Introduction

Much of the variation in the ecological and life-history patterns of animals is attributable to differences in body size (Peters, 1983; Losos, 1990; Blackburn et al., 1999). Therefore, understanding factors affecting specializations in this trait is a major challenge in evolutionary biology (Belk & Houston, 2002).

Bergmann’s rule predicts that body size in organisms tends to be positively correlated to latitude and altitude, and therefore, negatively correlated to environmental temperature (Bergmann, 1847; Blackburn et al., 1999). The justification for this relationship is that larger body size reduces rates of heat loss per unit mass. This represents an advantage for endothermic physiologies, but less obvious is its relevance to ectotherms. Indeed, for ectotherm vertebrates, evidence supporting the hypothesis that geographical gradients constrain variation in body size remains elusive and controversial (Blackburn et al., 1999; de Queiroz & Ashton, 2004). Instead, ecological adaptations such as perch preferences appear to be better predictors of divergence in this variable (Rummel & Roughgarden, 1985; Glossip & Losos, 1997).

The first non-phylogenetic studies testing Bergmann’s rule in ectotherms showed supporting evidence (Ray, 1960; Lindsey, 1966). However, later phylogenetic comparative analyses have suggested that only turtles and salamanders tend to follow patterns predicted by this model (Ashton & Feldman, 2003), whereas fish, anurans, snakes and lizards appear to reverse the trend (Ashton, 2002; Belk & Houston, 2002; de Queiroz & Ashton, 2004). Remarkably, a recent study conducted on South American Liolaemus lizards of the boulengeri clade showed that these species follow Bergmann’s rule (Cruz et al., 2005). This research provided the only known phylogenetic evidence supporting this model in a monophyletic squamate (lizards and snakes) clade. However, these non-significant results appear to be explained only by the inclusion of further species rather than by a different estimation of body size. Analyses conducted on the 16 species included in the previous study always revealed significant relationships between body size and latitude-altitude, whereas, the enlarged sample always rejected the pattern predicted by Bergmann’s rule.

Abstract

Bergmann’s rule predicts larger body sizes in species living in higher latitudes and altitudes. This rule appears to be valid for endotherms, but its relevance to ectotherm vertebrates has largely been debated. In squamate reptiles (lizards and snakes), only one study, based on Liolaemus species of the boulengeri clade, has provided phylogenetic evidence in favour of Bergmann’s clines. We reassessed this model in the same lizard clade, using a more representative measure of species body size and including a larger number of taxa in the sample. We found no evidence to support Bergmann’s rule in this lineage. However, these non-significant results appear to be explained only by the inclusion of further species rather than by a different estimation of body size. Analyses conducted on the 16 species included in the previous study always revealed significant relationships between body size and latitude-altitude, whereas, the enlarged sample always rejected the pattern predicted by Bergmann’s rule.

Keywords:
Bergmann’s rule; body size; environmental temperature; geographic clines; Liolaemus lizards; reptiles.
Brown et al. (1999), percentiles lower than the maximum SVL provide more accurate estimates for asymptotic size in lizards that do not follow asymptotic growth curves.

Here we reassess the problem of body size evolution under geographical gradients in the *Liolaemus* species of the *boulengeri* clade, to test for compliance with Bergmann’s rule. We use a larger sample of species belonging to this clade, and a different methodology to estimate SVL. Our aim is not to challenge the work of Cruz et al. (2005), but to clarify the importance of latitude and altitude in their influence on body size in lizards.

**Materials and methods**

We gathered data on body size with respect to latitude and altitude from 319 individuals representing 26 species of the *boulengeri* clade (Cruz et al., 2005; Supplementary Material). The sample comprises individuals from both sexes studied alive in the field and specimens housed in the institutions detailed in the Appendix. Museum specimens only include lizards preserved in the field immediately after collection, whereas those kept in captivity were omitted from these analyses. Additional geographical information was taken from previously published records (Cei, 1993; Etheridge, 1993; Cruz et al., 2005; Pincheira-Donoso & Núñez, 2005). We used SVL as a proxy for body size. We calculated the arithmetic average of the largest two-thirds of the total sample of SVL measurements for each studied species (see Losos et al., 2003). As *Liolaemus* species of the *boulengeri* clade may exhibit sexual size differences, with larger males, larger females or no sexual dimorphism (Cei, 1993; Etheridge, 1993, 2000; Pincheira-Donoso & Núñez, 2005; Pincheira-Donoso et al., 2007), and because Cruz et al. (2005) did not restrict their analyses to a single sex, these mean values were calculated on the basis of both males and females, in order to estimate a mean value for the species. Whenever possible (23 of 26 species) the two-thirds of the total sample comprised a similar number of males and females.

As environmental temperatures decrease with both increasing latitude and altitude (Lutgens & Tarbuck, 1998; Ashton, 2002), we used the adjusted latitudinal midpoint (ALM) scale recently calibrated by Cruz et al. (2005). This scale and similar versions, broadly used for estimations of species’ environmental conditions in comparative and multi-taxon studies (e.g. Espinoza et al., 2004; Wiens et al., 2007), combines the effects of latitude and altitude. The ALM scale is based on the assumption that environmental temperature in altitudinal transects declines 0.65 °C each 100 m of increased elevation (see also Lutgens & Tarbuck, 1998). Cruz et al. (2005) obtained a corrected latitudinal value for latitude and altitudinal thermal covariation using the formula $y = 0.009x - 6.2627$, where $x$ represents the latitudinal midpoint for each species, and $y$ the corrected temperature for latitude. Then, the $y$-value is added to the latitudinal midpoint for each species to give the ALM. We also calculated the adjusted latitudinal range (ALR) for each species, using the extremes of latitudinal and altitudinal distributions. For the regression analyses we used ln(SVL) as dependent variable, and ALM and ALR as predictor variables. Inclusion of ALR was necessary to compare species that shared a geographical centre but differed in their tolerance of ecological extremes.

We analysed data sets using two different methods (see Cruz et al., 2005), including our improved estimates of SVL for each species (see above). First, we used raw data on ln(SVL) and ALM, without explicit phylogenetic control. We analysed the 16 identifiable species of the *boulengeri* clade used by Cruz et al. (2005), and then a larger sample of 26 species belonging to this lineage. Second, we used independent contrasts (Felsenstein, 1985) calculated using COMPARE version 4.6b (Martins, 2004), to control for phylogenetic effects. In the first phylogenetic analysis, we re-analysed the relationship between ln(SVL) and ALM for the 16 identifiable species of the *boulengeri* clade used by Cruz et al. (2005). We then analysed our whole phylogenetic data set using the same procedure, but including additional species (see Supplementary Material). Variables were evaluated under the phylogenetic hypothesis of Cruz et al. (2005) and additional phylogenetic evidence provided by recent studies (Espinoza et al., 2004; Pincheira-Donoso et al., 2007; Fig. 1). As our phylogenetic hypothesis is based on

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**Fig. 1** Phylogenetic relationships between the *Liolaemus* species of the *boulengeri* clade.
different data sets, we applied a speciational model assuming branch lengths equal to 1.0 (Espinosa et al., 2004; Martins, 2004). Following Cruz et al. (2005), we checked for the absence of phylogenetic autocorrelation using Abouheif’s (1999) test for serial independence (TFSI). Analyses of standardized residuals and Cook’s distance values (< 1.0) revealed that the addition of new species did not introduce potential outliers into the regression model (Cook & Weisberg, 1982).

Results

Re-analysis of species used by Cruz et al. (2005)

Linear regression of ln(SVL) against ALM for a common subset of 16 species of the boulengeri clade supported Cruz et al.’s (2005) evidence for Bergmann’s rule in these lizards (raw data, $R^2 = 0.364, F_{1,15} = 8.002, P = 0.013$; independent contrasts, $R^2 = 0.284, F_{1,15} = 5.560, P = 0.033$, Fig. 2).

Analysis of the expanded clade

Bivariate regression analyses revealed that ALM does not predict increasing variation in species body size when using the entire data set of 26 species of the boulengeri clade (see above; also Supplementary Material) and estimating SVL on the basis of the two largest members of the original, smaller sample (see above; also Supplementary Material). In contrast, the species added to expand the clade sample may have been biased or ‘extreme’ in some way. We can discount both mechanisms. First, non-significant relationships were also observed if we analysed the maximum recorded SVL for the expanded clade (raw data, $R^2 = 0.091, F_{1,25} = 2.389, P = 0.135$; independent contrast analysis, $R^2 = 0.085, F_{1,18} = 1.585, P = 0.225$, see Cruz et al., 2005). Second, the species added to expand the clade sample do not exist outside the body size, altitude and latitude ranges of the original, smaller sample (see Supplementary Material).

Discussion

In agreement with previous studies conducted on ectotherm vertebrates (e.g. Ashton & Feldman, 2003; de Queiroz & Ashton, 2004), and in contrast to the findings of Cruz et al. (2005), our results do not provide support for Bergmann’s rule in the Liolaemus species of the boulengeri clade. Differences in latitude and altitude do not predict evolution of larger body sizes in the species belonging to the studied reptile lineage. Although we controlled the potential statistical bias that analysis of maximum recorded SVL may cause in lineages that do not experience asymptotic growth curves (see above; Brown et al., 1999), the disagreement between Cruz et al.’s (2005) study and our results appears to be explained by increasing the number of species in the analyses. Indeed, the analysis of the same 16 species included in the Cruz et al.’s (2005) study revealed a significant relation between ALM and increasing body size no matter which method was used to estimate SVL. In contrast, the study of the enlarged species sample weakened the relationship between SVL and ALM to such an extent as to prevent rejection of the null hypothesis. Hence our expanded sample provided no evidence for Bergmann’s rule, regardless of the methodology used to estimate body size.

It is not surprising to find that the species of this clade do not follow Bergmann’s rule. Smaller body sizes in cooler environments appear to be advantageous for cold-blooded vertebrates, because increasing body mass means that heating rates are slower (e.g. Shine, 1980; Ashton & Feldman, 2003). Therefore, the optimal body temperatures to allow basic biological activities (e.g. feeding, reproduction) can be reached in shorter spans of times (Jaksic, 1998; Mattison, 1999).

Fig. 2 Linear regression of independent contrasts for ln(SVL) against adjusted latitudinal midpoint of the Liolaemus species of the boulengeri clade, using the species analysed by Cruz et al. (2005; see above) (open circles, dashed line $y = -0.013x$) and a new phylogenetic model that includes additional taxa in the phylogeny (filled circles, solid line represents no significant linear relationship).
We conclude that adequately-replicated evidence supporting Bergmann’s rule in reptiles is so far restricted to turtle lineages (Ashton & Feldman, 2003). There remains no strong evidence for Bergmann’s clime in other reptile groups (de Queiroz & Ashton, 2004). Finally, we suggest the need to test Bergmann’s rule in species-rich monophyletic clades of ectotherms with taxa adapted to contrasting environmental conditions, based on samples covering a high proportion of their known diversity.

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References


Lindsey, C.C. 1966. Body sizes of poikilotherm vertebrates at contrasting environmental conditions, based on samples covering a high proportion of their known diversity.


Supplementary Material

The following supplementary material is available for this article:

Table S1. Summary of the Liolaemus species included in this study.
Appendix

Museo Nacional de Historia Natural de Chile (MNHNC), Zoological Museum, Universidad de Concepción, Chile (MZUC), Museo de Historia Natural de Concepción, Chile (MHNC), Institute for Animal Biology, Universidad Nacional de Cuyo, Argentina (IBAUNC), Instituto Argentino de Investigaciones en Zonas Áridas, Argentina (IADIZA), Division of Reptiles and Amphibians, Natural History Museum of London, UK (NHML), and diagnostic collections of J. M. Cei (JMC-DC), J. A. Scolaro (JAS-DC).

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