JOURNAL OF Evolutionary Biology

eseb European Society for Evolutionary Biology

doi: 10.1111/jeb.12546

Bergmann's Rule rules body size in an ectotherm: heat conservation in a lizard along a 2200-metre elevational gradient

F. J. ZAMORA-CAMACHO, S. REGUERA & G. MORENO-RUEDA

Departamento de Zoología, Facultad de Ciencias, Universidad de Granada, Granada, Spain

Keywords:

body size;
cooling rate;
elevation;
heating rate;
Psammodromus algirus.

Abstract

Bergmann's Rule predicts larger body sizes in colder habitats, increasing organisms' ability to conserve heat. Originally formulated for endotherms, it is controversial whether Bergmann's Rule may be applicable to ectotherms, given that larger ectotherms show diminished capacity for heating up. We predict that Bergmann's Rule will be applicable to ectotherms when the benefits of a higher conservation of heat due to a larger body size overcompensate for decreased capacity to heating up. We test this hypothesis in the lizard *Psammodromus algirus*, which shows increased body size with elevation in Sierra Nevada (SE Spain). We measured heating and cooling rates of lizards from different elevations (from 300 to 2500 m above sea level) under controlled conditions. We found no significant differences in the heating rate along an elevational gradient. However, the cooling rate diminished with elevation and body size: highland lizards, with larger masses, have a higher thermal inertia for cooling, which allows them to maintain heat for more time and keep a high body temperature despite the lower thermal availability. Consequently, the net gaining of heat increased with elevation and body size. This study highlights that the heat conservation mechanism for explaining Bergmann's Rule works and is applicable to ectotherms, depending on the thermal benefits and costs associated with larger body sizes.

Introduction

Physiological processes are possible only at certain temperature ranges (Xiang *et al.*, 1996; Clark *et al.*, 2005; Sun *et al.*, 2012). Nonetheless, environmental temperature is generally variable, frequently shifting away from organisms' physiological optima. Thus, organisms show a set of adaptations for keeping their internal temperature compatible with physiological processes in spite of the unsettled environmental temperature. Animals show two main thermal strategies according to the relative importance of metabolic and environmental heat in body temperature upkeep: ectothermy and endothermy. Ectotherms resort mainly to external environmental heat sources to maintain their internal body temperature inside the preferred temperature range (Hertz *et al.*, 1993), which endotherms achieve using internal metabolic heat sources (Bennett & Ruben, 1979).

Several macroecological rules arose from the influence of the thermal environment on animals' fitness, showing different applicability in ectotherms and endotherms. Bergmann's Rule establishes a general tendency of endotherms to achieve larger body sizes in higher latitudes, and thus, in colder environments (Bergmann, 1847). This increase in body size with decreasing environmental temperature, known as Bergmann's clines, could be explained by the positive relationship between body mass and thermal inertia (heat conservation hypothesis): heat is dissipated more slowly in larger animals as the surface-area to volume ratio diminishes, so it would be a thermal advantage in colder habitats (Meiri, 2011). Bergmann's Rule has been widely supported in endotherms (Meiri & Dayan, 2003; Millien *et al.*, 2006), although the mechanism causing Bergmann's Rule is still under discussion (Blackburn *et al.*, 1999; Rodríguez *et al.*, 2006; Yom-Tov

Correspondence: Francisco J. Zamora-Camacho, Departamento de Zoología, Facultad de Ciencias, Universidad de Granada, Granada E-18071, Spain. Tel.: +34 958 24 98 54; fax: +34 958 24 32 38; e-mail: zamcam@ugr.es

& Geffen, 2006; Meiri *et al.*, 2007; McNab, 2010; Watt *et al.*, 2010).

For ectotherms, the application of Bergmann's Rule is even less clear: although a larger ectotherm would retain body heat for a longer time, a big body mass could decrease its capacity to warm up from an external heat source, mainly in cold habitats (Stevenson, 1985). For this reason, most scientists consider that the traditional explanation for Bergmann's clines (the heat conservation hypothesis) is not applicable to ectotherms (Watt *et al.*, 2010; for exceptions to this view see Ashton & Feldman, 2003; Cruz *et al.*, 2005; Olalla-Tárraga *et al.*, 2006; Olalla-Tárraga & Rodríguez, 2007). Despite this point of view, many ectotherm groups show Bergmann's clines (e.g. aforementioned references; also see Ashton, 2002a; Blanckenhorn & Demont, 2004; Millien *et al.*, 2006). Both the converse of Bergmann's clines as well as the lack of covariation between body size and environmental temperature have also been found in several ectotherms (Mousseau, 1997; Ashton & Feldman, 2003; Olalla-Tárraga *et al.*, 2006; Adams & Church, 2008; Hu *et al.*, 2011), contributing to the controversy regarding the applicability of Bergmann's Rule to ectotherms.

Under the view that the heat conservation hypothesis fails to explain why ectotherms comply with Bergmann's Rule, several alternative hypotheses (not mutually exclusive) have been proposed to explain Bergmann's clines in ectotherms (Atkinson & Sibly, 1997; Arnett & Gotelli, 2003; Angilletta *et al.*, 2004a; Wilson, 2009; Arendt, 2011). However, we consider that arguments suggesting that the heat conservation hypothesis does not explain Bergmann's Rule in ectotherms rely on simplistic assumptions. In ectotherms, net heat gain (N) is a function of heat gain (G) minus heat loss (L). Both G and L are functions of body mass (m), everything else being equal, $G = -\alpha m$ and $L = -\beta m$. The parameters α and β indicate the slopes at which heat gain and heat loss decrease with body mass, and they are negative as thermal inertia increases with body mass (Carothers *et al.*, 1997). Therefore, the net gain of heat would be $N = (\beta - \alpha)m$. Typically, researchers have implicitly assumed that in ectotherms $\beta < \alpha$, and therefore, net gain of heat decreases with body mass, which would favour smaller body sizes in cold sites (the converse Bergmann's cline). Nevertheless, the fact is that for some ectotherms, $\beta < \alpha$ (*Iberolacerta monticola*; Carrascal *et al.*, 1992), but for others, $\beta > \alpha$ (*Liolaemus altissimus*; Carothers *et al.*, 1997).

We hypothesized that the heat conservation hypothesis may explain the occurrence of Bergmann's clines in ectotherms. Here, we test this hypothesis using the lizard *Psammodromus algirus* as a model system in Sierra Nevada (SE Spain). In Sierra Nevada, this lizard follows Bergmann's clines in a 2200-metre elevational gradient, lizards being larger at high elevations (see Results). During the activity period of this lizard, environmental temperature decreases an average of 8 °C from the lowest (300 m asl) to the highest elevation (2500 m asl) in our study area (Zamora-Camacho *et al.*, 2013). We predict that the advantage of increased thermal inertia in larger individuals inhabiting cold habitats should compensate for the disadvantage of reduced heating capabilities, explaining the body size cline with elevation in this population; that is, we expect to find $\beta > \alpha$. To test this hypothesis, we examined whether elevational differences in body size are related to different thermoregulatory capabilities, by measuring lizards' heating and cooling rates under controlled conditions (Yom-Tov & Geffen, 2011). The main novelty of this study is that, for the first time, we check whether the mechanism of the heat conservation hypothesis works in an animal showing a Bergmann cline.

Materials and methods

Psammodromus algirus is a medium-sized (53–95 mm snout-vent length (SVL) in our study area) generalist Lacertid inhabiting mid-moisture shrubby areas in south-western Europe and north-western Africa, from sea level to 2600 m asl (Salvador, 2011). Several lineages appear to comprise *P. algirus* (Verdú-Ricoy *et al.*, 2010), but all the populations in our study belong to the same lineage, thus avoiding phylogenetic divergence (Cruz *et al.*, 2005; Meiri & Thomas, 2007).

During June and July 2012, we caught lizards from sampling plots at 300, 700, 1200, 1700, 2200 and 2500 m asl in the southern slope of Sierra Nevada (SE Spain), in habitats chosen as similar as possible based on habitat structure (Zamora-Camacho *et al.*, 2013). All specimens caught were taken to the laboratory. We used males, nongravid females and gravid females. We distinguished males because they have wider heads, larger and more numerous femoral pores in the hind limbs and orange spots in the corners of their mouths. We recognized pregnant females by manual palpation of developing eggs inside the trunk. During their stay in the laboratory, we maintained each lizard in an individual terrarium, where water (in the form of nutritive aqueous gel) and food (mealworm larvae, *Tenebrio molitor*) were provided *ad libitum*, and a natural light source was provided for the circadian physiological processes. A heat source (heat cable) was put in one corner of the terrarium to permit natural thermoregulation behaviour of the animals.

Prior to the experiments, we measured biometric parameters likely involved in heat exchange, including body mass with a balance (model CDS-100, precision 0.01 g), snout-vent length (SVL; in mm) with a millimetre-marked ruler and back lightness with a SCM-2600d/2500d spectrophotometer (Clusella-Trullas *et al.*, 2007). Colour data provided by this device were composed of three coordinates (L*a*b*) from the *Commission Internationale d'Eclairage* chromatic value colour space. Darkness is the inverse of lightness (L, measured in % of reflectance; Montgomerie, 2006). We measured the colour of the central point of every lizard's dorsum. The spectrophotometer measured three times and provided the average value, which we used for the analyses. As body mass, more than SVL, is the physical attribute most involved in heat exchange (Carothers *et al.*, 1997; Fei *et al.*, 2012), we focused our analyses on body mass, avoiding the expectable collinearity of these biometrically related factors ($r = 0.85$; $P < 0.001$; $n = 61$).

To measure heat transfer rates, we immobilized lizards individually on a thermally stable synthetic cork plaque, using a soft lace knot around lizards' neck, and another one around lizards' waist, fastened firmly but loosely enough so that the lizards could not either escape or suffer any pain. We placed the lizards 13 cm below a 60-W blue-light bulb. In a laboratory at 22 °C room temperature, we started the trials when lizards attained 27 °C body temperature and switched off the bulb when their body temperature reached 35 °C. We chose a bulb over the animals as heat source because these lizards are heliothermic, and heat up mainly by sunbathing (Díaz & Cabezas-Díaz, 2004). The ranges of body temperature are below lethal temperature, being their optimum temperature range of 33–35 °C (Díaz *et al.*, 2006). Actually, the ranges of body temperature chosen are within the body-temperature range that animals show in the field when active (Zamora-Camacho *et al.*, 2013). Once the bulb was switched off, the experiment continued until body temperature diminished to 32 °C. Body temperature during the experiment was measured with a small catheter inserted 8 mm inside the cloaca and connected to a thermometer (Hybok-18). The body temperature of each animal was registered every 30 s during the whole process. No animal suffered damage during this study. Once the experiment ended, lizards were returned to the place where they were captured.

Graphing body temperature over time, the standard heat transfer curve of a lizard consisted of a linear temperature increase while the bulb was switched on, a variable-duration transition lapse after switching off the bulb, while body temperature remained almost unaltered, and a linear temperature decrease after the inertia lapse (Fig. 1). From those three phases, we obtained for each individual: (i) the heating rate, calculated as the regression slope of body temperature increase over time during the heating period, in °C min^{-1}; (ii) the transition lapse, as the time (in min) lapse since we switched off the bulb until lizard body temperature started to diminish; and (iii) the cooling rate, calculated as the regression slope of body temperature decrease over time during the cooling period, in °C min^{-1}.

Statistical analyses were performed with parametric statistics (Quinn & Keough, 2002). Data distributions matched the assumptions of parametric statistics (homoscedasticity and normality of residuals). The variables cooling rate and body mass required log-transformation. We performed an ANOVA to test for elevational differences in back lightness, SVL and body mass. Another ANOVA tested whether there were statistical differences in heat transfer processes among males, gravid females and nongravid females (a factor with three levels). Finally, we used ordinary least squares linear models to test for differences in heating rates, inertia lapses and cooling rates according to elevation and body mass. We did not include elevation and body mass in the same model because models with the two variables showed problems of collinearity (in an ANOVA, elevation explained body mass with a multiple $R = 0.68$). Therefore, to avoid multicollinearity, for each dependent variable, we performed two models, one with elevation and other with body mass. Given that sex and female reproductive status, as well as dorsal lightness, could affect thermoregulation (heating rate in the case of dorsal lightness), we controlled for these variables in the models. We performed those analyses with software Statistica 7.1 (StatSoft, Inc., Tulsa, OK, USA).

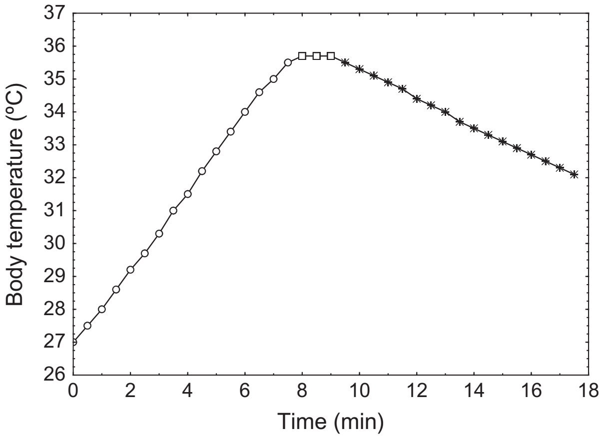

Fig. 1 Changes in body temperature during the main stages of the thermal experiment in a standard, hypothetical lizard. All lizards followed a similar pattern of temperatures during the trials: linear heating phase when the bulb is on (circle-dotted line), thermally stable transition lapse after switching the bulb off (square-dotted line) and linear cooling phase after the transition lapse (asterisk-dotted line).

Results

Morphological variation in elevation

Body mass ($F_{5,53} = 9.07$; $P < 0.001$; Fig. 2) and SVL ($F_{5,57} = 7.44$; $P < 0.001$) were significantly larger in highland than in mid- and lowland lizards, which is consistent with a Bergmann's cline. There were no differences in body mass ($F_{2,53} = 1.00$; $P = 0.376$) or SVL ($F_{2,57} = 0.99$; $P = 0.376$) among males, gravid and

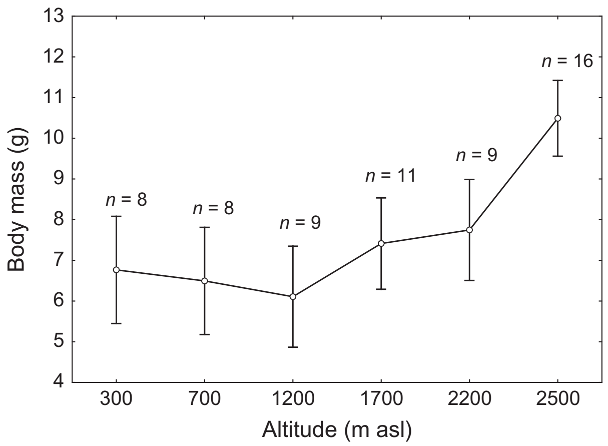

Fig. 2 Body mass was significantly bigger in the highlands, according to predictions of Bergmann's Rule. Vertical bars denote 0.95 confidence intervals. Sample size is indicated on bars.

nongravid females. Dorsal lightness (L*), inverse indicator of darkness, significantly decreased with elevation ($F_{5,56} = 5.92$; $P < 0.001$), so individuals' dorsum was significantly darker as elevation increased. There were no differences in lightness with sex and female reproductive status ($F_{2,56} = 1.973$; $P = 0.149$). Lizards' average body mass at every sampling elevation was negatively correlated with average environmental temperature during the activity period ($r = -0.836$; $P = 0.038$, $n = 6$ sampling points).

Heating rates

On average, lizards heated at a rate of 1.08 °C min^{-1}. Heating rates did not significantly differ with elevation ($F_{5,52} = 2.016$; $P = 0.092$), sex or female reproductive status ($F_{2,52} = 2.323$; $P = 0.108$), or dorsal lightness ($F_{1,53} = 1.656$; $P = 0.204$). When body mass was introduced in the model in the place of elevation, we found a concave downward relationship between body mass and heating rate (linear effect: $F_{1,52} = 4.454$; $P = 0.040$; quadratic effect: $F_{1,52} = 5.521$; $P = 0.023$; Fig. 3); the effect of sex and female reproductive status, and dorsal lightness remained nonsignificant (data not shown). Lizards from the highest elevation (where lizards are largest) showed a significant, negative relationship between body mass and heating rate ($r = -0.626$, $P = 0.009$), whereas no significant relationship between body mass and heating rate was found when considering lizards of populations below 2500 m asl ($r = 0.100$, $P = 0.513$).

Transition lapses

After switching off the bulb, lizards' body temperature remained stable for 1.27 min on average. Transition lapses tended to increase with elevation

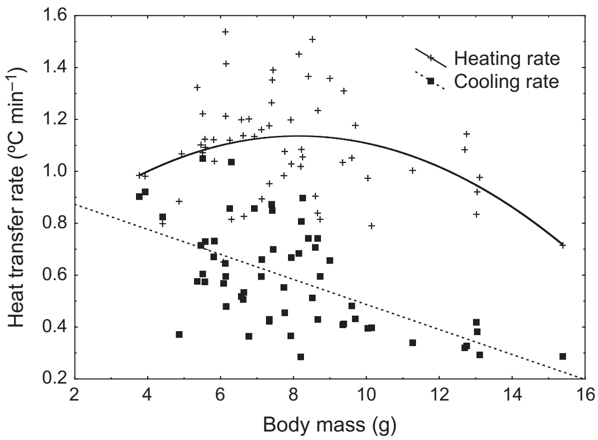

Fig. 3 Ordinary Least Squares Regression of heating rate (+) and cooling rate (■) over body mass. Although cooling rate had a significant, higher-sloped, negative relationship with body mass, heating rate showed a significant concave down relationship with body mass.

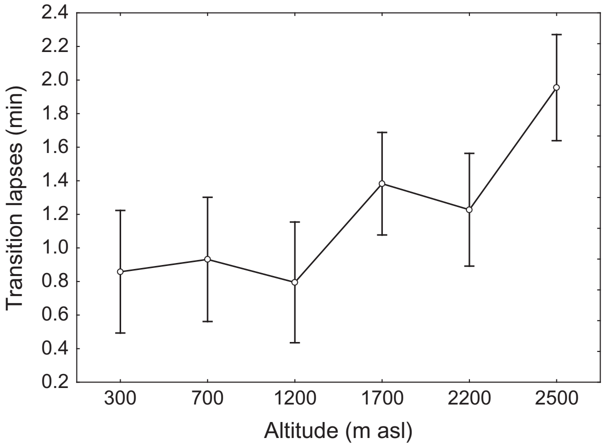

Fig. 4 Transition lapses, that is time elapsed from the moment we switched off the bulb until lizard started cooling down, were bigger in high elevations. Thus, larger-size high-elevation lizards showed increased thermal inertia, following the predictions of Bergmann's rule. Vertical bars denote 0.95 confidence intervals. Sample size was shown in Fig. 2.

($F_{5,57} = 12.554$; $P < 0.001$; Fig. 4). In this model, there were almost significant differences in transition lapses among males, nongravid females and gravid females ($F_{2,57} = 3.065$; $P = 0.054$; Fig. 5a), gravid females tending to have larger inertia lapses than males. When body mass was included in the model in the place of elevation, transition lapses significantly increased with body mass (effect of body mass: $\beta = 0.562$; $F_{1,57} = 30.153$; $P = 0.001$; effect of sex and female reproductive status: $F_{2,57} = 2.211$; $P = 0.119$). Neither lizards from the highest elevation ($r = 0.240$;

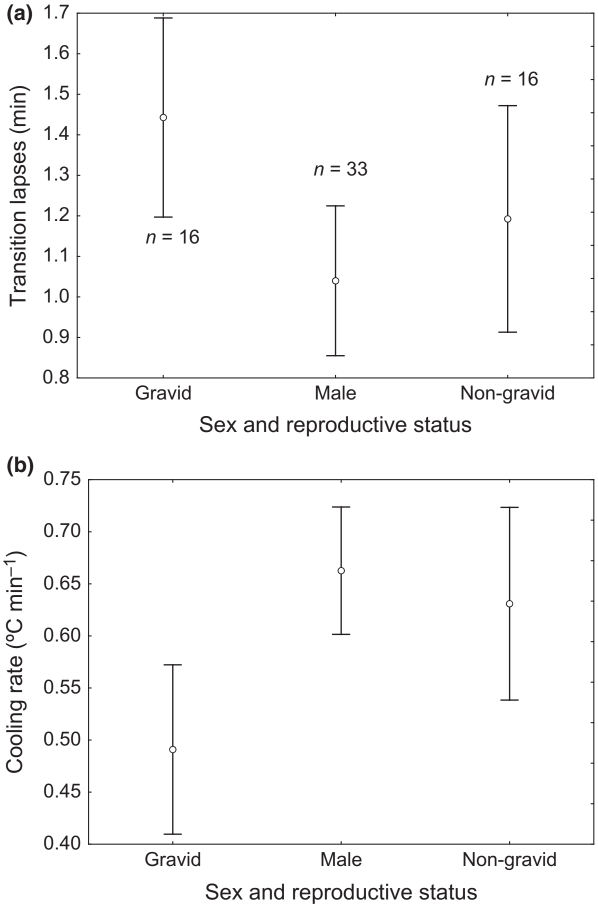

Fig. 5 Gravid females had higher transition lapses (a) and lower cooling rates (b) than males and nongravid females. Vertical bars denote 0.95 confidence intervals. Sample sizes on bars in (a).

$P = 0.370$) nor from populations below ($r = 0.238$; $P = 0.115$) showed a significant relationship between body mass and transition lapses.

Cooling rates

On average, lizards cooled by 0.58 °C min^{-1}. Similar to inertia lapses, cooling rates significantly decreased with elevation ($F_{5,52} = 11.068$, $P < 0.001$; Fig. 6). Consistent with our results for the inertia lapse, gravid females tended to lose heat more slowly than males ($F_{2,52} = 4.112$; $P = 0.022$; Fig. 5b). When body mass was introduced in the model in the place of elevation, cooling rates significantly decreased with body mass (effect of body mass: $\beta = -0.568$; $F_{1,56} = 37.582$, $P = 0.001$; Fig. 3; effect of sex and female reproductive status: $F_{2,56} = 2.801$, $P = 0.069$). That is, consistently with the heat conservation hypothesis, larger lizards lost heat more slowly than small lizards. Lizards from the highest elevation showed a significant, positive relationship between body mass and cooling rate ($r = 0.775$, $P < 0.001$), whereas no significant relationship between body mass and cooling rate was found when considering lizards of populations below 2500 m asl ($r = 0.241$, $P = 0.116$).

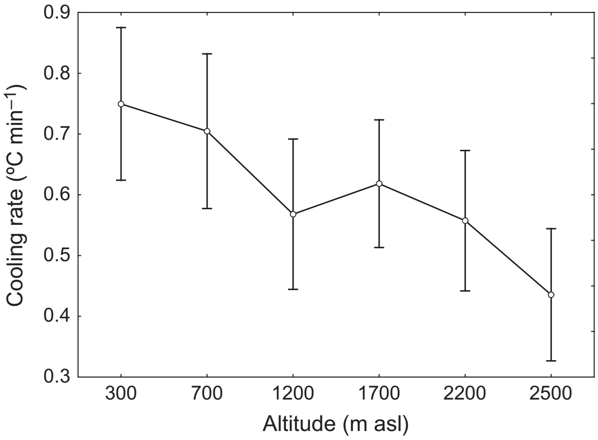

Fig. 6 Cooling rate diminished in elevation. Larger-sized highland lizards showed to retain heat for longer, supporting both the morphological and the thermal predictions of Bergmann's Rule. Vertical bars denote 0.95 confidence intervals. Sample sizes as in Fig. 2.

Net heating rate

We estimated the net heating rate as the heating rate minus the cooling rate. Net heating rate significantly increased with elevation ($F_{5,52} = 4.061$, $P = 0.003$; Fig. 7a; sex and female reproductive status, $F_{2,52} = 0.183$, $P = 0.833$). Similarly, net heating rate increased with body mass, suggesting a trend towards a concave down function (linear effect: $F_{1,53} = 5.965$, $P = 0.018$; quadratic effect: $F_{1,53} = 3.979$, $P = 0.051$; Fig. 7b; effect of sex and female reproductive status, $F_{2,53} = 1.453$, $P = 0.243$). Lizards from the highest elevation showed no significant relationship between body size and net heating rate ($r = -0.243$, $P = 0.365$), whereas a positive linear relationship between body size and net heating rate was found when considering lizards from populations below 2500 m asl ($r = 0.326$, $P = 0.035$; Fig. 7b).

Discussion

Bergmann's Rule, larger size in colder areas, has been validated in some endotherms (Ashton *et al.*, 2000; Ashton, 2002b; Meiri & Dayan, 2003; Millien *et al.*, 2006; Rodríguez *et al.*, 2006, 2008; Ramírez *et al.*, 2008). Nevertheless, its applicability for ectotherms remains controversial, since some of them follow Bergmann's cline, while numerous ectotherms do not, or even follow the converse to Bergmann's cline

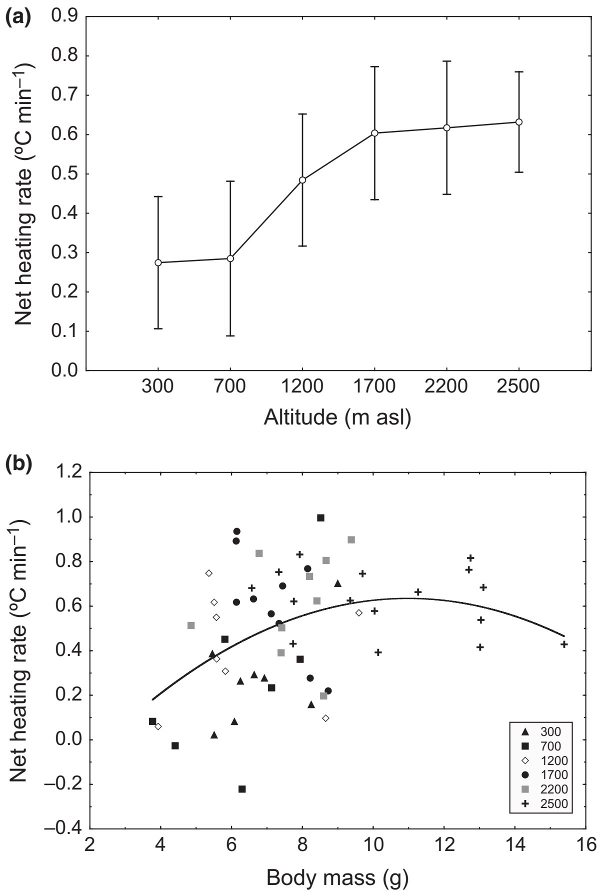

Fig. 7 Net heating rate (°C min^{-1}) tended to increase with elevation (a) and follow a concave down relationship with body mass (b). Sample sizes for (a) as in Fig. 2. Vertical bars denote 0.95 confidence intervals.

(Mousseau, 1997; Ashton & Feldman, 2003; Blanckenhorn & Demont, 2004; Olalla-Tárraga *et al.*, 2006; Olalla-Tárraga & Rodríguez, 2007; Adams & Church, 2008; Hu *et al.*, 2011; Oufiero *et al.*, 2011). The results of our study support Bergmann's Rule. In an elevational gradient of 2200 m, *P. algirus* populations showed larger size in high than in mid- and low elevations, and population average body size negatively correlated with temperature. The fact that the increase in body size is much more marked in high elevations matches with other studies showing that the increase in body size with decreasing temperature is stronger in cold habitats (Rodríguez *et al.*, 2008).

Nonetheless, the mechanism underlying Bergmann's clines is still under debate. Even for endotherms, many researchers have argued that the heat conservation hypothesis does not completely explain Bergmann's clines (McNab, 2010). In ectotherms, in which the heat conservation hypothesis has been generally (and prematurely) rejected, a set of hypotheses have been proposed to explain Bergmann's clines based on physiological by-products of temperature-dependent growth and development, or temperature-dependent life-history traits (mortality or fecundity; Angilletta *et al.*, 2004b). There is evidence that other ecological traits, besides thermoregulation, may cause body size divergence at interspecific or interpopulation levels, such as differences in longevity (Liao & Lu, 2011), habitat use (Collar *et al.*, 2011), predation pressure (de Barros *et al.*, 2010), feeding habits (Ochocińska & Taylor, 2003), food availability (Yom-Tov & Geffen, 2006), starvation resistance (Arnett & Gotelli, 2003) and life-history traits (Angilletta *et al.*, 2004b), among others. These factors are not mutually excluding, may act in contrasting directions and complicate enormously the interpretation of the causes of Bergmann's clines (Jones *et al.*, 2005).

However, the basis of the heat conservation hypothesis (higher inertia in larger animals in conjunction with a cline of increasing body size with decreasing environmental temperature) has not been properly tested until now (Partridge & Coyne, 1997). Evidence about body-size-dependent differences in heat transfer rates are needed to support this hypothesis (Watt *et al.*, 2010). In this sense, our study is novel because we showed that net heat gaining increased as lizards were larger. Nonetheless, the relationship between body size and net heating rate seemed to reach a limit, lizards at the highest elevation (the largest lizards) showing no relationship between body size and net heating rate. According to our results, larger lizards in cold habitats have an adaptive advantage over smaller lizards, which evolutionarily would favour larger sizes in alpine habitats, explaining the elevational pattern of lizard's body size found in our study. Our findings strongly support the heat conservation hypothesis and demonstrate that this hypothesis may operate in ectotherms, provided that the slope of cooling rate with body mass (β) is higher than the slope of heating rate with body mass (α; Figs 3 and 7b). In turn, we predict that when $\beta < \alpha$, ectotherms should tend to show the converse Bergmann's cline, which would explain the contrasting patterns found in several studies (Ashton & Feldman, 2003; Olalla-Tárraga *et al.*, 2006; Olalla-Tárraga & Rodríguez, 2007). In fact, the origin of a tendency to achieve larger body sizes in colder habitats is ancestral for tetrapods, before endothermy evolved (De Queiroz & Ashton, 2004); thus, we expect to find Bergmann's rule both in endotherms and ectotherms.

We found that heating rate showed a concave down relationship with body mass. This contrasts with previous studies showing that small lizards heat up faster than larger lizards (Carothers *et al.*, 1997). In our study system, highland lizards are darker; darker back colours could help these lizards to warm up faster (Clusella-Trullas *et al.*, 2007), counteracting the negative effect of larger body mass on heating capacity and smoothing out any elevational differences in heating rates (Cruz *et al.*, 2005; Harris *et al.*, 2012). Consequently, larger body mass would not limit heating rates in our study system. In fact, highland lizards reach field body temperatures similar to lowland lizards, despite lower environmental temperatures, which suggests an efficient exploitation of poorer heat sources in high elevations (Zamora-Camacho *et al.*, 2013). However, we failed to find convincing evidence of an effect of darker dorsal colour on heating rate.

We also found that gravid females had higher thermal inertia for cooling than males, nongravid females showing an intermediate inertia. Higher body mass is considered as a cause of higher thermal inertia (O'Connor, 1999), but no body mass difference arose among males and females in different reproductive status. This result implies that gravid females would be less dependent on external heat sources for maintaining body temperature during gestation. Pregnant females' ability to retain body heat could permit them to keep the optimal temperature for eggs or embryos when high predation risk makes them hide (Downes, 2001; Martín & López, 2005). Pregnant females in shelters during prolonged time to avoid predators show lower body temperatures than females in shelters for smaller periods, which provokes deterioration of body condition and immune response (Amo *et al.*, 2007). Therefore, slower cooling rate could help high elevation *P. algirus* females to prevent this worsening.

Conclusions

We show that *P. algirus* complies with Bergmann's Rule in an elevational system. We also demonstrate that larger lizards have a thermal advantage in colder habitats, as they retain accumulated heat for longer, but they heat up as fast as smaller lizards, providing the strongest empirical evidence that the heat conservation hypothesis may apply to ectotherm body size trends. According to the relative thermal costs and benefits of a larger body size, ectotherms may follow Bergmann's Rule, if the thermal benefits of a larger body size exceed the costs.

Acknowledgments

We thank the personnel from the *Espacio Natural de Sierra Nevada* for their constant support. This work was economically supported by the Ministerio de Ciencia e Innovación (project CGL2009-13185). FJZC and SR were supported by two predoctoral grants from the Ministerio de Ciencia e Innovación (FPU program). Animals capture was conducted in accordance with Junta de Andalucía research permits issued to the authors FJZC, SR and GMR. María Virtudes Rubiño Hispán, MariCruz Tuset Arcas, Miguel Leandro López Gracia, and Susana Silva González helped us during field work. Comments by Juan Manuel Pleguezuelos, Xavier Santos, Miguel Ángel Carretero, José Martín and José Antonio Hódar improved the manuscript. Jean Mattos-Reaño revised the English. The authors have no conflict of interests to declare.

References

Adams, D.C. & Church, J.O. 2008. Amphibians do not follow Bergmann's rule. *Evolution* **62**: 413–420.

Amo, L., López, P. & Martín, J. 2007. Pregnant female lizards *Iberolacerta cyreni* adjust refuge use to decrease thermal costs for their body condition and cell-mediated immune response. *J. Exp. Zool.* **307A**: 106–112.

Angilletta, M.J., Niewiarowski, P.H., Dunham, A.E., Leaché, A.D. & Porter, W.P. 2004a. Bergmann's clines in ectotherms: illustrating a life-history perspective with Sceloporine lizards. *Am. Nat.* **164**: 168–183.

Angilletta, M.J., Steury, T.D. & Sears, M.W. 2004b. Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integr. Comp. Biol.* **44**: 498–509.

Arendt, J.D. 2011. Size-fecundity relationships, growth trajectories, and the temperature-size rule for ectotherms. *Evolution* **65**: 43–51.

Arnett, A.E. & Gotelli, N.J. 2003. Bergmann's rule in larval ant lions: testing the starvation resistance hypothesis. *Ecol. Entomol.* **28**: 645–650.

Ashton, K.G. 2002a. Do amphibians follow Bergmann's rule? *Can. J. Zool.* **80**: 708–716.

Ashton, K.G. 2002b. Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. *Glob. Ecol. Biogeogr.* **11**: 505–523.

Ashton, K.G. & Feldman, C.R. 2003. Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution* **57**: 1151–1163.

Ashton, K.G., Tracy, M.C. & de Queiroz, A. 2000. Is Bergmann's rule valid for mammals? *Am. Nat.* **156**: 390–415.

Atkinson, D. & Sibly, R.M. 1997. Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends Ecol. Evol.* **12**: 235–239.

de Barros, F.C., de Carvalho, J.E., Abe, A.S. & Kohlsdorf, T. 2010. Fight versus flight: the interaction of temperature and body size determines antipredator behaviour in tegu lizards. *Anim. Behav.* **79**: 83–88.

Bennett, A.F. & Ruben, J.A. 1979. Endothermy and activity in vertebrates. *Science* **206**: 649–654.

Bergmann, C. 1847. Ueber die Verhaltnisse der warmeokonomie der thiere zu ihrer grosse. *Gottinger Studien* **3**: 595–708.

Blackburn, T.M., Gaston, K.J. & Loder, N. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. *Divers. Distrib.* **5**: 165–174.

Blanckenhorn, W.U. & Demont, M. 2004. Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum? *Integr. Comp. Biol.* **44**: 413–424.

Carothers, J.H., Fox, S.F., Marquet, P.A. & Jaksic, F.M. 1997. Thermal characteristics of ten Andean lizards of the genus *Liolaemus* in central Chile. *Rev. Chil. Hist. Nat.* **70**: 297–309.

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

Clark, T.D., Butler, P.J. & Frappell, P.B. 2005. Digestive state influences the heart rate hysteresis and rates of heat exchange in the varanid lizard *Varanus rosenbergi*. *J. Exp. Biol.* **208**: 2269–2276.

Clusella-Trullas, S., Van Wyk, J.H. & Spotila, J.R. 2007. Thermal melanism in ectotherms. *J. Therm. Biol* **32**: 235–245.

Collar, D.C., Schulte, J.A. & Losos, J.B. 2011. Evolution of extreme body size disparity in monitor lizards (*Varanus*). *Evolution* **65**: 2664–2680.

Cruz, F.B., Fitzgerald, L.A., Espinoza, R.E. & Schulte, J.A. 2005. The importance of phylogenetic scale in tests of Bergmann's and Rapoport's rules: lessons from a clade of South American lizards. *J. Evol. Biol.* **18**: 1559–1574.

De Queiroz, A. & Ashton, K.G. 2004. The phylogeny of a species-level tendency: species heritability and possible deep origins of Bergmann's rule in tetrapods. *Evolution* **58**: 1674–1684.

Díaz, J.A. & Cabezas-Díaz, S. 2004. Seasonal variation in the contribution of different behavioural mechanisms to lizard thermoregulation. *Funct. Ecol.* **18**: 867–875.

Díaz, J.A., 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.

Downes, S. 2001. Trading heat and food for safety: costs of predator avoidance in a lizard. *Ecology* **82**: 2870–2881.

Fei, T., Skidmore, A.K., Venus, V., Wang, T., Schlerf, M., Toxopeus, B. *et al.* 2012. A body temperature model for lizards as estimated from the thermal environment. *J. Therm. Biol* **37**: 56–64.

Harris, R., McQuillan, P. & Hughes, L. 2012. Patterns in body size and melanism along a latitudinal cline in the wingless grasshopper, *Phaulacridium vittatum*. *J. Biogeogr.* **39**: 1450–1461.

Hertz, P.E., Huey, R.B. & Stevenson, R.D. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am. Nat.* **142**: 796–818.

Hu, J., Xie, F., Li, C. & Jiang, J. 2011. Elevational patterns of species richness, range and body size for spiny frogs. *PLoS ONE* **6**: e19817.

Jones, J., Gibb, C.E., Millard, S.C., Barg, J.J., Girvan, M.K., Veit, M.L. *et al.* 2005. Multiple selection pressures generate adherence to Bergmann's rule in a Neotropical migratory songbird. *J. Biogeogr.* **32**: 1827–1833.

Liao, W. & Lu, X. 2011. Adult body size = f (initial size + growth rate × age): explaining the proximate cause of Bergman's cline in a toad along altitudinal gradients. *Evol. Ecol.* **26**: 579–590.

Martín, J. & López, P. 2005. Wall lizards modulate refuge use through continuous assessment of predation risk level. *Ethology* **111**: 207–219.

McNab, B.K. 2010. Geographic and temporal correlations of mammalian size reconsidered: a resource rule. *Oecologia* **164**: 13–23.

Meiri, S. 2011. Bergmann's Rule – what's in a name? *Glob. Ecol. Biogeogr.* **20**: 203–207.

Meiri, S. & Dayan, T. 2003. On the validity of Bergmann's rule. *J. Biogeogr.* **30**: 331–351.

Meiri, S. & Thomas, G.H. 2007. The geography of body size – challenges of the interspecific approach. *Glob. Ecol. Biogeogr.* **16**: 689–693.

Meiri, S., Yom-Tov, Y. & Geffen, E. 2007. What determines conformity to Bergmann's rule? *Glob. Ecol. Biogeogr.* **16**: 788–794.

Millien, V., Lyons, S.K., Olson, L., Smith, F.A., Wilson, A.B. & Yom-Tov, Y. 2006. Ecotypic variation in the context of global climate change: revisiting the rules. *Ecol. Lett.* **9**: 853–869.

Montgomerie, R. 2006. Analyzing colours. In: *Bird coloration. Vol. 1. Mechanisms and measurements* (G.E. Hill & K.J. McGraw, eds), pp. 90–140. Harvard University Press, Cambridge, MA.

Mousseau, T.A. 1997. Ectotherms follow the converse to Bergmann's rule. *Evolution* **51**: 630–632.

Ochocińska, D. & Taylor, J.R.E. 2003. Bergmann's rule in shrews: geographical variation of skull size in Palearctic *Sorex* species. *Biol. J. Linn. Soc.* **78**: 365–381.

O'Connor, M.P. 1999. Physiological and ecological implications of a simple model of heating and cooling in reptiles. *J. Therm. Biol* **24**: 113–136.

Olalla-Tárraga, M.Á. & Rodríguez, M.Á. 2007. Energy and interspecific body size patterns of amphibian faunas in Europe and North America: anurans follow Bergmann's rule, urodeles its converse. *Glob. Ecol. Biogeogr.* **16**: 606–617.

Olalla-Tárraga, M.Á., Rodríguez, M.Á. & Hawkins, B.A. 2006. Broad-scale patterns of body size in squamate reptiles of Europe and North America. *J. Biogeogr.* **33**: 781–793.

Oufiero, C.E., Gartner, G.E.A., Adolph, S.C. & Garland, T. 2011. Latitudinal and climatic variation in body size and dorsal scale counts in *Sceloporus* lizards: a phylogenetic perspective. *Evolution* **65**: 3590–3607.

Partridge, L. & Coyne, J.A. 1997. Bergmann's rule in ectotherms: is it adaptive? *Evolution* **51**: 632–635.

Quinn, G.P. & Keough, M.J. 2002. *Experimental Design and Data Analysis for Biologists*, 1st edn. Cambridge University Press, Cambridge, UK.

Ramírez, L., Diniz-Filho, J.A.F. & Hawkins, B.A. 2008. Partitioning phylogenetic and adaptive components of the geographical body-size pattern of New World birds. *Glob. Ecol. Biogeogr.* **17**: 100–110.

Rodríguez, M.Á., López-Sañudo, I.L. & Hawkins, B.A. 2006. The geographic distribution of mammal body size in Europe. *Glob. Ecol. Biogeogr.* **15**: 173–181.

Rodríguez, M.Á., Olalla-Tárraga, M.Á. & Hawkins, B.A. 2008. Bergmann's rule and the geography of mammal body size in the Western Hemisphere. *Glob. Ecol. Biogeogr.* **17**: 274–283.

Salvador, A. 2011. Lagartija colilarga – *Psammodromus algirus* (Linnaeus, 1758). In: *Enciclopedia Virtual de los Vertebrados Españoles* (A. Salvador & A. Marco, eds). Museo Nacional de Ciencias Naturales, Madrid. http://www.vertebradosibericos.org/.

Stevenson, R.D. 1985. Body size and limits to the daily range of body temperature in terrestrial ectotherms. *Am. Nat.* **125**: 102–117.

Sun, Y., Du, Y., Yang, J., Lin, C. & Ji, X. 2012. Climatic correlates of female and male reproductive cycles and plasma steroid hormone levels in the many-lined sun skink *Eutropis multifasciata*. *Gen. Comp. Endocrinol.* **178**: 363–371.

Verdú-Ricoy, J., Carranza, S., Salvador, A., Busack, S.D. & Díaz, J.A. 2010. Phylogeography of "*Psammodromus algirus*" (*Lacertidae*) revisited: systematic implications. *Amphib.-Reptil.* **31**: 576–582.

Watt, C., Mitchell, S. & Salewski, V. 2010. Bergmann's rule; a concept cluster? *Oikos* **119**: 89–100.

Wilson, A.B. 2009. Fecundity selection predicts Bergmann's rule in syngnathid fishes. *Mol. Ecol.* **18**: 1263–1272.

Xiang, J., Weiguo, D. & Pingyue, S. 1996. Body temperature, thermal tolerance and influence of temperature on sprint speed and food assimilation in adult grass lizards, *Takydromus septentrionalis*. *J. Therm. Biol* **21**: 155–161.

Yom-Tov, Y. & Geffen, E. 2006. Geographic variation in body size: the effects of ambient temperature and precipitation. *Oecologia* **148**: 213–218.

Yom-Tov, Y. & Geffen, E. 2011. Recent spatial and temporal changes in body size of terrestrial vertebrates: probable causes and pitfalls. *Biol. Rev. Camb. Philos. Soc.* **86**: 531–541.

Zamora-Camacho, F.J., Reguera, S., Moreno-Rueda, G. & Pleguezuelos, J.M. 2013. Patterns of seasonal activity in a Mediterranean lizard along a 2200 m altitudinal gradient. *J. Therm. Biol* **38**: 64–69.

Data deposited at Dryad: doi:10.5061/dryad.969q5

Received 12 August 2014; accepted 31 October 2014