Volume 27 (July 2017), 239-244

Herpetological Journal

FULL PAPER

Published by the British Herpetological Society

Aspects of the thermal ecology of the lizard *Iberolacerta monticola* of Serra da Estrela (Portugal)

Zaida Ortega[1,2], Abraham Mencía[1,3] & Valentín Pérez-Mellado[1]

[1]Department of Animal Biology, University of Salamanca, Campus Miguel de Unamuno, 37007, Salamanca, Spain.

[2]Programa de Pós-Graduação em Ecologia e Conservação, Universidade Federal do Mato Grosso do Sul, CEP 79070-900, Campo Grande, Mato Grosso do Sul, Brazil.

[3]Programa de Pós-Graduação em Biologia Animal, Universidade Federal do Mato Grosso do Sul, CEP 79070-900, Campo Grande, Mato Grosso do Sul, Brazil.

We studied the thermal ecology of the montane Iberian rock lizard, *Iberolacerta monticola*, in the western area of its distribution at the Serra da Estrela (Portugal). We calculated the precision of thermoregulation and the indices of thermal quality of the habitat, and accuracy and effectiveness of thermoregulation. To complete the study of the thermal ecology, we assessed the relationships between body and environmental temperatures, and we described the thermal and spatial heterogeneity of the habitat. Our results indicate that the Iberian rock lizard is a cold-specialist, with a preferred temperature range between 29.80 and 31.60 °C. Thus, precision of thermoregulation is 1.8 °C, which is a normal range in thermal specialists, like other species of the genus *Iberolacerta*. This result is important because being thermal specialists and living in mountaintops make Iberian mountain lizards particularly vulnerable to global warming. The habitat of *I. monticola* at the Serra da Estrela is formed of microhabitats offering different operative temperatures, which allows lizards to select the most suitable for thermoregulation at any time of the day. Iberian rock lizards achieve an effectiveness of thermoregulation of 0.86, thanks to careful thermoregulatory behaviour. Rocky microhabitats occupy more than 50% of its habitat, so is probable that lizards are selecting rocks to warm themselves faster, minimising the costs of thermoregulation. A possible thigmothermic component of this kind would be unique among the species of *Iberolacerta*.

Key words: thermoregulation, cold-specialist, global warming, lizard, mountains, *Iberolacerta monticola*, Lacertidae, thigmothermy

INTRODUCTION

Among environmental variables, temperature has probably one of the largest effects on the life and evolution of ectotherms. Thermoregulating ectotherms show two dimensions regarding temperature: thermal sensitivity, which describes the extent to which their physiological performance depends on temperature (e.g. Huey & Kingsolver, 1989) and thermoregulation (e.g. Hertz et al., 1993), which describes the ability to regulate body temperature (see a review in Angilletta, 2009). Lizards mainly thermoregulate by adjusting activity periods, shuttling between different thermal microhabitats or adjusting their body posture (Bauwens et al., 1996). The combination of these strategies depends on the balance between their costs and benefits (Huey & Slatkin, 1976; Blouin-Demers & Nadeau, 2005).

Lacertid lizards are heliothermic thermoregulators. Thermal preferences are considered a conservative phenotypic trait (Huey et al., 2003), so we could expect small variations within lacertid lizards due to their common phylogenetic history (Kapli et al., 2011; Mayer & Pavlicev, 2007). Nonetheless, substantial differences have been detected between species, populations, seasons, or even groups of individuals inside the same population (e.g. Díaz et al., 2006). In addition, the degree to which a population approach their thermal preferences (that is, the degree of thermoregulation) also varies within the Lacertidae regarding season, altitude, sex, or habitat traits (Sagonas et al., 2013; Ortega et al., 2016a; 2016c, 2016e; Zamora-Camacho et al., 2016). Iberian lizards of the genus *Iberolacerta* inhabit high mountain areas, where they migrated after the last glaciation probably escaping warming and competition with more thermophilic lizards (Crochet et al., 2004; Mouret et al., 2011). Most are highly endangered due to restricted distributions, the destruction of their habitats and global warming (Pérez-Mellado et al., 2009).

Iberolacerta monticola lizards are vulnerable to global warming and is predicted that they could lose their thermally suitable habitat between 2020 and 2050 (Araújo et al., 2006; Carvalho et al., 2010). Although predictions of habitat could be inaccurate, realistically the physiology of high mountain lizards also made them highly vulnerable to climate change (Huey et al., 2012). This is mainly because they are cold-specialists and, as they already live in the mountain tops, are unable to migrate to cooler areas (Huey et al., 2012). Iberian rock lizards from Portugal are completely isolated from other populations, and inhabit the highest possible area within its distributional range, so the chance of migration to cooler habitats is literally nonexistent

Correspondence: Zaida Ortega (zaidaortega@usal.es)

(Pérez-Mellado, 1982; Pérez-Mellado, 2004). Therefore, it is necessary to study their thermal biology in order to make more accurate predictions about their future that will help us to design the conservation measures that could prevent their extinction. Here we aim to study the thermal ecology of *I. monticola*, which is still unknown. We assessed the thermal sensitivity of the species, measuring thermal preferences in laboratory conditions, and thermoregulation, calculating the indices developed by Hertz et al. (1993). We also studied the thermal and spatial heterogeneity of the habitat (e.g. Sears & Angilletta, 2015; Logan et al., 2015). Thus, we aim to quantify the thermal requirements and the thermoregulation abilities of the species, as well as the thermal characteristics of the habitat of *I. monticola*, in order to deepen in the knowledge of the thermal biology of the Lacertidae, and to gain the knowledge on this species that is needed to establish conservation priorities under the global warming predictions.

MATERIALS AND METHODS

Study species and study area

The Iberian rock lizard, *I. monticola* (Boulenguer, 1905) is endemic to the Iberian Peninsula. Two subspecies are considered nowadays: *I. monticola cantabrica* (Mertens, 1929) in the Cantabrian Mountains and Galicia (Carranza et al., 2004; Remón et al., 2013), and *I. monticola monticola* (Boulenguer, 1905) in the Serra da Estrela in Portugal (Pérez-Mellado, 1982; Carranza et al., 2004; Crochet et al., 2004). In the Serra da Estrela, *I. monticola monticola* lives between 1500 m and 1993 m of altitude (Pérez-Mellado, 1997). It is an insectivorous species, and whilst some temperature data is known, thermoregulation has not been studied in depth (Arguëllo & Salvador, 1988; Pérez-Mellado, 1982; Arribas, 2014).

The study was conducted in "Fonte dos Perús" (Manteigas, Portugal) at 1800 m altitude, at the Natural Park of Serra da Estrela. "Fonte dos Perús" is about 4 km from the highest point of Portugal, the plateau known as Torre (1993 m). The area consists of tarns, screes and large granite rock formations, with sparse vegetation consisting of grasses and shrubs including *Cytisus* spp. and *Juniperus communis nana*, among others.

Field sampling

Body temperatures (T_b) were sampled during July of 2012. A total of 43 *I. monticola* adult lizards (27 males and 16 females) were captured by noosing, between 07.00 and 16.00 h GMT (Greenwich Mean Time). For each lizard we measured body temperature (T_b) immediately after capture, air temperature (T_a) 1 cm above the capture point, and substrate temperature (T_s) at the capture point. Temperatures were measured with a Testo® 925 digital thermometer (± 0.1 °C precision).

Operative temperatures (T_e) were recorded in the same area of study, and simultaneously to T_b sampling, in order to assure the same weather conditions. We used copper models as null T_e models (Bakken & Angilletta, 2014). One thermocouple probe was placed into each hollow model and connected to a data logger HOBO H8 (® Onset Computer Corporation) programmed to take a temperature recording every five minutes. The eight data loggers were randomly placed in different microhabitats: (1) under rock, (2) flat rock in shade, (3) grass in shade, (4) grass in full sun, (5) flat rock in full sun, (6) rock facing West in full sun, (7) rock facing North in full sun and (8) rock facing South in full sun. Thermal heterogeneity of the habitat was also quantified as the standard deviation of the mean operative temperatures of the data loggers (see Logan et al., 2015; Ortega et al., 2016e). Finally, spatial heterogeneity was described by mean values of the proportion of cover and the frequency of each microhabitat type of 15 lineal transects, 25 m long each (Ortega et al., 2016e).

Preferred temperature range (PTR)

We studied the PTR of *I. monticola* in July of 2012 during the same field work trip, in order to assure similar weather conditions. We captured 24 Iberian rock lizards (12 males and 12 females), that were housed in individual terraria, fed daily with mealworms and crickets, and provided with water ad libitum. The thermal gradient was built in a glass terrarium (100 x 60 x 60 cm) with a 150 W infrared lamp over one of the sides, obtaining a gradient between 20 to 60 ˚C. The behaviourally selected temperature (T_{sel}) of each lizard was recorded with a Testo® 925 digital thermometer each hour from 08.00 to 16.00 h (GMT), obtaining 150 selected temperature values. The 50% of central values of selected body temperatures was considered as the PTR to assess thermoregulation (Hertz et al., 1993; Blouin-Demers & Nadeau, 2005). Thus, we refer to each selected temperature as T_{sel} and the 50 % central values of the T_{sel} as PTR. These were used for calculation of the indices of thermoregulation. After the experiment, lizards were released in their capture places at "Fonte dos Perús".

Data analysis

In order to study the thermoregulation in *I. monticola*, we calculated the three indices developed by Hertz et al. (1993): (1) the index of accuracy of thermoregulation (mean d_b), calculated as the mean of absolute values of the deviations between each T_b from the PTR (as they measure deviation from the optimum, higher values of d_b indicate lower accuracy of thermoregulation, and vice-versa), (2) the index of habitat thermal quality (mean d_e), calculated as the mean of absolute values of the deviations of each T_e from the PTR (analogously to d_b, higher values of d_e indicate a lower habitat thermal quality, and vice-versa), and (3) the index of effectiveness of thermoregulation (E), calculated as $E = 1 - (d_b / d_e)$, which ranges from 0 to 1, where a higher effectiveness of thermoregulation translates into a higher value of E (see Hertz et al., 1993). Effectiveness of thermoregulation was calculated with THERMO, a Minitab module that has been used in previous studies of thermal biology (e.g. Ortega et al., 2014) and uses three kinds of input data: T_b, T_e and T_{sel} of the PTR, and was programmed to perform bootstraps of 100 iterations, building pseudo-distributions of three kinds of output values: d_b, d_e, and E. Mean values are accompanied by standard errors (SE).

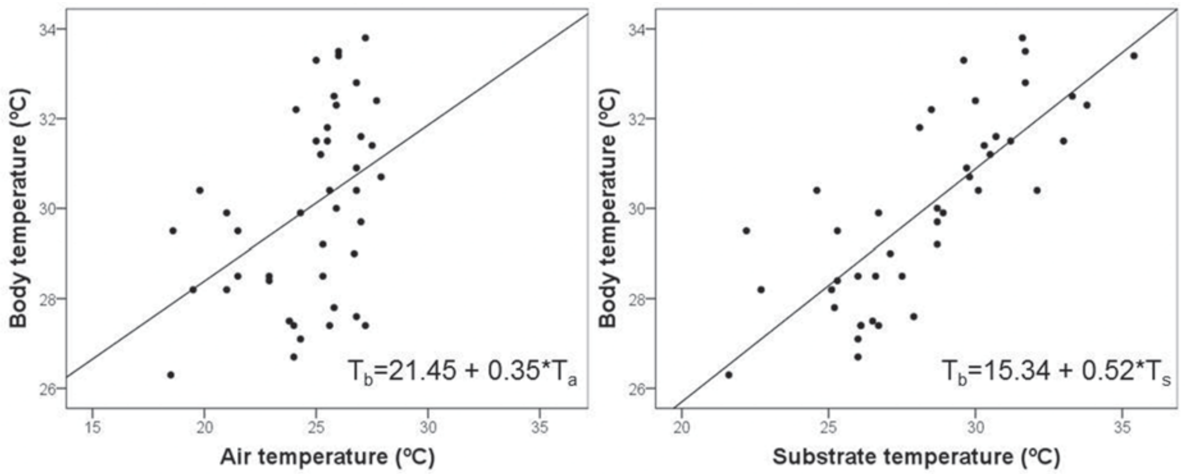

Figure 1. Lineal regression models of the relation between body temperature (T_b) and air temperature (T_a) and T_b and substrate temperature (T_s) are plotted, together with their equations, for *I. monticola*.

Table 1. Mean ± SE body temperatures (T_b), air temperatures (T_a), and substrate temperatures (T_s) for the 27 males and 16 females of *I. monticola* studied.

	Males	Females	Total
T_b	30.31 ± 0.42	29.69 ± 0.49	30.00 ± 0.32
T_a	24.58 ± 0.53	24.82 ± 0.59	24.66 ± 0.38
T_s	28.74 ± 0.69	27.76 ± 0.61	28.31 ± 0.48

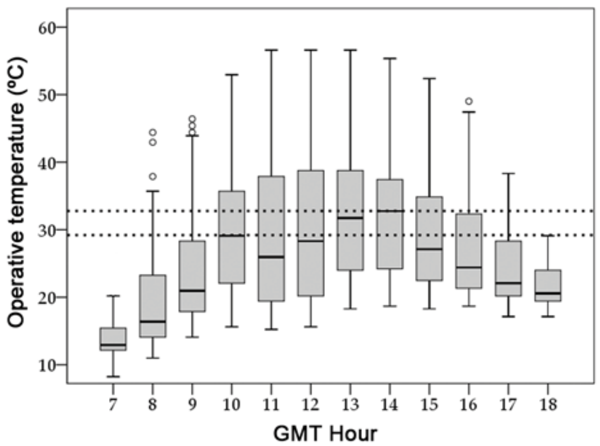

Figure 2. Boxplots of the operative temperatures (T_e) of each hour of the daily activity period of *I. monticola* at the Serra da Estrela.

Parametric statistics were performed when data followed the assumptions of normality and homogeneity of variances. If these assumptions were not fulfilled, even after log-transformation, non-parametric equivalents were carried out (Crawley, 2012; Sokal & Rohlf, 1995). Analyses were conducted on R, version 3.1.3 (R Core Team, 2015). Post-hoc comparisons of Kruskal-Wallis tests were computed with Nemenyi test with the package PMCMR (Pohlert, 2014).

RESULTS

The PTR of the studied lizards was 29.80 - 31.60 °C, and mean T_{sel} were similar among sexes (males: mean T_{sel} = 30.80 ± 0.08 °C, *N* = 40; females: mean T_{sel} = 30.74 ± 0.09 °C, *N* = 41; One-way ANOVA, $F_{1, 79}$ = 0.298, *p* = 0.587). Body temperatures (T_b) were also similar among sexes (One-way ANOVA, $F_{1, 40}$ = 0.876, *p* = 0.355), as well as air temperatures (T_a; One-way ANOVA, $F_{1, 40}$ = 0.084, *p* = 0.774), and substrate temperatures (T*s*; One-way ANOVA, $F_{1, 40}$ = 0.953 *p* = 0.335; Table 1). There was a positive significant correlation between T_b of *I. monticola* lizards and T_a (*r* = 0.420, *p* = 0.003, *N* = 43), although the goodness of fit of the lineal regression model was poor (R^2 = 0.176, Fig. 1). Correlation between T_b and T_s was significant and strong (*r* = 0.782, *p* < 0.0001, *N* = 43) and the goodness of fit of the model of lineal regression was high (R^2 = 0.611, Fig. 1).

The study area is formed of microhabitats offering different operative temperatures (T_e) for the thermoregulation of *I. monticola* (Kruskal-Wallis test, *N* = 4499, *d.f.* = 7, *H* = 1109.80, *p* < 0.0001), with suitable T_e during the most of the hours of the daily activity period (Fig. 2). The microhabitat under rock offered lower T_e than the other microhabitats (Table 2). Flat rock in shade offered similar T_e than grass in shade, and all microhabitats covering rock in full sun offered similar T_e among them, and higher than the others (Table 2). Thermal heterogeneity of the habitat was 7.54 °C (*N* = 20). The habitat was mainly formed by big rocks and granite slabs, with some shrubs and meadows (Table 3). Mean value of the index of thermal quality of the habitat was 7.60 ± 0.02 °C. Mean value of the index of accuracy of thermoregulation was 1.09 ± 0.01 °C, and mean effectiveness of thermoregulation was 0.85 ± 0.002 (Fig. 3).

DISCUSSION

The habitat of *I. monticola* at the Serra da Estrela is a mosaic of big granite slabs and big rock blocs, mixed with shrubs and meadows, which is similar to the habitat of

Table 2. P-values of the Nemenyi post-hoc paired comparisons between the operative temperatures of different microhabitats available for *I. monticola*.

	Under rock	Flat rock shade	Grass shade	Grass full sun	Flat rock full sun	Rock West full sun	Rock North full sun	Rock South full sun
Under rock	-	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Flat rock shade	<0.0001	-	1.000	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Grass shade	<0.0001	1.000	-	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Grass full sun	<0.0001	<0.0001	<0.0001	-	0.002	0.025	0.023	0.032
Flat rock full sun	<0.0001	<0.0001	<0.0001	0.002	-	1.000	1.000	1.000
Rock West full sun	<0.0001	<0.0001	<0.0001	0.025	1.000	-	1.000	1.000
Rock North full sun	<0.0001	<0.0001	<0.0001	0.023	1.000	1.000	-	1.000
Rock South full sun	<0.0001	<0.0001	<0.0001	0.032	1.000	1.000	1.000	-

Table 3. Spatial heterogeneity of the study area at Serra da Estrela was assessed by measuring the available microhabitats in lineal transects. Mean (SE) percentages of cover and frequency are provided for the 15 transects. Slab means a big flat rock that does not provide shelter for lizards.

	Slab	Rocks > 50cm	Rocks < 50cm	Loose Stones	Soil	Grass > 15cm	Grass < 15cm	Shrubs
Cover	19.84% (4.52)	26.81% (2.79)	5.48% (1.39)	3.65% (1.36)	2.61% (0.86)	4.64% (1.03)	16.67% (2.94)	20.29% (2.99)
Frequency	16.97% (1.99)	19.42% (1.67)	7.10% (1.63)	5.27% (1.92)	5.76% (1.53)	6.82% (1.18)	24.48% (2.23)	14.18% (1.99)

I. cyreni in the east area of the Sistema Central (Pérez-Mellado, 1982; Carrascal et al., 1992; Monasterio et al., 2010). Thermal heterogeneity of the habitat is large (7.54 °C), and habitat thermal quality was one of the best among the studied populations of *Iberolacerta* (Monasterio et al., 2009; Aguado & Braña, 2014; Ortega et al., 2016a, 2016b, 2016d, 2016e). Therefore, the habitat of the Iberian rock lizard is thermally and spatially heterogeneous enough, at least under current climatic conditions, to enable proper regulation of body temperature of this species (Goller et al., 2014; Sears & Angilletta, 2015).

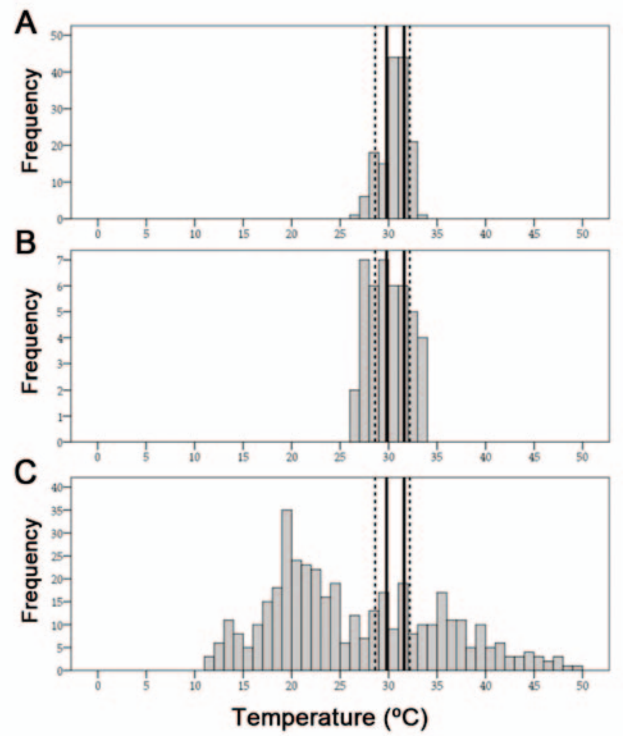

Figure 3. Histograms of: (A) selected temperatures, (B) body temperatures, and (C) operative temperatures for *I. monticola*. The dotted lines comprise the 80% preferred temperatures range (PTR) of the species and the continuous lines comprise the 50% PTR of the species.

The Iberian rock lizard is a cold-specialist species, with a preferred temperatures range between 29.80 and 31.60 °C, and, thus, a precision of thermoregulation of 1.8 °C, which is an intermediate value among the genus *Iberolacerta* (Aguado & Braña, 2014; Ortega et al., 2016a, 2016b, 2016d, 2016e, 2016f). The effectiveness of thermoregulation of *I. monticola* is 0.85, indicating that it is an effective thermoregulator. The relationship between body temperatures and substrate temperatures is greater for *I. monticola* than for other species of the genus (see Table 4), whereas the relation among body temperatures and air temperature is fairly weak. These results indicate that the Iberian rock lizard uses thigmothermy (that is, the conduction of heat from the substrate) to a great extent as a mechanism of thermoregulation. It is known that lacertids are able to select the type of heating source that provides the higher rate of warming (Belliure & Carrascal, 2002).

Being a cold-specialist and living at the highest area of distribution makes *I. monticola* highly vulnerable under the climate change projections for this century (Berg et al., 2010; Carvalho et al., 2010; Huey et al., 2012). Either way, *I. monticola* lizards have a great capacity for thermoregulation and may be able to adapt their thermoregulatory behaviour to buffer the impact of climate change (Kearney et al., 2009). However, if we

Table 4. Data of the correlations between body and air temperature ($r\ T_b$-T_a) and body and substrate temperature ($r\ T_b$-T_s) from the other studied species of *Iberolacerta*.

	Altitude	Season	N	r T_b-T_a	r T_b-T_s
Iberolacerta cyreni (Ortega et al. 2016b)	2200	Summer	40	0.505 p<0.0001	0.605 p<0.0001
I. galani (Ortega et al. 2016f)	1400	Spring	26	0.366 p=0.047	0.730 p<0.0001
I. galani (Ortega et al. 2016a)	1400	Summer	79	0.500 p<0.0001	0.698 p<0.0001
I. aurelioi (Ortega et al. 2016e)	2500	Summer	17	-0.382 p=0.065	0.277 p=0.141
I. aurelioi (Ortega et al. 2016e)	2700	Summer	17	-0.147 p=0.287	0.635 p=0.003
I. bonnali (Ortega et al. 2016d)	2200	Summer	46	0.306 p=0.019	0.440 p=0.001

want to prevent the extinction of this high mountain subspecies, these aspects of thermal biology should be considered when designing conservation actions of the Natural Park of Serra da Estrela, with the aim to preserve their current habitat as Iberian rock lizards do not have the possibility to migrate to colder places.

ACKNOWLEDGEMENTS

We thank M.T. Mencía and J. McIntyre for linguistic revision, Koko for helping with the transects, our lab mates for support during the writing process, and João for the nice moments in Portugal. Lizards were sampled under licenses of the Govern of Portugal. Financial support was provided to Zaida Ortega and Abraham Mencía by predoctoral grants of the University of Salamanca (FPI program). This work was also supported by the research project CGL2012-39850-CO2-02 from the Spanish Ministry of Science and Innovation. All research was conducted in compliance with ethical standards and procedures of the University of Salamanca.

REFERENCES

Aguado, S. & Braña, F. (2014). Thermoregulation in a cold-adapted species (Cyren's Rock Lizard, *Iberolacerta cyreni*): influence of thermal environment and associated costs. *Canadian Journal of Zoology* 92, 955-964.

Angilletta, M.J. (2009). Thermal adaptation: A theoretical and empirical synthesis. Oxford: Oxford University Press.

Araújo, M.B., Thuiller, W. & Pearson, R.G. (2006). Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography* 33, 1712-1728.

Argüello, J.A. & Salvador, A. (1988). Actividad, selección de hábitat y temperaturas corporales de *Lacerta monticola* en una localidad de la Cordillera Cantábrica (Sauria, Lacertidae). *Revista Española de Herpetología* 3, 29-40.

Arribas, O.J. (2014). *Iberolacerta* (*Iberolacerta*) *monticola* (Boulenger, 1905). In: *Fauna Ibérica Vol. 10, Reptiles, 2ª edición revisada y aumentada*. 419-432. Salvador, A. (Coord), Ramos, M. A. et al. (eds). Madrid: Consejo Superior de Investigaciones Científicas.

Bakken, G. S. & Angilletta, M. J. (2014). How to avoid errors when quantifying thermal environments. *Functional Ecology* 28, 96-107.

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. *Physiological and Biochemical Zoology* 75, 369-376.

Berg, M.P., Kiers, E.T., Driessen, G., Van Der Heijden, M., Kooi, B.W., Kuenen, F., Liefting, M., Verhoef, H.A. & Ellers, J. (2010). Adapt or disperse: understanding species persistence in a changing world. *Global Change Biology* 16, 587-598.

Blouin-Demers, G. & Nadeau, P. (2005). The cost-benefit model of thermoregulation does not predict lizard thermoregulatory behaviour. *Ecology* 86, 560-566.

Carranza, S., Arnold, E.N. & Amat, F. (2004). DNA phylogeny of *Lacerta* (*Iberolacerta*) and other lacertine lizards (Reptilia: Lacertidae): did competition cause long-term mountain restriction? *Systematics and Biodiversity* 2, 57-77.

Carrascal, L.M., López, P., Martín, J. & Salvador, A. (1992). Basking and antipredator behaviour in a high altitude lizard: implications of heat-exchange rate. *Ethology* 92, 143-154.

Carvalho, S.B., Brito, J.C., Crespo, E.J. & Possingham, H.P. (2010). From climate change predictions to actions – conserving vulnerable animal groups in hotspots at a regional scale. *Global Change Biology* 16, 3257-3270.

Crawley, M.J. (2012). *The R book*. Wiley, Chichester, UK.

Crochet, P.A., Chaline, O., Surget-Groba, Y., Debain, C. & Cheylan, M. (2004). Speciation in mountains: phylogeography and phylogeny of the rock lizards genus *Iberolacerta* (Reptilia: Lacertidae). *Molecular Phylogenetics and Evolution* 30, 860-866.

Díaz, J.A., Iraeta, P. & Monasterio, C. (2006). Seasonality provokes a shift of thermal preferences in a temperate lizard, but altitude does not. *Journal of Thermal Biology* 31, 237-242.

Goller, M., Goller, F. & French, S.S. (2014). A heterogeneous thermal environment enables remarkable behavioral thermoregulation in Uta stansburiana. *Ecology and Evolution* 4, 3319-3329.

Hertz, P.E., Huey, R.B. & Stevenson, R.D. (1993). Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropiate question. *The American Naturalist* 142, 796-818.

Huey, R. B. & Kingsolver, J. G. (1989). Evolution of thermal sensitivity of ectotherm performance. *Trends in Ecology &*

Evolution 4, 131-135.

Huey, R. B. & Slatkin, M. (1976). Cost and benefits of lizard thermoregulation. *Quarterly Review of Biology* 51, 363-384.

Huey, R.B., Hertz, P.E. & Sinervo, B. (2003). Behavioral drive versus behavioral inertia in evolution: a null model approach *The American Naturalist* 161, 357-366.

Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A., Jess, M. & Williams, S.E. (2012). Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. Philosophical Transactions of the Royal Society of London B: *Biological Sciences* 367, 1665-1679.

Kapli, P., Poulakakis, N., Lymberakis, P. & Mylonas, M. (2011). A re-analysis of the molecular phylogeny of Lacertidae with currently available data. *Basic and Applied Herpetology* 25, 97-104.

Kearney, M., Shine, R. & Porter, W.P. (2009). The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. *Proceedings of the National Academy of Sciences* 106, 3835-3840.

Logan, M.L., Fernandez, S.G. & Calsbeek, R. (2015). Abiotic constraints on the activity of tropical lizards. *Functional Ecology* 29, 694–700.

Mayer, W. & Pavlicev, M. (2007). The phylogeny of the family Lacertidae (Reptilia) based on nuclear DNA sequences: convergent adaptations to arid habitats within the subfamily Eremiainae. *Molecular Phylogenetics and Evolution* 44, 1155-1163.

Monasterio, C., Salvador, A. & Díaz, J.A. (2010). Altitude and Rock Cover Explain the Distribution and Abundance of a Mediterranean Alpine Lizard. *Journal of Herpetology* 44, 158-163.

Monasterio, C., Salvador, A., Iraeta, P. & Díaz, J.A. (2009). The effects of thermal biology and refuge availability on the restricted distribution of an alpine lizard. *Journal of Biogeography* 36, 1673-1684.

Mouret, V., Guillaumet, A., Cheylan, M., Pottier, G., Ferchaud, A. L. & Crochet, P. A. (2011). The legacy of ice ages in mountain species: post-glacial colonization of mountain tops rather than current range fragmentation determines mitochondrial genetic diversity in an endemic Pyrenean rock lizard. *Journal of Biogeography* 38, 1717-1731.

Ortega, Z., Mencía, A., & Pérez-Mellado, V. (2016a). Are mountain habitats becoming more suitable for generalist than cold-adapted lizards thermoregulation?. *PeerJ* 4, e2085.

Ortega, Z., Mencía, A., & Pérez-Mellado, V. (2016b). Behavioral buffering of global warming in a cold-adapted lizard. *Ecology and Evolution* 6, 4582-4590.

Ortega, Z., Mencía, A., & Pérez-Mellado, V. (2016c). Sexual differences in behavioral thermoregulation of the lizard *Scelarcis perspicillata*. *Journal of Thermal Biology* 61, 44-49.

Ortega, Z., Mencía, A., & Pérez-Mellado, V. (2016d). The peak of thermoregulation effectiveness: thermal biology of the Pyrenean rock lizard, *Iberolacerta bonnali* (Squamata, Lacertidae). *Journal of Thermal Biology* 56, 77-83.

Ortega, Z., Mencía, A., & Pérez-Mellado, V. (2016e). Wind constraints on the thermoregulation of high mountain lizards. *International Journal of Biometeorology*, DOI: 10.1007/s00484-016-1233-9.

Ortega, Z., Mencía, A., & Pérez-Mellado, V. (2016f). Adaptive seasonal shifts in the thermal preferences of the lizard *Iberolacerta galani* (Squamata, Lacertidae). *Journal of Thermal Biology* 62, 1-6.

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. *Journal of Thermal Biology* 39, 32-39.

Pérez-Mellado, V. (1982). Datos sobre *Lacerta monticola* Boulenger, 1905 (Sauria: Lacertidae) en el oeste del Sistema Central. *Doñana, Acta Vertebrata* 9, 107-129.

Pérez-Mellado, V. (1997). *Lacerta monticola* Boulenger, 1905. In: Pleguezuelos, J.M. (ed), *Distribución y biogeografía de los anfibios y reptiles en España y Portugal*. Granada: Monografías de Herpetología - Asociación Española de Herpetología, Universidad de Granada, pp. 225-227.

Pérez-Mellado, V. (2004). *Lacerta monticola* Boulenger, 1905. Lagartija serrana. In: Pleguezuelos, J. M., Márquez, R. & Lizana, M. (eds). *Atlas y libro rojo de los anfibios y reptiles de España*. Madrid: Dirección General de Conservación de la Naturaleza – Asociación Herpetológica Española, pp. 228-230.

Pérez-Mellado, V., Sá-Sousa, P., Marquez, R. & Martínez-Solano, I. (2009). *Iberolacerta monticola*. The IUCN Red List of Threatened Species 2009: e.T61448A12487278. http://dx.doi.org/10.2305/IUCN.UK.2009.RLTS.T61448A12487278.en . Downloaded on 29 October 2015.

Pohlert. T. (2014). The Pairwise Multiple Comparison of Mean Ranks Package (PMCMR). R package. URL: https://cran.r-project.org/web/packages/PMCMR/vignettes/PMCMR.pdf. Accessed on 31 October 2015.

R Core Team (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Remón, N., Galán, P., Vila, M., Arribas, O. & Naveira, H. (2013). Causes and evolutionary consequences of population subdivision of an Iberian mountain lizard, *Iberolacerta monticola*. *PLoS One* 8, e66034.

Sagonas, K., Meiri, S., Valakos, E. D., & Pafilis, P. (2013). The effect of body size on the thermoregulation of lizards on hot, dry Mediterranean islands. *Journal of Thermal Biology* 38, 92-97.

Sears, M.W. & Angilletta, M.J. (2015). Costs and benefits of thermoregulation revisited: both the heterogeneity and spatial structure of temperature drive energetic costs. *The American Naturalist* 185, E94-E102.

Sokal, R. R. & Rohlf, F. J. (1995). *Biometry: the principles and practice of statistics in biological research*. New York: State University of New York at Stony Brook.

Zamora-Camacho, F. J., Reguera, S., & Moreno-Rueda, G. (2016). Thermoregulation in the lizard *Psammodromus algirus* along a 2200-m elevational gradient in Sierra Nevada (Spain). *International Journal of Biometeorology* 60, 687-697.

Accepted: 20 October 2016