ORIGINAL ARTICLE

Main factors affecting lacertid lizard thermal ecology

Zaida ORTEGA[1,2] and Francisco Javier MARTÍN-VALLEJO[2]

[1]Postgraduate Program in Ecology and Conservation, Federal University of Mato Grosso do Sul, Campo Grande, Mato Grosso do Sul, Brazil and [2]Department of Statistics, University of Salamanca, Spain

Abstract

The thermal ecology of ectotherms has been studied for almost 2 centuries, but additional attention is currently being paid to it, to understand how organisms deal with the environment in a climate change context. A consensus is still far away due to the large number of factors involved and their complex interactions. In this context, 3 analyses in lacertid lizards were carried out: (i) a meta-analysis, to test for differences between body and air temperatures from 71 populations; (ii) a meta-analysis concerning correlations between body and air temperatures from 60 populations; and (iii) a multimodel inference of thermoregulation effectiveness indices from 45 populations. The importance of different factors, including body size, habitat, insularity, altitude, climate and season, was evaluated in all analyses to model the response variables. A strong seasonality effect was observed, with a consistent pattern of less effective thermoregulation in summer compared to other seasons. Altitude was the second most important factor, with a consistent higher thermoregulation effort in populations occurring at high elevations (>1000 m above sea level). Other factors, such as insularity or body size, can also be important, but did not exhibit a clear pattern. Finally, thermoregulation was less affected by climate and habitat type.

Key words: lizards, meta-analysis, seasonality, temperature, thermoregulation

INTRODUCTION

Temperature is a key environmental factor shaping animal ecology and evolution of ectotherms due to its effects on the performance of chemical reactions (Huey & Stevenson 1979; Adolph & Porter 1993; Pörtner

Correspondence: Zaida Ortega, 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.

Email: zaidaortega@usal.es

2002; Angilletta 2009). Environmental temperatures that organisms experience are influenced by many factors, such as altitude, latitude, habitat heterogeneity, weather conditions and climate change, which can interact to produce complex patterns (Díaz *et al*. 2006; Deutsch *et al*. 2008; Sears *et al*. 2011; Graae *et al*. 2012). Environmental temperatures determine lizard body temperature by means of physiology and thermoregulatory behavior, probably in a complex model concerning thermoregulation costs and benefits (Huey & Slatkin 1976; Sears & Angilletta 2015). Lizards usually thermoregulate by adjusting activity periods (Hertz 1992; Adolph & Porter 1993; Meiri *et al*. 2013), shifting between different thermal microhabitats (Heath 1970; Bauwens *et al*. 1996; Sagonas *et al*. 2017) or adjusting their body pos-

ture (Bauwens *et al.* 1996). The use of these strategies depends on the balance between their costs and benefits (Huey & Slatkin 1976; Blouin-Demers & Nadeau 2005).

Many factors affect thermoregulation degree in lizards. Body size is inversely related to thermal inertia, with larger individuals subjected to a higher risk of overheating, which, in turn, affects thermoregulatory behavior (Stevenson 1985; Olalla-Tárraga *et al.* 2006; Kingsolver & Huey 2008). Habitat spatial configuration where a specific population inhabits also affects its thermoregulation degree, because habitat heterogeneity is inversely related to thermoregulation energetic costs (Sears & Angilletta 2015; Sears *et al.* 2016; Basson *et al.* 2017). Insularity may also play a key role in thermoregulation because insular populations usually share traits, such as low predation pressure, scarcity of food resources and weather unpredictability (Sagonas *et al.* 2013b; Ortega *et al.* 2014). However, the effect of insularity strongly depends on the location and size of the island (e.g. Losos 2009). Furthermore, the altitude in which a population lives may have a great effect on their thermoregulation because environmental temperatures and atmospheric oxygen decrease with increasing altitude, whereas the intensity of solar radiation increases (Hertz 1981; Sunday *et al.* 2014; Ortega *et al.* 2016c). Finally, seasonality also strongly affects lizard thermoregulation because different environmental conditions lead to thermoregulatory behavior adaptations (Huey & Pianka 1977; Christian & Bedford 1995; Díaz & Cabezas-Díaz 2004).

Lacertid lizards are usually effective heliothermic thermoregulators (Arnold 1987; Castilla *et al.* 1999). However, the degree of thermoregulation of a population is affected by different factors that could potentially change due to global warming (Chamaillé-Jammes *et al.* 2006; Moreno-Rueda *et al.* 2012; Martín & López 2013). Currently, little consensus on the relative importance of different factors affecting the lacertid lizard thermoregulation is available (e.g. Castilla *et al.* 1999; Sagonas *et al.* 2013a,b; Ortega *et al.* 2014; Reguera *et al.* 2014). In this context, the relevance of different factors (body size, habitat type, insularity, altitude, climate and season) in dictating the thermoregulatory ability of lacertid lizards and their possible interactions were evaluated herein.

As thermal inertia increases with body size, smaller lizards (that heat and cool rapidly) would thermoregulate more effectively in thermally heterogeneous environments. In addition, thermal inertia leads to increased overheating risks in larger lizards, so they would thermoregulate less effectively under warm conditions. Habitat heterogeneity reduces energetic thermoregulation costs because lizards have many options of thermal microhabitats to cool and heat themselves. Thus, it is expected that more homogeneous habitats (such as forests or sandy areas) would lead lizards to thermoregulate less effectively. The effect of insularity on lizard thermoregulation is not well understood. As small islands are normally subjected to high unpredictability regarding weather conditions, the thermal ecology of insular lizards could be more flexible than that of continental lizards. In addition, seasonality is known to differently affect the thermoregulation effectiveness of nearby islands, probably interacting with habitat heterogeneity (Ortega *et al.* 2014). Finally, because predation pressure is often relaxed on islands, lizards could expend longer times in exposed microhabitats to heat or cool themselves, increasing thermoregulation effectiveness. Lacertid lizards are known to maintain high effective thermoregulation with altitude, probably by expending more time in thermoregulating activities (Gvoždík 2002). Due to the more extreme weather conditions on mountains, it is also expected that thermoregulation effectiveness could interact with seasonality, with thermoregulation being less effective in summer.

Thus, the aim of the present study is to test the expected effects of these factors assessed in published studies on lacertid lizards, to test the hypotheses related to the expectations on each factor (see above). To achieve this, meta-analysis (Hedges & Olkin 1985; Arnqvist & Wooster 1995; Hunter & Schmidt 2004) and model selection (Burnham & Anderson 2002) approaches were combined. Specifically, a meta-partition approach was applied, because interest lay in modeling the heterogeneity of effect sizes by different candidate moderators (Martín-Vallejo 1995; Nakagawa & Santos 2012; Ortega *et al.* 2016a). This approach allowed us not only to test the hypothesis regarding the effect of each factor on thermoregulation (and, if significant, to evaluate the magnitude and direction of the effect) but also allowed for comparisons concerning the relative importance of each factor and significant interactions among factors. Thus, this study also aimed to evaluate if the predicted interactions between body size and habitat heterogeneity and/or season, insularity and season, and altitude and season found on individual studies could be applied as general rules for lacertids.

MATERIALS AND METHODS

Data extraction

A search of published articles up to July 2016 was carried out in scientific databases (Scopus, Web of Knowledge and Google Scholar) using the following keywords: "thermal biology," "thermal ecology," "thermoregulation," "temperature regulation," "Lacertidae," "lacertid lizards" and "lacertids." In addition, "snowball searching" (i.e. following up references cited in the papers) was performed.

Traditional publication bias (Hunter & Schmidt 2004) does not affect studies on ectotherm thermal ecology, as all temperature data are likely to be published. The only bias is that some geographical areas are more thoroughly sampled than others (Koricheva *et al.* 2013; Fig. 1). Nonetheless, publication bias was evaluated using funnel plots (Light *e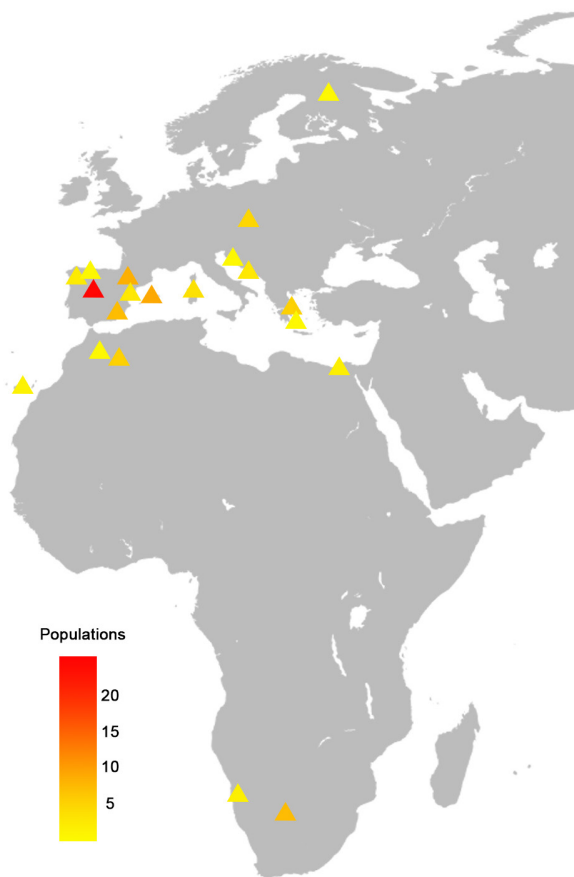t al.* 1994; Peters *et al.* 2008). First, all publications reporting data on body temperatures of any lacertid lizard were included, followed by removal of those that did not provide complete information for data analyses (see below).

Each population for which differences in thermal ecology were published was used as a sampling unit, considering spatial and temporal variations; that is, 2 populations at different altitudes, or data concerning 1 population studied during 2 seasons were considered as 2 different sampling units (see Electronic Supplementary Material 1).

Published studies on thermal ecology can be categorized into 3 groups: (1) those reporting mean body temperatures and, in some cases, mean air and substrate temperatures, but without addressing the relationships between these variables; (2) those addressing correlations between body temperatures and air and/or substrate temperatures; and (3) those addressing thermoregulation effectiveness (Hertz *et al.* 1993). For the first type of publication, a meta-analysis was conducted using the standardized differences of the means between body and air temperatures as effect size. Although the differences between mean body and air temperatures do not provide evidence for thermoregulation (see Heath 1964), many researchers have applied these data, including recently (e.g. Martins *et al.* 2014). However, it is interesting to understand the general patterns of different variables affecting this effect size, as this has been traditionally a proxy for thermoregulation and is still in use in macroecological research. For the second type of publication, another meta-analysis was conducted using the correlation between body and air temperatures as effect size, which is usually negatively related to thermoregulation ability. Again, a weak correlation between body and air temperatures does not provide evidence for thermoregulation (Hertz *et al.*1993), but many studies have used it as a proxy (e.g. Van Damme *et al.* 1990; Herczeg *et al.* 2004). Therefore, the results reported herein should be evaluated with caution and used only as a guide to identify limitations and gaps from past studies. Finally, most studies did not report a dispersion measure for thermoregulation indices, precluding their use in the meta-analysis.

A total of 82 publications were obtained reporting body temperatures, correlation coefficients, appropriate dispersion measure and lacertid lizard sample size, of which 42 were included in the following meta-analyses (Supplementary Material 1). Finally, the following were retrieved: (1) 71 sampling units (populations, from now on) for the analysis of differences of mean body

Figure 1 Map of all the lacertid lizard populations whose thermoregulation data were included in the present study.

and air temperatures, obtained from 39 publications; (2) 60 populations for the analysis of correlations between body and air temperatures, obtained from 34 publications; and (3) 45 populations for the analysis of thermoregulation effectiveness, obtained from 21 publications (see Supplementary Material 2).

Statistical analyses

Meta-partition was applied, allowing for modeling the heterogeneity of an effect size by potential moderators (Ortega *et al*. 2016a). The meta-partition algorithm consists of 3 steps: (1) detection of the heterogeneity of effect sizes under the assumption of a fixed-effect model; (2) if heterogeneity is found, partition by the moderator that minimizes heterogeneity within a subset, while maximizing it between subsets and, if the effect sizes of the subset are still heterogeneous, steps 1 and 2 are repeated; and (3) integration of effect sizes of final subsets, by a fixed-effect model if homogeneity is present, and by a random-effects model if heterogeneity is detected (see Fig. 2). Although several authors (Borenstein *et al*. 2010) argue against changing from the fixed-effect model to the random-effects model when heterogeneity has not been explained, this is applied herein to subgroups where the homogeneity test was significant. This is only used to include the heterogeneity that has not been explained in the calculation of effect sizes and is not related to the assumptions of the random-effects model. By using a meta-partition approach, the importance of moderators explaining the heterogeneity of effect sizes can be assessed, as well as the direction of these relations and the detection of interactions between moderators (Ortega *et al*. 2016a).

Moderators known to affect ectotherm thermal ecology and for which the category for a population is available in the literature were selected. Thus, 7 moderators were selected for the meta-partition: (1) "body size": "small" (*snout–vent length* [SVL] <60 mm), "median" (SVL 60–75 mm) or "large" (SVL >75 mm; where the 33 and 66 percentiles of the available data were used to establish the cut-off points); (2) "preferred habitat" (the habitat on which the population usually inhabits, obtained from the literature): "sandy areas," "rocky areas," "grasslands," "open areas," "scrublands" and "generalist" (prefer many types of habitats); (3) habitat (where the study was conducted): "sandy areas," "rocky areas," "scrublands," "unknown," "grasslands," "forest" and "rocky walls"; (4) "insularity": "yes" or "no"; (5) "altitude": "low-altitude" (<400 m), "mid-altitude" (400–1000 m), and "high-altitude" (>1000 m); (6) "climate,"

following the Köppen classification (Kottek *et al*. 2006); and (7) "season": "spring," "summer," "spring–summer" (the publication provides mixed results of both seasons), "autumn," "winter," "annual" (the publication provides mixed results for the whole year or the entire activity season) and "unknown." In cases where the information was not included in the original publication, the data was searched for in other publications. If a range of values was provided, the means were calculated before categorizing the moderator.

Two variables that can influence lacertid lizard thermoregulation were not included in the analysis: latitude and phylogeny. Although latitude affects the thermal biology of other lizards (Huey *et al*. 2009), this was not included herein because the latitudinal variation in the present dataset is low (Fig. 1), which, alongside a limited sample size would probable add more noise to the results. In addition, phylogeny was also not taken into account, as this study focused only on 1 family, and it would probably also add noise to the results (see also Huey & Pianka 2018). Nonetheless, the importance of testing the effects of geography and phylogeny on lizard
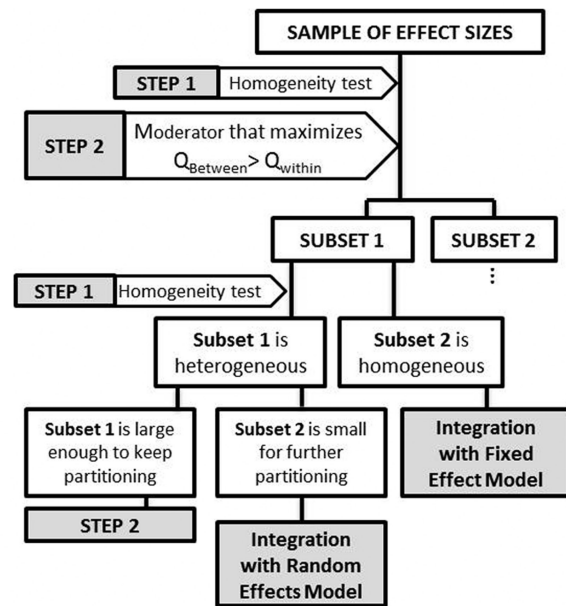

Figure 2 Summary of the meta-partition methodology: (1) step 1 is the assessment of heterogeneity with the homogeneity test and the value of I^2, (2) step 2 is the selection of the best moderator, according to the Logworth value with p-value correction, and (3) step 3 is the integration of effect sizes in final subsets (Ortega *et al*. 2016a).

thermoregulation is noteworthy (Felsenstein 1985; Garland *et al*. 2005). As studies reporting lizard thermoregulation indices are becoming more common, a further meta-analysis testing the effects of those factors shall be carried out.

Two effect sizes were applied: (1) standardized differences between mean body temperatures and mean air temperatures; and (2) correlation between body and air temperatures. According to the former, the higher the mean body temperature above the mean air temperature, the greater the thermoregulatory ability of the population. Although this estimate of effect size provides limited information, because it is only based on mean values (Heath 1964), it is useful for comparisons between populations. Comparisons address the relative influence of environmental factors on the differences between body and air temperatures between populations.

The Hedges' *d* was used to calculate the difference between mean body temperatures and mean air temperatures (Hedges & Olkin 1985). The association between body and air temperatures was measured in the original publications by the correlation coefficient. Fisher's *Z* transformation of the correlation coefficient as the effect size for analyzing correlations was applied (Fisher 1921; Fleiss 1993). For populations where the correlation coefficient was not reported, it was calculated from the regression coefficient. Meta-analyses were conducted using the Metawin 2.0 (Rosenberg *et al*. 2000) and JMP-12 (SAS Institute, Cary, NC, USA) software.

Multimodel inference

Thermoregulation effectiveness could not be subjected to meta-analysis, as dispersion measures of thermoregulation indices are usually not provided (this data was available only for 14 out of 45 populations). Thus, these data were analyzed using a theoretical information approach.

As a response variable, the thermoregulation effectiveness index was used (Hertz *et al*. 1993), ranging between 0 and 1. The higher the value, the higher the thermoregulatory ability. The first step was to explore the data, to select the explanatory variables and biologically meaningful interactions observed to potentially affect the response variable (Burnham & Anderson 2004; Zuur *et al*. 2010). The results from both meta-analyses were used, as well as data exploring thermoregulation effectiveness, to decide the best explanatory variables to include in the global model. Generalized linear mixed models (GLMM) with Gaussian errors were applied for the data analysis. The analysis was carried out using the

lme4 R package (Bates *et al*. 2016; R Core Team 2016).

Because the explanatory variables were carefully selected based on the meta-analyses and data exploration results, the set of models was restricted, and it was considered appropriate to select the top $2AIC_c$ (a second-order Akaike information criterion [AIC], required for small samples; see Burnham & Anderson 2004) of the models as the "top model set" (Burnham & Anderson 2004; Grueber *et al*. 2011). The *arm* package was used to standardize parameters from the global model (Gelman & Su 2016) and the *MuMIn* R package was used to obtain the model set (Barton 2016). As the aim was to determine the averaged effect of the main factors affecting thermoregulation effectiveness, the zero method for model averaging was chosen (Nakagawa & Freckleton 2010).

RESULTS

Differences between mean body and air temperatures

The data on mean body and air temperatures for the 71 lizard populations is highly heterogeneous for the fixed-effect model (Q_H = 2333.37, P < 0.00001), and 97% of the variability of effect sizes is intrinsic to the studies themselves. The main moderator affecting effect size is season (Q_B = 241.92, Logworth = 1.10; where Logworth = $-\log10[P$-value]), with populations studied in the winter and summer exhibiting a lower effect size compared to populations studied during other seasons (Fig. 3).

Lacertids studied in the winter (n = 1) and summer (n = 26) exhibit a mean effect size (under the random effect model) of 1.8562 (95% CI: 1.4104/2.3019). However, this group is still heterogeneous (Q_H = 869.77, P < 0.00001; I^2 = 97.02%), with the next partition by altitude (Q_B = 106.54, Logworth = 0.99), with the low-altitude + mid-altitude group (i.e. below 1000 m above sea level) on one side (n = 15) and the high-altitude group (> 1000 m above sea level) on the other (n = 12). The complete meta-partition of this effect size is reported in the Supplementary Material 2. Upon integration of the effect sizes, lacertids in the winter and summer living at <1000 m above sea level display a common effect size of 1.3454 (95% CI: 0.8504/1.8405), while lacertids in summer living at >1000 m above sea level show a common effect size of 2.5075 (95% CI: 1.5918/3.4232). The difference in effect sizes for lacertids studied during the summer (and 1 population in winter) is considerable

(Fig. 4).

Lacertids studied during other seasons ($n = 44$) exhibit a mean effect size (under the random effect model) of 0.0304 (95% CI: −0.0226/0.0834). Within this group, effect sizes are highly heterogeneous ($Q_H = 1221.68$, $P < 0.00001$; $I^2 = 96.48\%$). The complete meta-partition is provided in the Electronic Supplementary Material 2. The meta-analysis revealed that season is the main factor affecting the differences between mean body temperatures and mean air temperatures. Hence, the studies for which temperatures from different seasons pooled into in one common mean may include poor quality data, and further partitions could, consequently, be confounded.

Correlations between body and air temperatures

The initial 60 population sample where correlations between body and air are available is heterogeneous ($Q_H = 803.36$, $P < 0.00001$, $I^2 = 92.65\%$) and the first partition is by the altitude moderator ($Q_B = 157.44$, Logworth = 3.52; Fig. 5). As in the first meta-analysis, the groups resulting from the partition by altitude are high-altitude and low-altitude + mid-altitude. The effect of altitude is congruent with the first meta-analysis (Fig. 6).

For the 27 lizard populations inhabiting areas >1000 m above sea level, effect sizes are still heterogeneous ($Q_H = 81.74$, $P < 0.00001$, $I^2 = 68.19\%$). The next partition is by body size ($Q_B = 19.26$, Logworth = 1.90), grouping medium body size (60–75 mm) on one side ($n = 11$) and small (<60 mm) and large lizards (>75 mm) on the other ($n = 16$; Fig. 5). Both groups are still heterogeneous, but, as in the first meta-analysis, it is better to stop partitioning at this level, avoiding spurious results when the sample size is decreased and moderators could confound the meta-partition. The integrated effect size of the medium-sized lacertids living at >1000 m above sea level is 0.2984 (95% CI: 0.1536/0.4432), and that of the small-sized + large-sized is 0.4467 (95% CI: 0.3298/0.5636).

One outlier of the 33 populations living at <1000 m above sea level was removed [the population of *Zootoca vivipara* in Herczeg *et al*. 2004, whose effect size is 2.1095 (see Fig A9 in the Electronic Supplementary Material 2]. The effect sizes of the 32 remaining populations are still heterogeneous under the fixed-effect model ($Q_H = 424.88$, $P < 0.00001$, $I^2 = 92.70\%$), with the next partition occurring by *season* ($Q_B = 122.33$, Log-
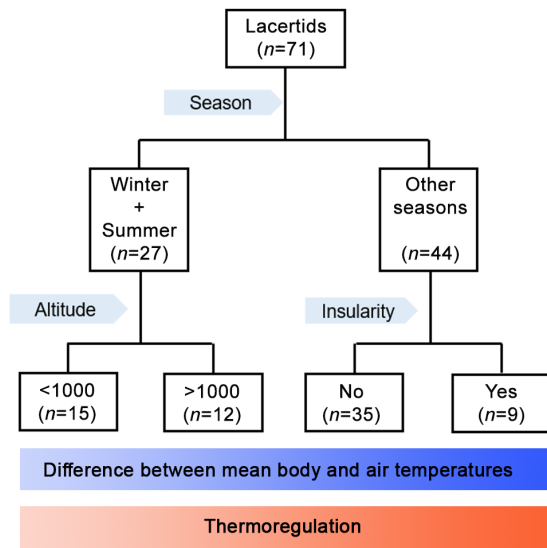

Figure 3 Summary tree of the first meta-analysis, exhibiting the difference of the means between body temperatures and air temperatures as the effect size of each population. Among the proposed moderators, season was the most important in explaining the heterogeneity of the effect sizes of the 71 lacertid populations with available data. See Supplementary Material 2 for the complete results of the meta-analysis.
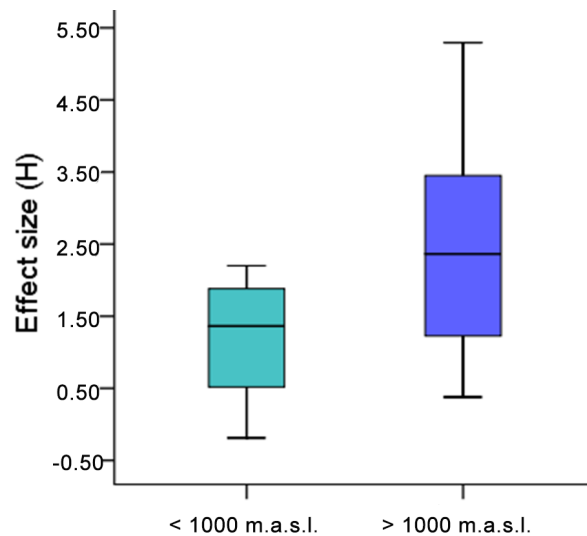

Figure 4 Influence of the altitude of the population on the effect size of the differences of means between body and air temperatures (estimated using Hedge's H) of the lacertid lizards studied during summer ($n = 26$) and winter ($n = 1$).

worth = 1.87). This partition forms 2 groups, lizards living <1000 m above sea level studied during other seasons ($n = 25$) on one side and those living at <1000 m above sea level studied during the summer ($n = 7$; Fig. 5). As in the first meta-analysis, the group comprising *other seasons* must be evaluated with caution, because season strongly affects lacertid thermoregulation, and the values within this group are mixed. The integrated effect size of this group is 0.5925 (95% CI: 0.4595/0.7254). Lacertids living at <1000 m above sea level and studied during the summer exhibit an integrated effect size of 1.1066 (95% CI: 0.9546/1.2086).

Multimodel inference for thermoregulation effectiveness

The following predictor variables were included, based on the results of the previous meta-analyses, to explain lizard thermoregulation effectiveness: (1) season (one factor with 3 levels: 1 = "spring," 2 = "summer," 3 = "others"); (2) altitude (a continuous variable, in m above sea level; when a range for 1 population was reported, the mean value of the range was used); (3) insularity (factor with 2 levels: 1 = "yes," 2 = "no"); and (4) body size (a continuous variable: the mean SVL reported for each population, in mm).

Thus, the global model was:

E ~ size + season + altitude + insularity + season:altitude + size:altitude.

The whole set of models included 26 models. The top $2AIC_c$ models included 3 models, whose averaged parameters are provided in Table 1. The relative importance of the explanatory variables is: season > body size > altitude > insularity. Season and body size appeared in the 3 top models, with significant inverse relationships with thermoregulation effectiveness (Fig. 7), while altitude and insularity each appeared in 1 of the 3 top models each.

DISCUSSION

To the best of our knowledge, this is the first meta-analytical, integrative study on the relative importance of different factors, and their interactions, on animal thermal ecology, precluding comparisons with other taxa. The first remarkable result was the high heterogeneity of effect sizes on the meta-partitions, with an $I^2 > 96\%$ for the initial datasets. This means that more than the 90%
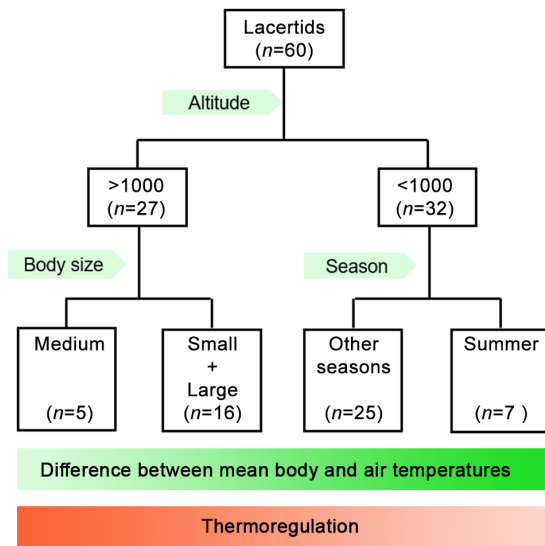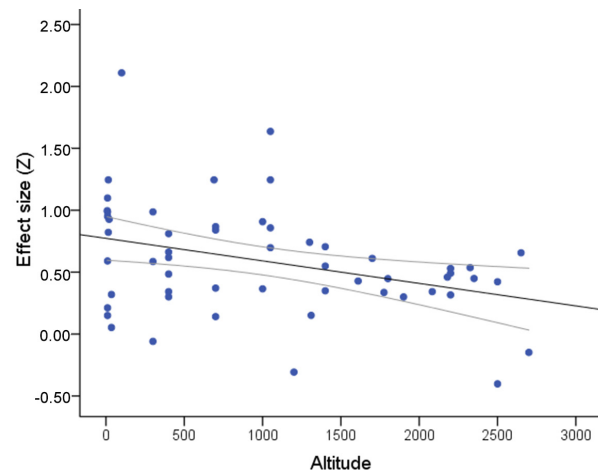

Figure 5 Summary tree of the second meta-analysis, with correlations between body temperatures and air temperatures as effect size. Among the proposed moderators, altitude was the most important in explaining the heterogeneity of the effect sizes of the 60 lacertid populations with available data. See Supplementary Material 2 for the complete results of the meta-analysis.

Figure 6 Influence of altitude on the effect size of the correlation between body and air temperatures (estimated using Fisher's Z) of the 60 lacertid lizard populations for which data are currently available. The greater the correlation, the lesser the degree of thermoregulation, and vice-versa. The black line is the linear regression slope line and the grey lines are the 95% confidence intervals.

Table 1 The upper part of the table reports the averaged parameters of the top 2AIC$_c$ models for the effect of the proposed factors on thermoregulaion effectiveness (E)

	Estimate	SE	Adjusted SE	Z	P
(Intercept)	0.88556	0.04843	0.04988	17.755	<2e-16***
Factor(Season) "Spring"	−0.04823	0.05599	0.05770	0.836	0.40324
Factor(Season) "Others"	−0.17380	0.05458	0.05625	3.090	0.00200**
Size	−0.10581	0.03874	0.03993	2.650	0.00805**
Altitude	−0.04067	0.03229	0.03329	1.222	0.22184
Factor(Insularity) "No"	−0.03111	0.03412	0.03519	0.884	0.37667
	Degrees of freedom	logLik[1]	AIC$_c$	DAICc	Akaike weight
24	5	39.21	−66.89	0.00	0.49
234	6	40.09	−65.97	0.92	0.31
124	6	39.68	−65.14	1.75	0.20

†Maximum likelihood of the model. Coefficients are averaged based on their Akaike weights for each of the top models. The lower part of the table provides information on the 3 top models and their weight in the averaged parameters.
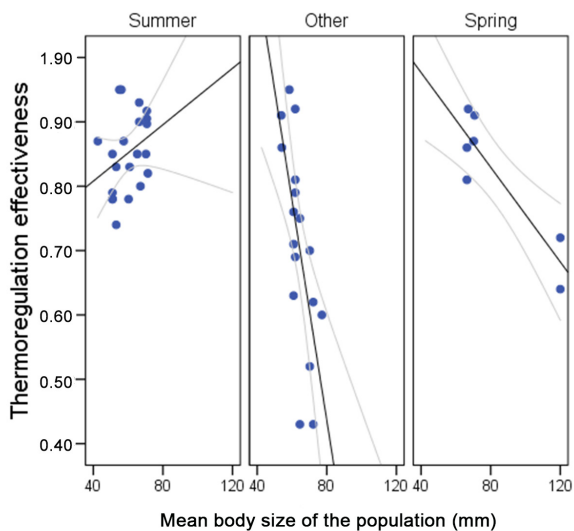

Figure 7 Scatterplot of the relation between body size (mean snout–vent length of the population, in mm) and the thermo-regulation effectiveness index for published Lacertidae data. The scatterplot is paneled by season to illustrate the multimodel inference analysis findings. The linear regression slope is depicted for each season, alongside the 95% confidence interval.

each factor explains the variability of effect sizes in ecological meta-analyses. Instead of focusing on *P*-values, it would be more interesting to address the sources of heterogeneity in effect sizes (Nakagawa & Poulin 2012; Nakagawa & Santos 2012; Lortie *et al*. 2013).

The first meta-partition revealed that season was the main trait affecting the differences between body and air temperatures, where lizard body temperatures are closer to air temperatures in summer compared to the other seasons. Some published studies have addressed the effect of seasonal changes on lacertid thermal ecology (Díaz & Cabezas-Díaz 2004; Díaz *et al*. 2006; Ortega *et al*. 2014; Ortega & Pérez-Mellado 2016), and some have detected seasonal differences between preferred temperatures (Díaz *et al*. 2006; Ortega *et al*. 2016b). Among lizards studied in the summer, altitude was the most important variable explaining differences between body and air temperatures, with a general trend for a greater increase of body temperatures above air temperatures in populations inhabiting high elevations (above 1000 m above sea level). For populations studied during other seasons, both the small sample size and data mixing hamper the understanding of the role of other variables. Obviously, the smaller differences between body and air temperatures in summer would be due to the habitat being thermally more suitable for lizards during this season. Similarly, higher differences in high altitude populations would be due to the harsher thermal conditions at higher altitudes. The extent of thermoregulation ability has been negatively related to correlations between

of the variability of effect sizes is due to the heterogeneity concerning the responses of lizard populations or studies, and not chance (Higgins & Thompson 2002). This underscores the importance of understanding how

body and air temperatures (Hertz *et al*. 1993; Mitchell & Angilletta 2009). The second meta-partition revealed that the central variable affecting correlations between body and air temperature was altitude, with lizards living above 1000 m above sea level showing weaker correlations and vice-versa. Body size was the most important factor affecting correlations between body and air temperatures in lizards living at high elevations. However, the pattern is not clear, because medium-sized lacertids show weaker correlations and small and large lacertids show stronger correlations. Lacertids inhabiting lower altitudes were most affected by season, with populations studied in summer displaying the highest correlations between body and air temperatures. This pattern is consistent with that found in the other meta-partition: during summer, lacertids achieve body temperatures closer to air temperatures in their habitats.

Results regarding thermoregulation effectiveness highlight the roles of season and body size. Nonetheless, the effect of season on thermoregulation effectiveness should be evaluated cautiously, due to the mixing of data from different seasons and small sample size. Body size seems to be positively related to thermoregulation effectiveness in summer and negatively in other seasons. Two interactions were detected, between altitude and season and between body size and altitude. None were significant in the best models explaining thermoregulation effectiveness, and none were the main effect of altitude, but their appearance in the top model set suggest some effect that deserves further research.

Previous studies (e.g. Blouim-Demers & Nadeau 2005) report that lizards, especially those living in thermally challenging habitats, must thermoregulate effectively. General conclusions of the present results consistently support this fact as the most remarkable in lacertid thermal ecology, with season (summer *vs* other seasons) and altitude as the main drivers of this phenomenon. In addition to thermal habitat suitability, body size seems to have a general effect on lacertid thermal ecology, probably interacting with altitude. Hence, future studies should focus on the interrelations of body size, altitude and season in shaping lacertid lizard thermoregulation ability. It is, thus, recommended that researchers always report study dates and control for the effects of season, altitude and body size when studying the effect of other variables on lacertid lizard thermoregulation. Otherwise, if researchers mix data from various seasons or altitudes in thermal ecology studies without accounting for it, results could be misleading.

As ectotherms, lizards are highly susceptible to cli-

mate change impacts. It is predicted that almost one-fifth of the lizard species will disappear up to 2080 due to anthropogenic climate change (Sinervo *et al*. 2010). Regarding lacertids, as with basic thermal ecology research, there is a strong geographical bias towards European species (Winter *et al*. 2016), while the impact on Asian and African lacertids is less known (see Martínez-Freiría *et al*. 2013). Some European lizards are predicted to expand their ranges in the early stages of climate warming (Araújo *et al*. 2006; Le Galliard *et al*. 2012). Predicted range expansions may occur for lizards of cold and humid areas, while those from the Mediterranean basin could be more negatively impacted due to increasing droughts (Foufopoulos *et al*. 2010; Belasen *et al*. 2017). The fact that all studied lacertid lizards presented body temperatures closet to their thermal preference, reflects the flexibility of their thermoregulatory strategies and behavioral adaptations, which could compensate for climate change, at least in the short term. In addition, the mean thermoregulation effectiveness of the 45 lacertids for which data is available is 0.78 (ranging from 0.43 to 0.95). This indicates that lizards from this family are effective thermoregulators, apt at buffering the impacts of climate change by means of behavioral thermoregulation during the first stages of climate warming (Ortega *et al*. 2016d). In any case, the results presented herein highlight the importance of season and elevation for lacertid lizard thermal ecology. Thus, special attention should be paid to the impact of climate alterations on seasonality and mountain habitats. In addition, body size seems to interact with altitude, and is predicted to decline with climate change (Gardner *et al*. 2011; Caruso *et al*. 2014). This fact prompts the need for further understanding of how body size interacts with altitude to model lacertid lizard thermoregulation effectiveness, with the aim of improving the predictions concerning these lizards under climate change conditions, as well as possible conservation measures.

ACKNOWLEDGMENTS

the manuscript.

REFERENCES

Adolph SC, Porter WP (1993). Temperature, activity, and lizard life histories. *The American Naturalist* **142**, 273–95.

Angilletta MJ (2009). *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford University Press, Oxford.

Arnold EN (1987). Resource partition among lacertid lizards in southern Europe. *Journal of Zoology* **1**, 739–82.

Araújo MB, Thuiller W, Pearson RG (2006). Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography* **33**, 1712–28.

Arnqvist G, Wooster D (1995). Meta-analysis: Synthesizing research findings in ecology and evolution. *Trends in Ecology and Evolution* **10**, 236–40.

Barton K (2016). *MuMIn: Multi-Model Inference. R package version 1.15.6.* [Cited 21 Feb 2018.] Available from URL: https://CRAN.R-project.org/package=MuMIn.

Basson CH, Levy O, Angilletta MJ, Clusella-Trullas S (2017). Lizards paid a greater opportunity cost to thermoregulate in a less heterogeneous environment. *Functional Ecology* **31**, 856–65.

Bates D, Mächler M, Bolker B, Walker S (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical So ftware* **67**, 1–48.

Bauwens D, Hertz PE, Castilla AM (1996). Thermoregulation in a lacertid lizard: The relative contributions of distinct behavioral mechanisms. *Ecology* **77**, 1818–30.

Belasen A, Brock K, Li B *et al.* (2017). Fine with heat, problems with water: Microclimate alters water loss in a thermally adapted insular lizard. *Oikos* **126**, 447–57.

Blouin-Demers G, Nadeau P (2005). The cost–benefit model of thermoregulation does not predict lizard thermoregulatory behaviour. *Ecology* **86**, 560–6.

Borenstein M, Hedges LV, Higgins J, Rothstein HR (2010). A basic introduction to fixed-effect and random effects models for meta-analysis. *Research Synthesis Methods* **1**, 97–111.

Burnham KP, Anderson DR (2004). Multimodel inference understanding AIC and BIC in model selection. *Sociological Methods & Research* **33**, 261–304.

Caruso NM, Sears MW, Adams DC, Lips KR (2014). Widespread rapid reductions in body size of adult salamanders in response to climate change. *Global Change Biology* **20**, 1751–9.

Castilla AM, Van Damme R, Bauwens D (1999). Field body temperatures, mechanisms of thermoregulation and evolution of thermal characteristics in lacertid lizards. *Natura Croatica* **8**, 253–74.

Chamaillé-Jammes S, Massot M, Aragon P, Clobert J (2006). Global warming and positive fitness response in mountain populations of common lizards *Lacerta vivipara*. *Global Change Biology* **12**, 392–402.

Christian KA, Bedford GS (1995). Seasonal changes in thermoregulation by the frillneck lizard, *Chlamydosaurus kingii*, in tropical Australia. *Ecology* **76**, 124–32.

Deutsch CA, Tewksbury JJ, Huey RB *et al.* (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences* **105**, 6668–72.

Díaz JA, Cabezas-Díaz S (2004). Seasonal variation in the contribution of different behavioural mechanisms to lizard thermoregulation. *Functional Ecology* **18**, 867–75.

Díaz JA, 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**, 237–42.

Felsenstein J (1985). Phylogenies and the comparative method. *The American Naturalist* **125**, 1–15.

Fisher RA (1921). Some remarks on the methods formulated in a recent article on "The quantitative analysis of plant growth." *Annals of Applied Biology* **7**, 367–72.

Fleiss JL (1993). Review papers: The statistical basis of meta-analysis. *Statistical Methods in Medical Research* **2**, 121–45.

Foufopoulos J, Kilpatrick AM, Ives AR (2010). Climate change and elevated extinction rates of reptiles from Mediterranean islands. *The American Naturalist* **177**, 119–29.

Gardner JL, Peters A, Kearney MR, Joseph L, Heinsohn R (2011). Declining body size: A third universal response to warming? *Trends in Ecology & Evolution* **26**, 285–91.

Garland T, Bennett AF, Rezende EL (2005). Phylogenetic approaches in comparative physiology. *Journal of Experimental Biology* **208**, 3015–35.

Gelman A, Su YS (2016). *arm: Data Analysis Using Regression and Multilevel/Hierarchical Models. R package version 1.9-3.* [Cited 21 Feb 2018.] Available from URL: https://CRAN.R-project.org/package=arm.

Graae BJ, De Frenne P, Kolb A *et al.* (2012). On the use of weather data in ecological studies along altitudinal and latitudinal gradients. *Oikos* **121**, 3–19.

Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011). Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology* **24**, 699–711.

Gvoždík, L. (2002). To heat or to save time? Thermoregulation in the lizard *Zootoca vivipara* (Squamata: Lacertidae) in different thermal environments along an altitudinal gradient. *Canadian Journal of Zoology* **80**, 479–92.

Heath JE (1964). Reptilian thermoregulation: Evaluation of field studies. *Science* **146**, 784–5.

Heath JE (1970). Behavioral regulation of body temperature in poikilotherms. *The Physiologist* **13**, 399.

Hedges LV, Olkin I (1985). *Statistical Methods for Meta-Analysis*. Academic Press, Orlando.

Herczeg G, Kovács T, Tóth T, Török J, Korsós Z, Merilä J (2004). Tail loss and thermoregulation in the common lizard *Zootoca vivipara*. *Naturwissenschaften* **91**, 485–8.

Hertz PE (1981). Adaptation to altitude in two West Indian anoles (Reptilia: Iguanidae): Field thermal biology and physiological ecology. *Journal of Zoology* **195**, 25–37.

Hertz PE (1992). Temperature regulation in Puerto Rican *Anolis* lizards: A field test using null hypotheses. *Ecology* **73**, 1405–17.

Hertz PE, Huey RB, Stevenson RD (1993). Evaluating temperature regulation by field-active ectotherms: The fallacy of the inappropriate question. *The American Naturalist* **142**, 796–818.

Higgins JP, Thompson SG (2002). Quantifying heterogeneity in a meta-analysis. *Statistics in Medicine* **21**, 1539–58.

Huey RB, Pianka ER (1977). Seasonal variation in thermoregulatory behavior and body temperature of diurnal Kalahari lizards. *Ecology* **58**, 1066–75.

Huey RB, Pianka ER (2018). Body temperature distributions of active diurnal lizards in three deserts: Skewed up or skewed down? *Functional Ecology* **32**, 334–44.

Huey RB, Slatkin M (1976). Costs and benefits of lizard thermoregulation. *The Quarterly Review of Biology* **51**, 363–84.

Huey RB, Stevenson RD (1979). Integrating thermal physiology and ecology of ectotherms: A discussion of approaches. *The American Zoologist* **19**, 357–66.

Huey RB, Deutsch CA, Tewksbury JJ *et al.* (2009). Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society of London B: Biological Sciences* **276**, 1939–48.

Hunter JE, Schmidt FL (2004). *Methods of Meta-Analysis*. Sage Publications, Thousand Oaks, CA.

Kingsolver JG, Huey RB (2008). Size, temperature, and fitness: Three rules. *Evolutionary Ecology Research* **10**, 251–68.

Koricheva J, Gurevitch J, Mengersen K (2013). *Handbook of Meta-analysis in Ecology and Evolution*. Princeton University Press, Princeton, NJ.

Kottek M, Grieser J, Beck C, Rudolf B, Rubel F (2006). World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift* **15**, 259–63.

Le Galliard JF, Massot M, Baron JP, Clobert J (2012). Ecological effects of climate change on European reptiles. In: Brodie J, Post E, Doak D, eds. *Wildlife Conservation in a Changing Climate*, pp. 179–203.

Light RJ, Singer JD, Willett JB (1994). The visual presentation and interpretation of meta-analyses. In: Cooper HM, Hedges LV, eds. *The Handbook of Research Synthesis*. Russell Sage Foundation, New York, pp. 439–53.

Lortie CJ, Stewart G, Rothstein H, Lau J (2013). How to critically read ecological meta-analyses. *Research Synthesis Methods* **6**, 124–33.

Losos JB (2009). *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. University of California Press, Oakland, CA.

Martín J, Lopez P (2013). Effects of global warming on sensory ecology of rock lizards: Increased temperatures alter the efficacy of sexual chemical signals. *Functional Ecology* **27**, 1332–40.

Martins LS, Verrastro L, Tozetti AM (2014). The influences of habitat on body temperature control in a southern population of *Liolaemus occipitalis* (Boulenger, 1885) in Brazil. *South American Journal of Herpetology* **9**, 9–13.

Martínez-Freiría F, Argaz H, Fahd S, Brito JC (2013). Climate change is predicted to negatively influence Moroccan endemic reptile richness. Implications for

conservation in protected areas. *Naturwissenschaften* **100**, 877–89.

Martín-Vallejo J (1995). Métodos estadísticos en meta-análisis (PhD thesis). University of Salamanca, Spain.

Meiri S, Bauer AM, Chirio L *et al.* (2013). Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. *Global Ecology and Biogeography* **22**, 834–45.

Mitchell WA, Angilletta MJ (2009). Thermal games: Frequency-dependent models of thermal adaptation. *Functional Ecology* **23**, 510–20.

Moreno-Rueda G. Pleguezuelos JM, Pizarro M, Montori A (2012). Northward shifts of the distributions of Spanish reptiles in association with climate change. *Conservation Biology* **26**, 278–83.

Nakagawa S, Freckleton RP (2011). Model averaging, missing data and multiple imputation: A case study for behavioural ecology. *Behavioral Ecology and Sociobiology* **65**, 103–16.

Nakagawa S, Poulin R (2012). Meta-analytic insights into evolutionary ecology: An introduction and synthesis. *Evolutionary Ecology* **26**, 1085–99.

Nakagawa S, Santos EA (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology* **26**, 1253–74.

Olalla-Tárraga MÁ, Rodríguez MÁ, Hawkins BA (2006). Broad-scale patterns of body size in squamate reptiles of Europe and North America. *Journal of Biogeography* **33**, 781–93.

Ortega Z, Pérez-Mellado V (2016). Seasonal patterns of body temperature and microhabitat selection in a lacertid lizard. *Acta Oecologica* **77**, 201–6.

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**, 32–9.

Ortega Z, Martin-Vallejo J, Mencía A, Galindo-Villardón MP, Pérez-Mellado V (2016a). Meta-partition, a useful methodology to explore factors that influence ecological effect sizes. *PLoS ONE* **11**, e0158624.

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

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

Ortega Z, Mencía A, Pérez-Mellado V (2016d). Behavioral buffering of global warming in a cold-adapted lizard. *Ecology and Evolution* **6**, 4582–90.

Peters JL, Sutton AJ, Jones DR, Abrams KR, Rushton L (2008). Contour-enhanced meta-analysis funnel plots help distinguish publication bias from other causes of asymmetry. *Journal of Clinical Epidemiology* **61**, 991–6.

Pörtner HO (2002). Climate variations and the physiological basis of temperature dependent biogeography: Systemic to molecular hierarchy of thermal tolerance in animals. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **132**, 739–61.

R Core Team (2016). *R: A Language and Environment for Statistical Computing. – R Foundation for Statistical Computing*, Vienna, Austria. [Cited 21 Feb 2018.] Available from URL: https://www.R-project.org/.

Reguera S, Zamora-Camacho FJ, Moreno-Rueda G (2014). The lizard *Psammodromus algirus* (Squamata: Lacertidae) is darker at high altitudes. *Biological Journal of the Linnean Society* **112**, 132–41.

Rosenberg MS, Adams DC, Gurevitch J (2000). *MetaWin: Statistical Software for Meta-analysis with Resampling Tests*. Sinauer Associates, Sunderland, MA.

Sagonas K, Kapsalas G, Valakos E, Pafilis P (2017). Living in sympatry: The effect of habitat partitioning on the thermoregulation of three Mediterranean lizards. *Journal of Thermal Biology* **65**, 130–7.

Sagonas K, Meiri S, Valakos ED, Pafilis P (2013a). The effect of body size on the thermoregulation of lizards on hot, dry Mediterranean islands. *Journal of Thermal Biology* **38**, 92–7.

Sagonas K, Valakos ED, Pafilis P (2013b). The impact of insularity on the thermoregulation of a Mediterranean lizard. *Journal of Thermal Biology* **38**, 480–86.

Sears MW, Angilletta MJ (2015). Costs and benefits of thermoregulation revisited: Both the heterogeneity and spatial structure of temperature drive energetic costs. *The American Naturalist* **185**, E94–102.

Sears MW, Raskin E, Angilletta MJ (2011). The world is not flat: Defining relevant thermal landscapes in the context of climate change. *Integrative and Comparative Biology* **51**, 666–75.

Sears MW, Angilletta MJ, Schuler MS *et al.* (2016).

Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. *Proceedings of the National Academy of Sciences* **113**, 10595–600.

Sunday JM, Bates AE, Kearney MR *et al.* (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences* **111**, 5610–15.

Stevenson RD (1985). Body size and limits to the daily range of body temperature in terrestrial ectotherms. *The American Naturalist* **125**, 102–17.

Van Damme R, Bauwens D, Castilla AM, Verheyen RF (1990). Comparative thermal ecology of the sympatric lizards *Podarcis tiliguerta* and *Podarcis sicula*. *Acta Oecologica* **11**, 503–12.

Zuur AF, Ieno EN, Elphick CS (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* **1**, 3–14.

SUPPLEMENTARY MATERIALS

Detailed Results

Cite this article as:

Ortega Z, Martín-Vallejo FJ (2019). Main factors affecting lacertid lizard thermal ecology. *Integrative Zoology* **14**, 293–305.