

# Wind constraints on the thermoregulation of high mountain lizards

Zaida Ortega<sup>1</sup>  · Abraham Mencía<sup>1</sup> · Valentín Pérez-Mellado<sup>1</sup>

Received: 29 October 2015 / Revised: 13 July 2016 / Accepted: 8 August 2016  
© ISB 2016

**Abstract** Thermal biology of lizards affects their overall physiological performance. Thus, it is crucial to study how abiotic constraints influence thermoregulation. We studied the effect of wind speed on thermoregulation in an endangered mountain lizard (*Iberolacerta aurelioi*). We compared two populations of lizards: one living in a sheltered rocky area and the other living in a mountain ridge, exposed to strong winds. The preferred temperature range of *I. aurelioi*, which reflects thermal physiology, was similar in both areas, and it was typical of a cold specialist. Although the thermal physiology of lizards and the structure of the habitat were similar, the higher wind speed in the exposed population was correlated with a significant decrease in the effectiveness thermoregulation, dropping from 0.83 to 0.74. Our results suggest that wind reduces body temperatures in two ways: via direct convective cooling of the animal and via convective cooling of the substrate, which causes conductive cooling of the animal. The detrimental effect of wind on thermoregulatory effectiveness is surprising, since lizards are expected to thermoregulate more effectively in more challenging habitats. However, wind speed would affect the costs and benefits of thermoregulation in more complex ways than just the cooling of animals and their habitats. For example, it may reduce the daily activity, increase desiccation, or complicate the hunting of prey. Finally, our results imply that wind should also be considered when developing conservation strategies for threatened ectotherms.

**Keywords** Wind · Abiotic constraints · Thermoregulation · Climate change · Lizard · Mountains

## Introduction

Temperature is probably the meteorological factor that most affects animals, particularly ectotherms, conditioning all aspects of their lives, and eventually, survival (Huey and Stevenson 1979; Adolph and Porter 1993; Angilletta 2009). Environmental temperatures available for organisms vary with latitude, altitude, weather conditions, and habitat composition (Díaz et al. 2006; Deutsch et al. 2008; Sears et al. 2011; Graae et al. 2012). An animal's survival in a given climate is dictated by two main features: the animal's thermal sensitivity and its ability to thermoregulate (Angilletta, 2009). Thermal sensitivity describes the extent to which physiological performance of an organism depends on temperature, with a gradient between thermal specialists, whose performance is optimal in a narrow range of temperatures, and thermal generalists, which are able to perform well in a wide range of temperatures (Angilletta et al. 2002; Angilletta 2009). Thermoregulation is the ability to actively regulate body temperature, with a gradient from thermoconformers, whose body temperatures would always be similar to ambient temperatures, and to perfect thermoregulators, whose body temperatures would be independent of ambient temperature (Heath 1970; Huey 1974; Hertz et al. 1993; Sears and Angilletta 2015).

Other abiotic factors, such as wind, can deeply affect the activity and thermoregulation of ectotherms (Scheers and Van Damme 2002; Maia-Carneiro et al. 2012; Logan et al. 2015). Wind speed affects the heat exchange between the animal and the environment (Porter and Gates 1969; Stevenson 1985). Wind would decrease air temperature, which would also promote the heat loss of the animal by convection. In addition,

---

✉ Zaida Ortega  
zaidaortega@usal.es

<sup>1</sup> Department of Animal Biology, University of Salamanca, Campus Miguel de Unamuno, 37007 Salamanca, Spain

wind can also cool the substrates, like rocks, decreasing the heat that the animal can gain through conduction or even by the infrared radiation reflected by rocks (Porter and Gates 1969; Kearney and Porter 2009). Furthermore, wind speed would also increase water loss, but this would be less important for reptiles than for other ectotherms, such as amphibians (e.g., Tracy and Christian 2005; but see Winne et al. 2001). Moreover, a negative effect of wind exposure on activity has been reported for some vipers and tropical lizards (Logan et al. 2015; Sun et al. 2001). The effects of wind in the energy budget of ectotherms have been studied by biophysical approaches (e.g., Kearney and Porter 2009), and experimental studies may add strength to their conclusions.

High mountain lizards could be seriously threatened by climate change for three main reasons: (1) they are often cold specialists, which increases the decline of individual fitness once body temperatures exceed the optimal temperatures (Martin and Huey 2008; Huey et al. 2012), (2) phenotypic plasticity or genetic evolution seems difficult to keep pace with fast environmental warming (Buckley et al. 2015; Chevin and Lande 2015; Gunderson and Stillman 2015), and (3) they have no place to migrate from mountaintops in order to find thermally suitable areas (Berg et al. 2010; McCain 2010; Bestion et al. 2015). These circumstances highlight the need to develop conservation plans to prevent the extinction of high mountains ectotherms, particularly in the rich and vulnerable Mediterranean mountains (Araújo et al. 2006, 2011; Carvalho et al. 2010; Crossman et al. 2012; Maiorano et al. 2013).

Here, we use an endangered mountain lizard (*Iberolacerta aurelioi*) as a model organism to assess the effect of wind in thermoregulation. Therefore, we compare two populations that differ in wind exposure but are similar in other characteristics.

## Materials and methods

### Study species and study area

The Aurelio's rock lizard, *I. aurelioi* (Arribas 1994), is an endemic lacertid lizard of the Pyrenees that inhabits fragmented areas, between 2100 and 2942 m of altitude, in Pallars region (Spain), Ariège (France), and Andorra (Arribas 2002). *I. aurelioi* prefers slopes facing south, protected from the wind, and with good insulation (Arribas 1997, 2002, 2010). Due to the presence of snow covering the ground during, at least, 6 to 9 months (Arribas and Galán 2005), Pyrenean lizards are characterized by a short activity period. *I. aurelioi* is classified as "endangered" (EN) in the IUCN red list, because its area of occupancy is less than 500 km<sup>2</sup>, with highly fragmented and declining populations, mainly threatened by direct destruction of the habitat by human activities and climate change (Pérez-Mellado et al. 2009).

The study took place in the mountains of Comapedrosa (La Massana, Andorra). To assess the effect of the wind, we selected two areas of study. The first area (hereafter, *ski slope*) is a protected slate scree, located at the end of a ski slope at the Vallnord ski resort (2500 m a.s.l.). The second area (hereafter, *Sanfons*) is a slate scree located in a mountain ridge (2700 m a.s.l.), continuously exposed to the wind. Both areas belong to the alpine bioclimatic region, so they almost lack shrub vegetation (Nicolau and Baró 2009).

### Field sampling

Body temperatures ( $T_b$ ) were obtained during June 2012, simultaneously to the record of operative temperatures ( $T_e$ ). We captured lizards by noosing, from 09.00 to 16.00 h GMT. For each captured lizard, we measured body temperature ( $T_b$ ) with a Testo® 925 digital thermometer ( $\pm 0.1$  °C precision) immediately after capture, as well as air temperature ( $T_a$ ) 1 cm above the capture point and substrate temperature ( $T_s$ ) at the capture point. We also measured the speed of the wind with a 3000 Kestrel™ anemometer (in ms<sup>-1</sup>), and the distance of the lizard to the nearest refuge (in cm), and registered the type of substrate (rock, soil, grass, or loose stones). In order to compare body condition between areas, we recorded snout-vent length (SVL, with a steel rule, in mm) and weight of lizards (with a Pesola® dynamometer, in g). Body condition was computed as the residual values from the regression of body mass on SVL (Schulte-Hostedde et al. 2005).

We recorded operative temperatures ( $T_e$ ) simultaneously to  $T_b$ , and in the same two areas of study. We employed copper models as null  $T_e$  models (Bakken and 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 record every 5 min. We used ten data loggers. Copper models were randomly placed in different microhabitats, replicating the distribution for the two areas of study, the *ski slope* ( $N = 2686 T_e$ ) and *Sanfons* ( $N = 2439 T_e$ ). Following Logan et al. (2015), for both areas, thermal heterogeneity of the habitat was quantified as the standard deviation of the mean operative temperatures from data loggers. Furthermore, we measured spatial heterogeneity of both areas with 17 linear transects (7 in the *ski slope* and 10 in *Sanfons*). The spatial heterogeneity was described by mean values of the cover proportion of each microhabitat (the mean percent microhabitat cover) and the mean microhabitat frequency (the mean number of times that each microhabitat occurred on the total).

### Preferred temperature range

The preferred temperature range of *I. aurelioi* was also measured in June 2012. We captured 24 lizards (12 males and 12 females) in both study areas. Lizards 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 × 60 × 60 cm) with a 150-W infrared lamp over one of the sides, obtaining a gradient between 20 to 60 °C. Lizards were introduced in the thermal gradient 24 h prior to the first measurement, in order to let them explore the new surroundings before resuming normal thermoregulatory behavior (e.g., Ladyman and Bradshaw 2003). Each hour, from 08.00 to 18.00 h (GMT), individual values of selected temperatures ( $T_{\text{set}}$ ) of lizards were recorded with a digital thermometer, obtaining 157 values of selected temperatures. The 50 % of central values of selected body temperatures were considered as the preferred temperature range to assess thermoregulation (Hertz et al. 1993; Blouin-Demers and Nadeau 2005). After the experiment, lizards were released at the same places of capture.

### Data analysis

To test the null hypothesis of thermoregulation (that is, if lizards use microhabitats randomly regarding temperature), we followed the protocol developed by Hertz et al. (1993) and calculated their three indexes of thermoregulation. The first is the index of accuracy of thermoregulation ( $d_b$ ), which is the mean of absolute values of the deviations between each  $T_b$  from the preferred temperature range. Thus, the values of the index of accuracy of thermoregulation are counterintuitive: higher values of  $\bar{d}_b$  indicate lower accuracy of thermoregulation and vice versa. The second is the index of thermal quality of habitat ( $\bar{d}_e$ ), calculated as the mean of absolute values of the deviations between each  $T_e$  from the preferred temperature range. Accordingly, the values of the index of thermal quality of the habitat are also counterintuitive: higher values of ( $\bar{d}_e$ ) indicate a lower thermal quality of the habitat and vice versa. The third is the index of effectiveness of thermoregulation ( $E$ ), which is calculated as  $E = 1 - (d_b/d_e)$ . Values of  $E$  can range from 0 to 1, where a larger  $E$  means a higher effectiveness of thermoregulation (see Hertz et al. 1993). Effectiveness of thermoregulation was calculated with THERMO, a Minitab module written by Richard Brown. THERMO has been used in previous studies of thermal biology of lizards (e.g., Ortega et al. 2014, 2016a, b). It uses three kinds of input data, namely  $T_b$ ,  $T_e$ , and  $T_{\text{set}}$  of the preferred temperature range, and was programmed to perform bootstraps of 100 iterations, building pseudo-distributions of three kinds of output values: the arithmetic mean of the index of accuracy of thermoregulation ( $d_b$ ), the arithmetic mean of the index of thermal quality of the habitat ( $\bar{d}_e$ ), and the arithmetic mean of the index of effectiveness of thermoregulation ( $E$ ).

Mean values are accompanied by standard errors (SE). 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 and 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).

To assess the effect of wind on body temperatures, we fitted a generalized linear model (GLM) with normal errors (Crawley 2012). We considered the wind speed, the study area, the substrate temperature and the air temperature 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, with a stepwise procedure, non-significant variables and interactions ( $p > 0.05$ ). In this way, we obtained the simplest significant model to explain body temperatures of active *I. aurelioi*. For each model, we evaluated data dispersion and the distribution of residual values (Crawley 2012).

### Results

Body size of *I. aurelioi* lizards was  $53.14 \pm 0.70$  mm (mean SVL  $\pm$  SE,  $N = 27$ ), without differences between sexes (one-way ANOVA,  $F_{1, 25} = 0.121$ ,  $p = 0.731$ ) nor between areas (one-way ANOVA,  $F_{1, 25} = 0.174$ ,  $p = 0.680$ ). Mean body mass was  $2.96 \pm 0.11$  g ( $N = 27$ ), without differences between sexes (Mann-Whitney  $U$  test,  $U = 84.50$ ,  $p = 0.756$ ) nor between areas (one-way ANOVA,  $F_{1, 25} = 2.296$ ,  $p = 0.142$ ). Mean body condition was also similar between areas (one-way ANOVA,  $F_{1, 25} = 2.686$ ,  $p = 0.114$ ).

Selected temperatures ( $T_{\text{set}}$ ) were similar for both sexes (one-way ANOVA,  $F_{1, 84} = 1.394$ ,  $p = 0.241$ ). Furthermore,  $T_{\text{set}}$  were also similar between the two areas of study (Mann-Whitney  $U$  test,  $U = 510.50$ ,  $p = 0.878$ ,  $N = 86$ ), so a unique preferred temperature range, between 30.75 and 32.00 °C, was considered for *I. aurelioi*. Body temperatures ( $T_b$ ) of *I. aurelioi* were also similar in males and females (one-way ANOVA,  $F_{1, 34} = 0.069$ ,  $p = 0.794$ ). Thus, we pooled data of both sexes for further analyses. Body temperatures were significantly higher in the *ski slope* area than in *Sanfons* (one-way ANOVA,  $F_{1, 34} = 7.729$ ,  $p = 0.009$ ), as well as substrate temperatures ( $T_s$ ; Mann-Whitney  $U$  test,  $U = 17.50$ ,  $p < 0.0001$ ), while air temperatures ( $T_a$ ) were similar in both areas (Mann-Whitney  $U$  test,  $U = 118.0$ ,  $p = 0.375$ ; Table 1).

Correlation between  $T_b$  and  $T_a$  was only marginally significant in the *ski slope* area ( $r = -0.382$ ,  $p = 0.065$ ,  $N = 17$ ) and not significantly different from zero in *Sanfons* ( $r = -0.147$ ,  $p = 0.287$ ,  $N = 17$ ). Correlation between  $T_b$  and  $T_s$  was not significantly different from zero in the *ski slope* ( $r = 0.277$ ,  $p = 0.141$ ,  $N = 17$ ), but it was statistically different in *Sanfons*

**Table 1** Mean  $\pm$  SE ( $N$ ) body temperatures ( $T_b$ ), air temperatures ( $T_a$ ), substrate temperatures ( $T_s$ ), the index of thermal quality of the habitat ( $d_e$ ), the index of accuracy of thermoregulation ( $d_b$ ), and the index effectiveness of thermoregulation ( $E$ ) of *Iberolacerta aurelioi* lizards in the wind-sheltered *ski slope* area and the wind-exposed *Sanfons*

	<i>Ski slope</i>	<i>Sanfons</i>
$T_b$	30.95 $\pm$ 0.53 °C (19)	28.63 $\pm$ 0.64 °C (18)
$T_a$	25.92 $\pm$ 0.40 °C (17)	24.29 $\pm$ 1.06 °C (17)
$T_s$	34.84 $\pm$ 0.94 °C (17)	29.12 $\pm$ 0.50 °C (17)
$\bar{d}_e$	7.44 $\pm$ 0.36 °C	10.15 $\pm$ 0.39 °C
$\bar{d}_b$	1.23 $\pm$ 0.06 °C	2.63 $\pm$ 0.05 °C
$\bar{E}$	0.83 $\pm$ 0.004	0.74 $\pm$ 0.005

( $r = 0.635$ ,  $p = 0.003$ ,  $N = 17$ ). Linear relations showed a different tendency for both areas between  $T_b$  and  $T_a$  (*ski slope*  $T_b = 44.67 - 0.53 * T_a$ ,  $p$  of the regression coefficient = 0.131,  $R^2 = 0.146$ ,  $N = 17$ ; *Sanfons*  $T_b = 31.00 - 0.09 * T_a$ ,  $p$  of the regression coefficient = 0.574,  $R^2 = 0.022$ ,  $N = 17$ ), although slopes were not significantly different for both areas (ANCOVA slopes test,  $F_{1, 30} = 1.170$ ,  $p = 0.288$ ). However, the slopes of linear regressions between  $T_b$  and  $T_s$  were significantly different between study areas (*ski slope*  $T_b = 25.30 + 0.16 * T_s$ ,  $p$  of the regression coefficient = 0.282,  $R^2 = 0.077$ ,  $N = 17$ ; *Sanfons*  $T_b = 4.36 + 0.84 * T_s$ ,  $p$  of the regression coefficient = 0.006,  $R^2 = 0.404$ ,  $N = 17$ ; ANCOVA slopes test,  $F_{1, 30} = 4.855$ ,  $p = 0.035$ ; Fig. 1b).

Wind speed was significantly higher in *Sanfons* than in the *ski slope* area (*ski slope*  $0.71 \pm 0.18 \text{ m s}^{-1}$ ,  $N = 19$ ; *Sanfons*  $1.73 \pm 0.26 \text{ m s}^{-1}$ ,  $N = 18$ ; one-way ANOVA,  $F_{1, 35} = 10.634$ ,  $p = 0.002$ ). The best-fitted GLM shows that wind speed had a significant effect decreasing the  $T_b$  of lizards (Table 2). The interaction between wind speed and the study area is significant, as well as the interaction between wind speed and  $T_s$

(Table 2). These results suggest that wind reduces body temperatures in two ways: via direct convective cooling of the animal and via convective cooling of the substrate which causes conductive cooling of the animal (Fig. 1).

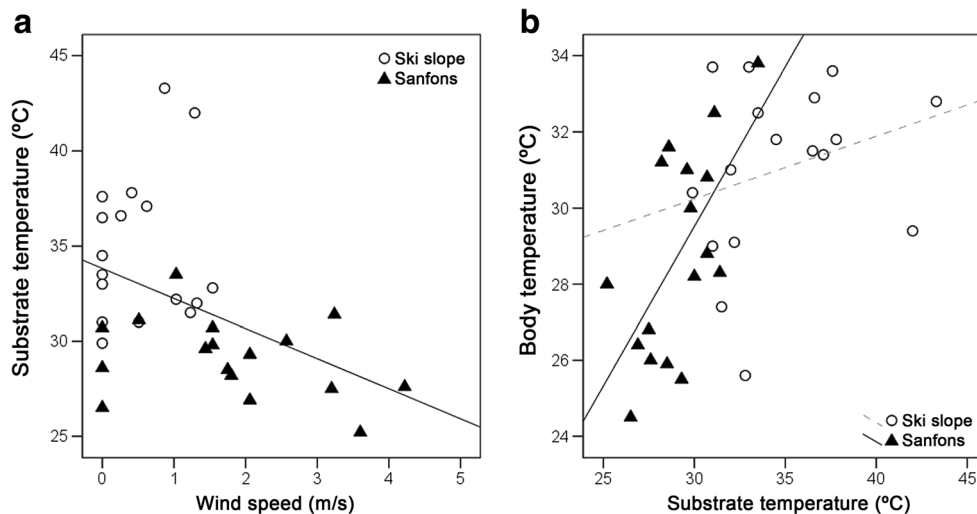
Operative temperatures ( $T_e$ ) varied significantly through the day in the *ski slope* (Kruskal-Wallis test,  $H = 1293.75$ , d.f. = 10,  $p < 0.0001$ ) as well as in *Sanfons* (Kruskal-Wallis test,  $H = 1169.59$ , d.f. = 10,  $p < 0.0001$ ). For all microhabitats,  $T_e$  were significantly higher in the *ski slope* than in *Sanfons* and they only reach the preferred temperature range of *I. aurelioi* for *ski slope*, being suboptimal in *Sanfons* (Table 3; Fig. 2). Thus, the proportion of  $T_e$  above the preferred temperature range was higher in the *ski slope* than in *Sanfons* ( $\chi^2 = 628.287$ , d.f. = 2,  $p < 0.0001$ ). In addition, mean distance to the nearest potential refuge was similar for lizards of both areas (*ski slope*  $6.79 \pm 1.35 \text{ cm}$ ,  $N = 14$ ; *Sanfons*  $5.38 \pm 1.05 \text{ cm}$ ,  $N = 13$ ; one-way ANOVA,  $F_{1, 25} = 0.657$ ,  $p = 0.425$ ) and the structure of the *ski slope* and *Sanfons*, in terms of microhabitat composition and its distribution, was also similar (Table 4). Thermal heterogeneity was similar in both areas (*ski slope*  $sd = 5.26 \text{ °C}$ ,  $N = 11$ ; *Sanfons*  $sd = 3.43 \text{ °C}$ ,  $N = 10$ ; Levene's test,  $F_{1, 19} = 1.774$ ,  $p = 0.199$ ).

Finally, the index of thermal quality of the habitat ( $d_e$ ) was significantly lower for the *ski slope* (one-way ANOVA,  $F_{1, 198} = 2630.21$ ,  $p < 0.0001$ ), as well as the index of accuracy of thermoregulation (Mann-Whitney  $U$  test,  $U = 65.50$ ,  $p < 0.0001$ ), and effectiveness of thermoregulation was significantly higher for lizards of the *ski slope* (Mann-Whitney  $U$  test,  $U = 686.00$ ,  $p < 0.0001$ ; Table 1; Fig. 3).

## Discussion

Our results show that *I. aurelioi* is a cold-specialist lizard, as other species of the genus *Iberolacerta* (Martin and Salvador 1993; Aguado and Braña 2014; Žagar et al. 2015; Ortega et al.

**Fig. 1 a** As the wind speed increased, the substrate temperature ( $T_s$ ) decreased, being the linear relationship similar in both areas (ANCOVA slopes test,  $F_{1, 30} = 0.718$ ,  $p = 0.404$ ; see the common regression slope in the plot). **b** As  $T_s$  decreased, body temperature ( $T_b$ ) also decreased, and the slope or regression is significantly steeper in the wind-exposed area of *Sanfons* than in the wind-protected area if the *ski slope* (see both regression slopes in the plot)





**Table 2** Parameters of the simplest GLM that explains body temperature ( $T_b$ ) of *Iberolacerta aurelioi*

	Coefficient	SE	<i>t</i>	<i>p</i> value
Intercept	25.1560	4.1469	6.066	<0.0005
<i>Sanfons</i> area	-17.6528	8.1912	-2.155	0.0399
Wind speed	-3.1786	0.8134	-3.908	0.0005
Substrate temperature ( $T_s$ )	0.2175	0.1191	1.826	0.0785
<i>Sanfons</i> area: wind speed	2.7598	0.8971	3.077	0.0046
<i>Sanfons</i> area: $T_s$	0.5390	0.2622	2.055	0.0493

Deviance residual: 93.989, with 28 degrees of freedom. AIC = 145.06, lower than the AIC of more complex models. Residuals are normally distributed (Shapiro-Wilk test,  $W = 0.9802$ ,  $p = 0.7777$ )

2016a, b), with a preferred temperature range of 30.75–32.00 °C. The preferred temperature range was consistent between sexes and areas of study, and it is the narrowest found to date in Lacertidae. The fact that the preferred temperature range did not differ between both populations, exposed to different wind regimes, also reflects the conservative pattern of this phenotypic trait in evolution (Huey et al. 2003).

Operative temperatures were significantly lower in the wind-exposed area of *Sanfons* than in the wind-protected area of the *ski slope* for all replicated microhabitats. Thermal habitat quality was significantly lower for *Sanfons* (indicated by a higher  $d_e$  value), and *Sanfons* lizards showed less accurate thermoregulation (indicated by a higher  $d_b$ ). Effectiveness of thermoregulation of *I. aurelioi* clearly decreased as the wind speed increased, from 0.83 in the *ski slope*, with an average wind of 0.71 to 0.74 m s<sup>-1</sup> in *Sanfons*, with an average wind of 1.73 m s<sup>-1</sup>. Other traits were similar between the two study sites, as the distance to the nearest refuge and the spatial heterogeneity and thermal heterogeneity of the habitat. So, the clear difference between both areas was wind speed, which sharply reduced operative temperatures and body temperatures of lizards in *Sanfons* area. Our results of the GLM suggest that wind reduces body temperatures in two ways: via direct convective cooling of the animal and via convective cooling of the substrate which causes conductive cooling of the animal. Wind should cause accuracy of thermoregulation to decrease, but so long as the wind also causes habitat thermal quality to decrease to the same extent, effectiveness may be

unchanged. Since *I. aurelioi* effectiveness decreased with the increase of wind, our results suggest that accuracy is decreasing faster than thermal quality ( $d_b$  is increasing faster than  $d_e$ ). This means that the wind-exposed lizards may be actually exploiting a smaller proportion of the possible time they could be at their optimal temperatures, thus, reducing daily activity.

Previous studies support that ectotherms may increase their effectiveness of thermoregulation when the thermal quality of the habitat decreases, that is, that they would thermoregulate more carefully in challenging habitats (Blouin-Demers and Weatherhead 2001, 2002; Sagonas et al. 2013). Surprisingly, our results do not support this pattern, since *I. aurelioi* lizards thermoregulate less effectively in the less thermally suitable habitat, as it happens for other mountain populations of lizards (e.g., Monasterio et al. 2009; Zamora-Camacho et al. 2015). It is possible that wind impacts the behavior of *I. aurelioi* through more than just a reduction in body temperatures. Wind may add additional costs associated with feeding opportunities or water balance (Logan et al. 2015; Sun et al. 2001). Energetic benefits of thermoregulation would be clearly lower in wind-exposed high mountain areas (Huey and Slatkin 1976; Angilletta 2009). Nonetheless, body condition of lizards did not change between both areas, so the drop in the effectiveness of thermoregulation apparently does not affect the energetic status of *I. aurelioi*, as has been reported in *Iberolacerta cyreni* living in areas with human disturbance (Amo et al. 2007).

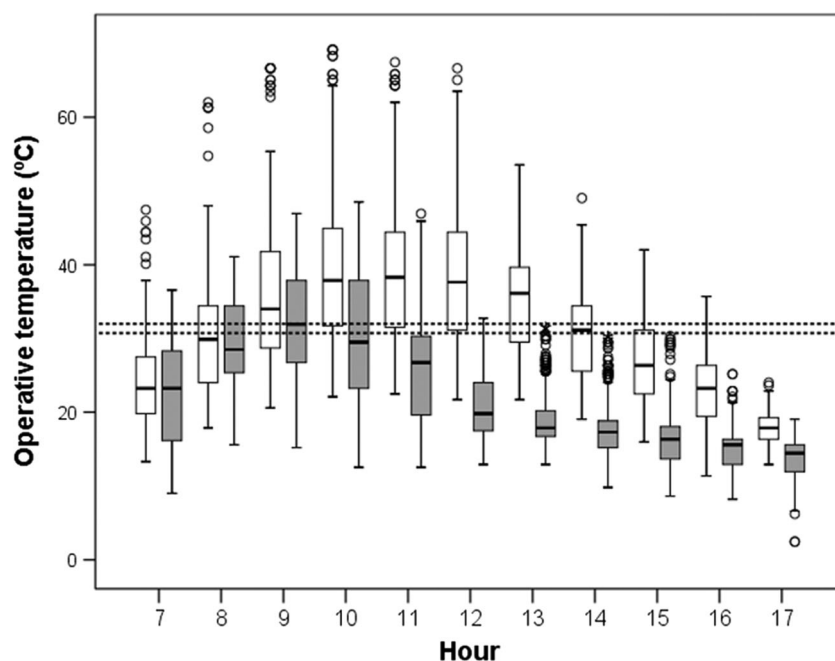
Although thermal biology of lizards has been extensively studied, it has been given little attention to the role of the wind in the thermoregulation, and the scarce available studies show that it may be a key constraint on the activity of lizards of open areas (Sun et al. 2001; Maia-Carneiro et al. 2012; Logan et al. 2015). If wind (above some critical speed that may change for different species and habitats) causes thermal accuracy to decrease at a faster rate than thermal quality of the habitat, resulting in a decrease of thermal effectiveness, this would be the cause for the reduction of activity observed in some lizards and snakes (Sun et al. 2001; Logan et al. 2015). In addition, wind may increase desiccation rates (Claussen 1967) or inhibit prey detection, increasing the energetic costs of maintaining a preferred body temperature. Wind could also inhibit predator detection, adding additional risks to

**Table 3** Mean ± SE (N) operative temperatures ( $T_e$ ) in °C

	<i>Ski slope</i>	<i>Sanfons</i>	Comparison
Rock facing east	32.53 ± 0.46 (242)	23.06 ± 0.37 (243)	$U = 9454.00$ , $p < 0.0001$
Flat rock	31.50 ± 0.23 (1455)	22.25 ± 0.25 (1221)	$U = 387,081.00$ , $p < 0.0001$
Under rock	29.80 ± 0.35 (496)	22.84 ± 0.36 (486)	$U = 65,461.00$ , $p < 0.0001$
Grass	33.10 ± 0.68 (493)	21.45 ± 0.40 (484)	$U = 62,482.00$ , $p < 0.0001$
Global	31.57 ± 0.19 (2686)	22.28 ± 0.17 (2439)	

Data are compared with the Mann-Whitney  $U$  test, resulting in lower  $T_e$  in all microhabitats in the wind-exposed area of *Sanfons*

**Fig. 2** Daily variation of operative temperatures ( $T_e$ ) in the both areas of study: the *ski slope* (white boxes) and *Sanfons* (gray boxes).  $T_e$  were significantly lower in *Sanfons* for all microhabitats. The dotted lines represent the 50 % preferred temperature range of *Iberolacerta aurelioi* (30.75–32.00 °C). The little white circles that accompany the boxes are the outlier values of  $T_e$  between the 90th and 95th percentiles



thermoregulation in habitats with high predation pressures. In any case, more research is needed to understand how the effect of the wind affects the ecology and evolution of ectotherms.

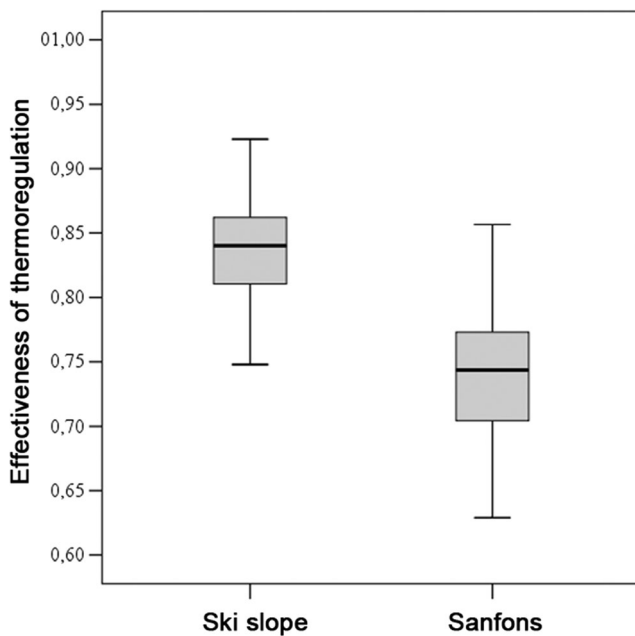
The wind-protected area exhibited suitable conditions for the thermoregulation of *I. aurelioi*, while the wind-exposed area exhibited a suboptimal habitat. Therefore, it would be interesting to study the thermal quality of the habitat when considering the conservation strategies of these endangered species (Groves et al. 2012; Seebacher and Franklin 2012). Small differences in abiotic constraints such as wind can make big differences to lizard populations (Ortega et al. 2014; Logan et al. 2015). On the other hand, it is important to keep in mind that the negative impact of wind on the thermoregulation occurs under current climatic conditions, which are rapidly changing. A specific study on the effects of climate change on amphibians and reptiles of the Iberian Peninsula predicts that, even in the best case scenario for reducing greenhouse gas emissions, *I. aurelioi* will lose all its suitable habitats by 2020 (Carvalho et al. 2010). Another research for the

Mediterranean mountains predicts an increase between 1.4 and 5.18 °C till 2085, accompanied by a sharp increase in drought (Nogués-Bravo et al. 2008). The overall increase of temperature predicted for the planet is 4.3 °C in 2100 (Pacifi et al. 2015). Thus, all predictions lead us to warn about the high risk of extinction of the Mediterranean mountain lizards along the twenty-first century. Among the conservation strategies that are being proposed to cope with climate change, the most useful for high mountain ectotherms seems to be the complete protection of high mountain habitats, and the creation of climate corridors to improve connectivity of populations (Groves et al. 2012; Keppel et al. 2012). Hence, cold areas have been proposed to serve as climate refugia to allow the conservation of mountain biodiversity once the warming would turn damaging (Araújo et al. 2011; Crossman et al. 2012; Maiorano et al. 2013). The understanding of the effects of the different meteorological constraints in thermal biology of ectotherms will surely help us to design effective conservation plans to preserve mountain ectotherms that cannot

**Table 4** Spatial heterogeneity of both study areas was assessed by measuring available microhabitat cover in 25 m linear transects. Mean (SE) percent microhabitat cover and microhabitat frequency are provided for the *ski slope* area ( $N = 7$ ) and for *Sanfons* ( $N = 10$ )

	Slab	Rocks >50 cm	Rocks <50 cm	Loose stones	Soil	Grass >15 cm	Grass <15 cm	Shrubs
<i>Ski slope</i>								
Cover	1.03 % (0.40)	5.31 % (1.24)	27.60 % (5.77)	42.83 % (5.21)	1.37 % (0.34)	14.11 % (5.38)	8.34 % (2.44)	0
Frequency	1.46 % (0.44)	6.80 % (1.70)	24.58 % (3.47)	39.16 % (3.58)	3.51 % (1.08)	14.69 % (4.36)	9.80 % (2.76)	0
<i>Sanfons</i>								
Cover	4.76 % (0.95)	22.32 % (2.99)	27.28 % (3.83)	18.76 % (4.24)	5.32 % (3.30)	7.64 % (3.97)	13.24 % (2.02)	0.68 % (0.46)
Frequency	8.62 % (1.76)	17.58 % (2.41)	23.10 % (1.92)	20.00 % (3.55)	5.12 % (1.72)	4.41 % (1.24)	20.69 % (1.94)	0.46 % (0.33)

Slab means a big flat rock that does not provide refuges for lizards



**Fig. 3** Effectiveness of thermoregulation of *Iberolacerta aurelioi* was significantly lower in *Sanfons*, as a consequence of the higher wind, than in the *ski slope*

migrate to higher latitudes (Berg et al. 2010; Groves et al. 2012). We still do not fully understand the effect of wind in the thermoregulation of lizards, and we do not know how these wind-exposed areas are going to change with global warming, so much more research is needed before the conservation implications of wind can be assessed.

## Conclusions

*I. aurelioi* is a cold-specialist lizard, with consistent thermal preferences in two populations exposed to different wind conditions. For this species, thermoregulatory effectiveness, thermoregulatory accuracy, and thermal quality of habitat all decrease with wind. We are confident that wind is driving this pattern, since our two study sites were very similar in all other characteristics. This decrease of thermoregulatory efficiency with increased wind is initially surprising, since it is often the case that in more challenging habitats, lizards show improved thermoregulatory effectiveness. However, the reason the pattern is different in our study may be because wind affects costs and benefits of lizards' thermoregulation in more complex ways than just the cooling of lizards and their habitats, as it can also reduce the daily activity, increase desiccation, and complicate hunting of prey.

Furthermore, these results show that wind, while often overlooked, can dramatically influence the thermal quality of a habitat and should therefore be considered when developing conservation strategies for threatened ectotherms. As climates warm, it is possible that, for some species, wind may become a

beneficial habitat quality. However, much more research is needed before the conservation implications of wind can be known.

**Acknowledgments** We thank two anonymous reviewers for their useful comments that helped us to improve the manuscript. We thank Sergi Riba and Jordi Nicolau for their great help providing us accommodation and guidance in Andorra. We thank Alberto Parada for helping with fieldwork, as well as Mario Garrido, Ana Pérez-Cembranos, Gonzalo Rodríguez and Alicia León for their support during writing. We also thank Mary Trini Mencia and Joe McIntyre for linguistic revision. Lizards were sampled under licences of the Ministeri de Turismo i Medi ambient of the Govern d'Andorra. Financial support was provided to ZO and AM by predoctoral grants 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. All research was conducted in compliance with ethical standards and procedures of the University of Salamanca.

## References

- Adolph SC, Porter WP (1993) Temperature, activity, and lizard life histories. *Am Nat* 142:272–295
- Aguado S, Braña F (2014) Thermoregulation in a cold-adapted species (Cyren's rock lizard, *Iberolacerta cyreni*): influence of thermal environment and associated costs. *Can J Zool* 92:955–964. doi:10.1139/cjz-2014-0096
- Amo L, López P, Martín J (2007) Habitat deterioration affects body condition of lizards: a behavioral approach with *Iberolacerta cyreni* lizards inhabiting ski resorts. *Biol Conserv* 135:77–85. doi:10.1016/j.biocon.2006.09.020
- Angilletta MJ (2009) Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, Oxford
- Angilletta MJ, Niewiarowski PH, Navas CA (2002) The evolution of thermal physiology in ectotherms. *J Therm Biol* 27:249–268. doi:10.1016/S0306-4565(01)00094-8
- Araújo MB, Alagador D, Cabeza M, Nogués-Bravo D, Thuiller W (2011) Climate change threatens European conservation areas. *Ecol Lett* 14:484–492. doi:10.1111/j.1461-0248.2011.01610.x
- Araújo MB, Thuiller W, Pearson RG (2006) Climate warming and the decline of amphibians and reptiles in Europe. *J Biogeogr* 33:1712–1728. doi:10.1111/j.1365-2699.2006.01482.x
- Arribas O (1994) Una nueva especie de lagartija de los Pirineos Orientales: *Lacerta (Archaeolacerta) aurelioi* sp. nov. (Reptilia: Lacertidae). *Bollettino del Museo Regionale di Scienze Naturali di Torino* 12:327–351
- Arribas O (1997) *Lacerta aurelioi* Arribas, 1994. In: Pleguezuelos JM (ed) Distribución y Biogeografía de los Anfibios y Reptiles de España y Portugal. Monografías de Herpetología, vol. 3. Colección Monográfica Tierras del Sur. Universidad de Granada – Asociación Herpetológica Española, Granada, pp. 216–218
- Arribas O (2002) *Lacerta aurelioi*. In: Pleguezuelos JM, Márquez R, Lizana M (eds) Atlas y Libro Rojo de los anfibios y reptiles de España. Dirección General de Conservación de la Naturaleza-Asociación Herpetológica Española, Madrid, pp. 218–219
- Arribas O (2010) Activity, microhabitat selection and thermal behavior of the Pyrenean rock lizards *Iberolacerta aranica* (Arribas, 1993), *I. aurelioi* (Arribas, 1994) and *I. bonnali* (Lantz, 1927) (Squamata: Sauria: Lacertidae). *Herpetozoa* 23:3–23
- Arribas O, Galán P (2005) Reproductive characteristics of the Pyrenean High-Mountain lizards: *Iberolacerta aranica* (Arribas, 1993), *Ib.*

- aurelioi* (Arribas, 1994) and *Ib. bonnali* (Lantz, 1927). *Anim Biol* 55:163–190. doi:10.1163/1570756053993505
- Bakken GS, Angilletta MJ (2014) How to avoid errors when quantifying thermal environments. *Funct Ecol* 28:96–107. doi:10.1111/1365-2435.12149
- Berg MP, Kiens ET, Driessen G, Van Der Heijden M, Kooi BW, Kuenen F, Liefing M, Verhoef HA, Ellers J (2010) Adapt or disperse: understanding species persistence in a changing world. *Glob Change Biol* 16:587–598. doi:10.1111/j.1365-2486.2009.02014.x
- Bestion E, Clobert J, Cote J (2015) Dispersal response to climate change: scaling down to intraspecific variation. *Ecol Lett* 18:1226–1233. doi:10.1111/ele.12502
- Blouin-Demers G, Nadeau P (2005) The cost-benefit model of thermoregulation does not predict lizard thermoregulatory behaviour. *Ecology* 86:560–566. doi:10.1890/04-1403
- Blouin-Demers G, Weatherhead PJ (2001) Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. *Ecology* 82:3025–3043. doi:10.1890/0012-9658(2001)082[3025:TEOBRS]2.0.CO;2
- Blouin-Demers G, Weatherhead PJ (2002) Habitat-specific behavioural thermoregulation by black rat snakes (*Elaphe obsoleta obsoleta*). *Oikos* 97:59–68. doi:10.1034/j.1600-0706.2002.970106.x
- Buckley LB, Ehrenberger JC, Angilletta MJ (2015) Thermoregulatory behaviour limits local adaptation of thermal niches and confers sensitivity to climate change. *Funct Ecol* 29:1038–1047. doi:10.1111/1365-2435.12406
- Burnham KP, Anderson DR (2004) Multimodel inference understanding AIC and BIC in model selection. *Sociol Method Res* 33:261–304. doi:10.1177/0049124104268644
- Carvalho SB, Brito JC, Crespo EJ, Possingham HP (2010) From climate change predictions to actions—conserving vulnerable animal groups in hotspots at a regional scale. *Glob Change Biol* 16:3257–3270. doi:10.1111/j.1365-2486.2010.02212.x
- Chevin LM, Lande R (2015) Evolution of environmental cues for phenotypic plasticity. *Evolution* 69:2767–2775. doi:10.1111/evo.12755
- Claussen DL (1967) Studies of water loss in two species of lizards. *Comp Biochem Physiol* 20:115–130. doi:10.1016/0010-406X(67)90728-1
- Crawley MJ (2012) *The R book*. Wiley, Chichester, UK
- Crossman ND, Bryan BA, Summers DM (2012) Identifying priority areas for reducing species vulnerability to climate change. *Divers Distrib* 18:60–72. doi:10.1111/j.1472-4642.2011.00851.x
- Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *P Natl Acad Sci USA* 105:6668–6672. doi:10.1073/pnas.0709472105
- Díaz JA, 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. doi:10.1016/j.jtherbio.2005.10.001
- Graae BJ, De Freene P, Kolb A, Brunet J, Chabrierie O, Verheyen K, Pepin N, Heinken T, Zobel M, Shevtsova A, Nijs I, Milbau A (2012) On the use of weather data in ecological studies along altitudinal and latitudinal gradients. *Oikos* 121:3–19. doi:10.1111/j.1600-0706.2011.19694.x
- Groves CR, Game ET, Anderson MG, Cross M, Enquist C, Ferdana Z, Girvetz E, Gondor A, Hall KR, Higgins J, Marshall R, Popper K, Schill S, Shafer SL (2012) Incorporating climate change into systematic conservation planning. *Biodivers Conserv* 21:1651–1671. doi:10.1007/s10531-012-0269-3
- Gunderson AR, Stillman JH (2015) Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *P Roy Soc Lond B Bio* 282:20150401. doi:10.1098/rspb.2015.0401
- Heath JE (1970) Behavioral regulation of body temperature in poikilotherms. *Physiologist* 13:399–410
- Hertz PE, Huey RB, Stevenson RD (1993) Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am Nat* 142:796–818
- Huey RB (1974) Behavioral thermoregulation in lizards: importance of associated costs. *Science* 184:1001–1003. doi:10.1126/science.184.4140.1001
- Huey RB, Slatkin M (1976) Cost and benefits of lizard thermoregulation. *Q Rev Biol* 51:363–384
- Huey RB, Stevenson RD (1979) Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am Zool* 19:357–366
- Huey RB, Hertz PE, Sinervo B (2003) Behavioral drive versus behavioral inertia in evolution: a null model approach. *Am Nat* 161:357–366. doi:10.1086/346135
- Huey RB, Kearney MR, Krockenberger A, Holtum JA, Jess M, Williams SE (2012) Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philos T Roy Soc B* 367:1665–1679. doi:10.1098/rstb.2012.0005
- Kearney M, Porter W (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol Lett* 12:334–350. doi:10.1111/j.1461-0248.2008.01277.x
- Keppel G, Van Niel KP, Wardell-Johnson GW, Yates CJ, Byrne M, Mucina L, Schut AGT, Hopper SD, Franklin SE (2012) Refugia: identifying and understanding safe havens for biodiversity under climate change. *Glob Ecol Biogeogr* 21:393–404. doi:10.1111/j.1466-8238.2011.00686.x
- Ladyman M, Bradshaw D (2003) The influence of dehydration on the thermal preferences of the western tiger snake, *Notechis scutatus*. *J Comp Physiol B* 173:239–246. doi:10.1007/s00360-003-0328-x
- Logan ML, Fernandez SG, Calsbeek R (2015) Abiotic constraints on the activity of tropical lizards. *Funct Ecol* 29:694–700. doi:10.1111/1365-2435.12379
- Maia-Carneiro T, Dorigo TA, Rocha CFD (2012) Influences of seasonality, thermal environment and wind intensity on the thermal ecology of Brazilian sand lizards in a restinga remnant. *South American Journal of Herpetology* 7:241–251. doi:10.2994/057.007.0306
- Maiorano L, Amori G, Capula M, Falcucci A, Masi M, Montemaggiore A, Pottier J, Psomas A, Rondinini C, Russo D, Zimmermann NE, Boitani L, Guisan A (2013) Threats from climate change to terrestrial vertebrate hotspots in Europe. *PLoS One* 8:e74989. doi:10.1371/journal.pone.0074989
- Martín J, Salvador A (1993) Thermoregulatory behaviour of rock lizards in response to tail loss. *Behaviour* 124:123–136. doi:10.1163/156853993X00533
- Martin TL, Huey RB (2008) Why “suboptimal” is optimal: Jensen's inequality and ectotherm thermal preferences. *Am Nat* 171:E102–E118. doi:10.1086/527502
- McCain CM (2010) Global analysis of reptile elevational diversity. *Glob Ecol Biogeogr* 19:541–553. doi:10.1111/j.1466-8238.2010.00528.x
- Monasterio C, Salvador A, Iraeta P, Díaz JA (2009) The effects of thermal biology and refuge availability on the restricted distribution of an alpine lizard. *J Biogeog* 36:1673–1684. doi:10.1111/j.1365-2699.2009.02113.x
- Nicolau J, Baró M (2009) El Parc Natural Comunal de les Valls del Comapedrosa. Planificació i gestió d'un nou espai protegit al Principat d'Andorra. *Revista del CENMA* 3:3–11
- Nogués-Bravo D, Araújo MB, Lasanta T, Moreno JIL (2008) Climate change in Mediterranean Mountains during the 21st century. *Ambio* 37:280–285. doi:10.1579/0044-7447(2008)37[280:CCIMMD]2.0.CO;2
- Ortega Z, Mencía A, Pérez-Mellado V (2016a) Are becoming mountain habitats more suitable for thermoregulation of generalist than cold-adapted lizards? *PeerJ* 4:e2085. doi:10.7717/peerj.2085
- 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. doi:10.1016/j.jtherbio.2016.01.005
- 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. doi:10.1016/j.jtherbio.2013.11.006
- Pacifici M, Foden WB, Visconti P, Watson JE, Butchart SH, Kovacs KM, Scheffers BR, Hole DG, Martin TG, Akçakaya HR, Corlett RT, Huntley B, Bickford D, Carr JA, Hoffmann AA, Midgley GF, Pearce-Kelly P, Pearson RG, Williams SE, Willis SG, Young B, Rondinini C (2015) Assessing species vulnerability to climate change. *Nature Clim Change* 5:215–224. doi:10.1038/nclimate2448
- Pérez-Mellado V, Cheylan M, Martínez-Solano I (2009) *Iberolacerta aurelioi*. The IUCN Red List of Threatened Species. Version 2015.2. URL: [www.iucnredlist.org](http://www.iucnredlist.org). Accessed 29 Oct 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 29 Oct 2015
- Porter WP, Gates DM (1969) Thermodynamic equilibria of animals with environment. *Ecol Monogr* 39:227–244. doi:10.2307/1948545
- 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/>. Accessed 29 Oct 2015
- Sagonas K, Valakos ED, Pafilis P (2013) The impact of insularity on the thermoregulation of a Mediterranean lizard. *J Therm Biol* 38:480–486. doi:10.1016/j.jtherbio.2013.08.004
- Scheers H, Van Damme R (2002) Micro-scale differences in thermal habitat quality and a possible case of flexibility in the thermal physiology of lacertid lizards. *Oecologia* 132:323–331. doi:10.1007/s00442-002-0970-0
- Schulte-Hostedde AI, Zinner B, Millar JS, Hickling GJ (2005) Restitution of mass-size residuals: validating body condition indices. *Ecology* 86:155–163. doi:10.1890/04-0232
- Sears MW, Angilletta MJ (2015) Costs and benefits of thermoregulation revisited: both the heterogeneity and spatial structure of temperature drive energetic costs. *Am Nat*. doi:10.1086/680008
- Sears MW, Raskin E, Angilletta MJ (2011) The world is not flat: defining relevant thermal landscapes in the context of climate change. *Integr Comp Biol* 51:666–675. doi:10.1093/icb/ict111
- Seebacher F, Franklin CE (2012) Determining environmental causes of biological effects: the need for a mechanistic physiological dimension in conservation biology. *Philos T Roy Soc B* 367:1607–1614. doi:10.1098/rstb.2012.0036
- Sokal RR, Rohlf FJ (1995) *Biometry: the principles and practice of statistics in biological research*. State University of New York at Stony Brook, New York
- Stevenson RD (1985) The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *Am Nat* 126:362–386
- Sun LX, Shine R, Debi Z, Zhengren T (2001) Biotic and abiotic influences on activity patterns of insular pit-vipers (*Gloydus shedaensis*, Viperidae) from north-eastern China. *Biol Conserv* 97:387–398
- Tracy CR, Christian KA (2005) Preferred temperature correlates with evaporative water loss in hylid frogs from northern Australia. *Physiol Biochem Zool* 78:839–846. doi:10.1086/432151
- Winne CT, Ryan TJ, Leiden Y, Dorcas ME (2001) Evaporative water loss in two natricine snakes, *Nerodia fasciata* and *Seminatrix pygaea*. *J Herpetol* 35:129–133. doi:10.2307/1566035
- Žagar A, Carretero M, Osojnik N, Sillero N, Vrežec A (2015) A place in the sun: interspecific interference affects thermoregulation in coexisting lizards. *Behav Ecol Sociobiol* 69:1127–1137. doi:10.1007/s00265-015-1927-8
- Zamora-Camacho FJ, Reguera S, Moreno-Rueda G (2015) Thermoregulation in the lizard *Psammodromus algirus* along a 2200-m elevational gradient in Sierra Nevada (Spain). *Int J Biometeorol*:1–11. doi:10.1007/s00484-015-1063-1