_{wind}), of the capture points of lizards and the mean availability values of each variable associated to each capture point, respectively, for each season. The second part of the table reports the p-values of the Kruskal-Wallis post-hoc paired comparisons between the seasons. Significant differences are marked in bold.

		d_s (°C)	d_a (°C)	d_{wind} (ms ⁻¹)
Season (N)	Spring (66)	0.353 ± 0.254	-0.003 ± 0.169	-0.060 ± 0.055
	Summer (112)	0.019 ± 0.188	-0.016 ± 0.126	-0.018 ± 0.039
	Autumn (44)	0.983 ± 0.257	0.844 ± 0.201	0.032 ± 0.031
	Winter (71)	1.474 ± 0.220	0.675 ± 0.139	-0.130 ± 0.063
Paired comparisons	Spring – Summer	0.684	1.000	<0.0001
	Spring – Autumn	0.342	0.005	<0.0001
	Spring – Winter	0.005	0.013	0.395
	Summer – Autumn	0.028	0.001	1.000
	Summer – Winter	<0.0001	0.003	<0.0001
	Autumn – Winter	0.551	0.905	<0.0001

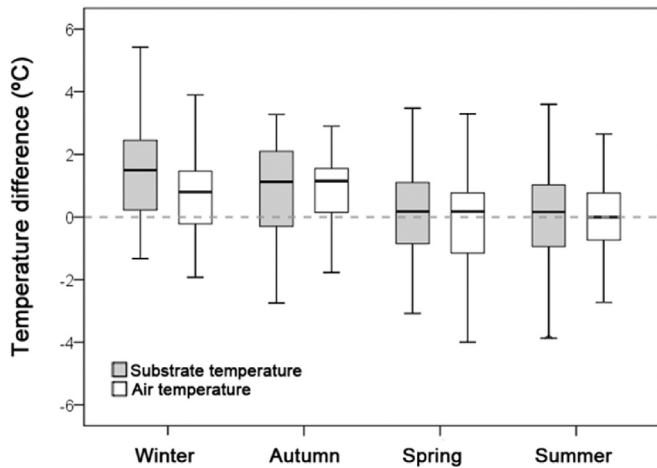


Fig. 2. Boxplots of the deviations between substrate and air temperatures of the capture point of lizards and the mean availability of the microhabitats for *Podarcis guadarramae* in all seasons.

Table 4
Results of the G-tests for the sunlight exposure categories (full sun, filtered sun, full shade) of the capture points of *Podarcis guadarramae* lizards vs the mean availability in their microhabitat for the four seasons. Significant results are marked in bold.

		G	p-value
Spring	Full sun – Filtered sun	0.334	0.436
	Full sun – Full shade	0.001	0.002
	Filtered sun – Full shade	0.002	0.020
Summer	Full sun – Filtered sun	0.129	0.173
	Full sun – Full shade	0.571	0.640
	Filtered sun – Full shade	0.369	0.412
Autumn	Full sun – Filtered sun	0.045	0.075
	Full sun – Full shade	0.001	0.008
	Filtered sun – Full shade	0.101	0.490
Winter	Full sun – Filtered sun	0.026	0.036
	Full sun – Full shade	0.042	0.080
	Filtered sun – Full shade	0.528	0.723

test, spring: $H = 3.284, P = 0.070, N = 66$; summer: $H = 0.000, P = 0.996, N = 112$; autumn: $H = 0.066, P = 0.797, N = 44$; winter: $H = 0.309, P = 0.579, N = 71$). However it was significantly different between seasons (Kruskal-Wallis test, $H = 61.505, P < 0.0001, N = 293$). There were significant differences between all paired comparisons except for spring and winter, and summer and autumn (Table 3). Hence, lizards avoided the wind to a greater extend in spring than summer and autumn, and in winter than summer and autumn (Table 3). Finally, lizards avoided shaded

microhabitats and preferred microhabitats in filtered sun in spring, while they did not show preferences regarding sunlight in summer, avoided shaded microhabitats in autumn, and avoided filtered sun areas in winter (Table 4 and Fig. 3).

4. Discussion

Adult individuals of *P. guadarramae* showed sexual size dimorphism, with significantly bigger males than females. A recent study reported that males of the Lusitanian wall lizard have slower heating rates than females, due to their bigger body size (Gabirot et al., 2013). However, body temperatures of adult males and females, as well as those of juvenile individuals, were similar within each season. Although body size is known to affect body temperature of small lizards (Herczeg et al., 2007), such effect would be smaller than the effect of the environmental traits experienced by lizards on their habitats.

Body temperature was significantly higher in summer than in the other seasons, and in spring than in winter. The same pattern was found regarding substrate and air temperatures of the microhabitats selected by lizards. Wind speed and air temperature did not affect body temperature of lizards, while body length was marginally significant and substrate temperature and season significantly affected the body temperatures of lizards. The important role of substrate temperature is probably reflecting the use of thigmothermy as a mechanism of thermoregulation by this species (Pérez-Mellado, 1983). In any case, our results studying the thermal biology during the whole year support the conclusion that seasonality is the most important factor affecting body temperatures of this temperate lacertid. The important role of seasonality in thermal biology of lizards has been addressed in previous studies, although the effect of seasons was not assessed throughout the whole annual activity period (Díaz and Cabezas-Díaz, 2004; Díaz et al., 2005; Sepúlveda et al., 2008; Ortega et al., 2014).

Regarding microhabitat selection, we have demonstrated that environmental constraints, as environmental temperatures and wind speed, affected the seasonal changes on behavioural thermoregulation of lizards. This effect was similar between sexes and age classes, and is independent of body size. Hence, environmental constraints were the main forces driving seasonal changes in microhabitat selection of *Podarcis guadarramae*. The role of sun radiation in microhabitat selection also changed significantly between seasons. Lizards avoided shaded microhabitats in spring and autumn. They preferred microhabitats in filtered sun in spring, while they even avoided these filtered-sun places in winter. However, the sunlight exposure was irrelevant to microhabitat choice during summer. These results emphasize the behavioural flexibility of lizards to adapt to seasonal climatic variations. Probably, within

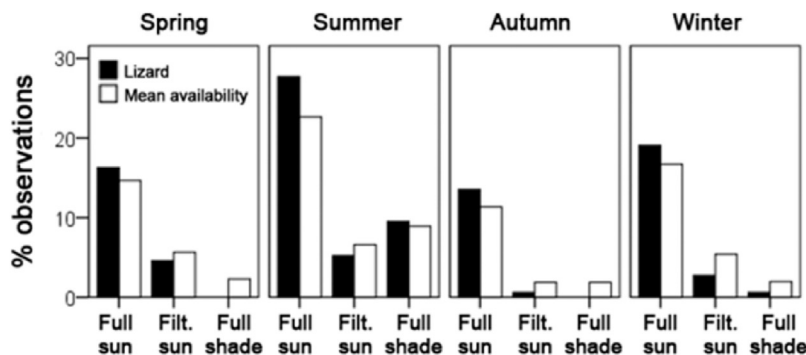


Fig. 3. Seasonal comparison of the frequencies of the sunlight exposure categories of *Podarcis guadarramae* capture places vs the mean availability of the habitat. 'Filt. sun' = filtered sun.

their possibilities, also conditioned by mating, predation or other intrinsic constraints, lizards would adapt their behaviour to choose the substrates with the more suitable heating rates depending on their thermal requirements on each season. This idea is also supported by the fact that lizards are able to select the heat resource that provides the more suitable heat transmission mode for different moments of the daily activity period (Belluere and Carrascal, 2002).

Since thermal preferences of lizards may also shift seasonally (e.g. Patterson and Davies, 1978; Díaz et al., 2006; Clusella-Trullas and Chown, 2014), and we only had data on thermal preferences of summer, we did not assess the seasonal shifts in thermal quality of the habitat and accuracy and effectiveness of thermoregulation (Hertz et al., 1993). The study of the patterns of influence of the different intrinsic and environmental traits in the indexes of thermoregulation of lizards would throw more light in the seasonal drivers of lizard thermoregulation. Even though, we have shown that season was the most important factor conditioning body temperature in the big picture, over body size, sex, or age of lizards, or the climatic variables of the microhabitats separately. In addition, we have shown that the drivers of microhabitat selection of Lusitanian wall lizards, and, probably, other Mediterranean lizards, change their roles between seasons. In winter, the preferences are clear: sunny substrates with higher temperatures and lower wind speed than the surroundings. In spring and autumn, the effect of sun, temperature and wind was also significant, but not so strong. However, wind, sun and temperature were irrelevant to microhabitat preferences in summer, and other traits, as protection against predators or access to food would be more important. Finally, our results could have important implications regarding the predictions for ectotherms under climate change, and underscore the necessity to incorporate seasonal changes to these projections, at least for Mediterranean habitats.

Role of each author

VPM designed the study; ZO conducted the study, analyzed the data and wrote and corrected the manuscript.

Acknowledgements

Lizards were sampled under permits number EP/CYL/472/2010 and EP/CYL/381/2011 of the Castilla y León Environmental Agency. We thank Pili Mary, Ignacio, Koko and Jero for their support during fieldwork, Mario Garrido and Abraham Mencía for their support during analysis and writing, and Mary Trini Mencía and Joe McIntyre for linguistic revision. Financial support was provided to Zaida Ortega by a predoctoral grant of the University of Salamanca. This work was also supported by the research project CGL2012-39850-CO2-02 from the Spanish Ministry of Science and Innovation. We conducted all research in compliance with ethical standards and procedures of the University of Salamanca.

References

- Adolph, S.C., Porter, W.P., 1993. Temperature, activity, and lizard life histories. *Am. Nat.* 142, 273–295.
- Angilletta, M.J., 2009. *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford University Press, Oxford.
- Avery, R.A., 1976. Thermoregulation, metabolism and social behaviour in Lacertidae. In: *Morphology and Biology of Reptiles*, vol. 3. Academic Press, Cambridge, pp. 245–260.
- Basson, C.H., Clusella-Trullas, S., 2015. The behavior–physiology nexus: behavioral and physiological compensation are relied on to different extents between seasons. *Physiol. Biochem. Zool.* 88, 384–394.
- Bauwens, D., Hertz, P.E., Castilla, A.M., 1996. Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. *Ecology* 77, 1818–1830.
- Belliure, J., Carrascal, L.M., 2002. Influence of heat transmission mode on heating rates and on the selection of patches for heating in a Mediterranean lizard. *P. Physiol. Biochem. Zool.* 75, 369–376.
- Burnham, K.P., Anderson, D.R., 2004. Multimodel inference understanding AIC and BIC in model selection. *Sociol. Method Res.* 33, 261–304.
- Cowles, R.B., Bogert, C.M., 1944. A preliminary study of the thermal requirements of desert reptiles. *Bull. Am. Mus. Nat. Hist.* 83, 261–296.
- Christian, K.A., Bedford, G.S., 1995. Seasonal changes in thermoregulation by the frillneck lizard, *Chlamydosaurus kingii*, in tropical Australia. *Ecology* 76, 124–132.
- Clusella-Trullas, S., Chown, S.L., 2014. Lizard thermal trait variation at multiple scales: a review. *J. Comp. Physiol. B* 184, 5–21.
- Crawley, M.J., 2012. *The R Book*, second ed. Wiley, Chichester, UK.
- Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., Martin, P.R., 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Nat. Acad. Sci.* 105, 6668–6672.
- Díaz, J.A., Bauwens, D., Asensio, B., 1996. A comparative study of the relation between heating rates and ambient temperatures in lacertid lizards. *Physiol. Zool.* 69, 1359–1383.
- Díaz, J.A., Cabezas-Díaz, S., 2004. Seasonal variation in the contribution of different behavioural mechanisms to lizard thermoregulation. *Funct. Ecol.* 18, 867–875.
- Díaz, J.A., Cabezas-Díaz, S., Salvador, A., 2005. Seasonal changes in the thermal environment do not affect microhabitat selection by *Psammotromus algirus* lizards. *Herpetol. J.* 15, 295–298.
- Díaz, J.A., Iraeta, P., Monasterio, C., 2006. Seasonality provokes a shift of thermal preferences in a temperate lizard, but altitude does not. *J. Therm. Biol.* 31, 237–242.
- Diego-Rasilla, F.J., Pérez-Mellado, V., 2003. Home range and habitat selection by *Podarcis hispanica* (Squamata, Lacertidae) in western Spain. *Folia Zool.* 52, 87–98.
- Gabirot, M., Balleri, A., López, P., Martín, J., 2013. Differences in thermal biology between two morphologically distinct populations of Iberian wall lizards inhabiting different environments. *Ann. Zool. Fenn.* 50, 225–236.
- Geniez, P., Sá-Sousa, P., Guillaume, C.P., Cluchier, A., Crochet, P.A., 2014. Systematics of the *Podarcis hispanicus* complex (Sauria, Lacertidae) III: valid nomina of the western and central Iberian forms. *Zootaxa* 3794, 1–51.
- Graae, B.J., De Freene, P., Kolb, A., Brunet, J., Chabrierie, O., Verheyen, K., Pepin, N., Heinken, T., Zobel, M., Shevtsova, A., Nijls, I., Milbau, A., 2012. On the use of weather data in ecological studies along altitudinal and latitudinal gradients. *Oikos* 121, 3–19.
- Heath, J.E., 1970. Behavioral regulation of body temperature in poikilotherms. *The Physiol.* 13, 399–410.
- Herczeg, G., Török, J., Korsós, Z., 2007. Size-dependent heating rates determine the spatial and temporal distribution of small-bodied lizards. *Amphibia-Reptilia* 28, 347–356.
- Hertz, P.E., 1992. Evaluating thermal resource partitioning. *Oecologia* 90, 127–136.
- Hertz, P.E., Huey, R.B., Stevenson, R.D., 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am. Nat.* 142, 796–818.
- Huey, R.B., 1974. Behavioral thermoregulation in lizards: importance of associated costs. *Science* 184, 1001–1003.
- Huey, R.B., 1982. Temperature, physiology, and the ecology of reptiles. In: Gans, C., Pough, F.H. (Eds.), *Biology of the Reptilia*. Vol. 12. Physiology C. Physiological Ecology. Academic Press, New York, pp. 25–91.
- Huey, R.B., Slatkin, M., 1976. Cost and benefits of lizard thermoregulation. *Q. Rev. Biol.* 51, 363–384.
- Kalioztopoulou, A., Pinho, C., Harris, D.J., Carretero, M.A., 2011. When cryptic diversity blurs the picture: a cautionary tale from Iberian and North African *Podarcis* wall lizards. *Biol. J. Linn. Soc.* 103, 779–800.
- Ortega, Z., Mencía, A., Pérez-Mellado, V., 2016a. Are mountain habitats becoming more suitable for generalist than cold-adapted lizards thermoregulation? *Peer J.* 4, e2085.
- Ortega, Z., Mencía, A., Pérez-Mellado, V., 2016b. The peak of thermoregulation effectiveness: thermal biology of the Pyrenean rock lizard, *Iberolacerta bonnali* (Squamata, Lacertidae). *J. Therm. Biol.* 56, 77–83.
- Ortega, Z., Pérez-Mellado, V., Garrido, M., Guerra, C., Villa-García, A., Alonso-Fernández, T., 2014. Seasonal changes in thermal biology of *Podarcis lilfordi* (Squamata, Lacertidae) consistently depend on habitat traits. *J. Therm. Biol.* 39, 32–39.
- Patterson, J.W., Davies, P.M.C., 1978. Preferred body temperature: seasonal and sexual differences in the lizard *Lacerta vivipara*. *J. Therm. Biol.* 3, 39–41.
- Pérez-Mellado, V., 1983. Activity and thermoregulation patterns in two species of Lacertidae: *Podarcis hispanica* (Steindachner, 1870) and *Podarcis bocagei* (Seoane, 1884). *Cienc. Biol. Ecol. Syst.* 5, 5–12.
- Pinho, C., Harris, D.J., Ferrand, N., 2007. Contrasting patterns of population subdivision and historical demography in three western Mediterranean lizard species inferred from mitochondrial DNA variation. *Mol. Ecol.* 16, 1191–1205.
- R Core Team, 2015. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/> (accessed 11.05.16).
- Salvador, A., Carretero, M.A., 2014. *Podarcis hispanicus* (Steindachner, 1870). In: Salvador, A., Ramos (Eds.), *Reptiles*, 2ª Edición Revisada Y Aumentada. Fauna Ibérica, vol. 10. Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, Madrid, pp. 537–556.
- Sears, M.W., Angilletta, M.J., 2015. Costs and benefits of thermoregulation revisited:

- both the heterogeneity and spatial structure of temperature drive energetic costs. *Am. Nat.* 185, E94–E102.
- Sears, M.W., Raskin, E., Angilletta, M.J., 2011. The world is not flat: defining relevant thermal landscapes in the context of climate change. *Integr. Comp. Biol.* 51, 666–675.
- Sepúlveda, M., Vidal, M.A., Fariña, J.M., Sabat, P., 2008. Seasonal and geographic variation in thermal biology of the lizard *Microlophus atacamensis* (Squamata: Tropiduridae). *J. Therm. Biol.* 33, 141–148.
- Solomon, S., Qin, D., Manning, M., Marquis, M., Averyt, K., Tignor, M.M.B., Miller, H.L., Chen, Z. (Eds.), 2007. *Climate Change 2007: the Physical Science Basis*. Cambridge University Press, Cambridge, UK.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry: the Principles and Practice of Statistics in Biological Research*. State University of New York at Stony Brook, New York.
- Van Damme, R., Bauwens, D., Verheyen, R.F., 1990. Evolutionary rigidity of thermal physiology: the case of the cool temperate lizard *Lacerta vivipara*. *Oikos* 57, 61–67.