Global Ecology and Biogeography, (Global Ecol. Biogeogr.) (2008) **17**, 274–283

RESEARCH PAPER

Bergmann's rule and the geography of mammal body size in the Western Hemisphere

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ABSTRACT

Aim To describe the geographical pattern of mean body size of the non-volant mammals of the Nearctic and Neotropics and evaluate the influence of five environmental variables that are likely to affect body size gradients.

Location The Western Hemisphere.

Methods We calculated mean body size (average log mass) values in 110 × 110 km cells covering the continental Nearctic and Neotropics. We also generated cell averages for mean annual temperature, range in elevation, their interaction, actual evapotranspiration, and the global vegetation index and its coefficient of variation. Associations between mean body size and environmental variables were tested with simple correlations and ordinary least squares multiple regression, complemented with spatial autocorrelation analyses and split-line regression. We evaluated the relative support for each multiple-regression model using AIC.

Results Mean body size increases to the north in the Nearctic and is negatively correlated with temperature. In contrast, across the Neotropics mammals are largest in the tropical and subtropical lowlands and smaller in the Andes, generating a positive correlation with temperature. Finally, body size and temperature are nonlinearly related in both regions, and split-line linear regression found temperature thresholds marking clear shifts in these relationships (Nearctic 10.9 °C; Neotropics 12.6 °C). The increase in body sizes with decreasing temperature is strongest in the northern Nearctic, whereas a decrease in body size in mountains dominates the body size gradients in the warmer parts of both regions.

Main conclusions We confirm previous work finding strong broad-scale Bergmann trends in cold macroclimates but not in warmer areas. For the latter regions (i.e. the southern Nearctic and the Neotropics), our analyses also suggest that both local and broad-scale patterns of mammal body size variation are influenced in part by the strong mesoscale climatic gradients existing in mountainous areas. A likely explanation is that reduced habitat sizes in mountains limit the presence of larger-sized mammals.

Keywords

Body size, climatic gradients, habitat zonation, heat tolerance, macroecology, New World mammals.

INTRODUCTION

An increase in body size in cold climates (Bergmann's rule) is one of the best known empirical generalizations of geographical ecology. Research on body size gradients has been intense in recent decades, likely because body size can be related to key physiological, ecological and evolutionary characteristics of animals (McNab, 1979; Peters, 1983; Lindstedt & Boyce, 1985; Cushman *et al.*, 1993) and, consequently, identifying the factors underlying geographical variation in body sizes may increase our understanding of the organization of animal communities (Lawton, 1990; Brown & Nicoletto, 1991).

DOI: 10.1111/j.1466-8238.2007.00363.x

Studies on broad-scale patterns of body size variation can be divided into those focused on intraspecific patterns and those focused on interspecific patterns. Intraspecific patterns have received the most attention (Ray, 1960; Lindsey, 1966; Ashton *et al*., 2000; Meiri & Dayan, 2003; Meiri *et al*., 2004), although interspecific gradients have also been studied, especially for endotherms (mammals: Zeveloff & Boyce, 1988; Cotgreave & Stockley, 1994; Blackburn & Hawkins, 2004; Rodríguez *et al*., 2006; Diniz-Filho *et al*., 2007; Medina, *et al*., 2007; birds: Cousins, 1989; Blackburn & Gaston, 1996; Gaston & Blackburn, 2000; Ramirez *et al*., 2007). In the case of mammals, two recent interspecific studies involving the northern Nearctic (Blackburn & Hawkins, 2004) and the Western Palaearctic (Rodríguez *et al*., 2006) found clear Bergmann-like patterns and strong negative associations between mean body size and mean annual temperature. This is consistent with the heat conservation mechanism proposed by Bergmann, that cold climates should harbour more large-bodied species because of the reduced surface area to volume ratios (Bergmann, 1847) and/or thicker insulation layers (Blackburn *et al*., 1999) of larger animals. However, Rodríguez *et al.* (2006) also suggested that this hypothesis might need to be reformulated to include nonlinear relationships between body size and temperature over very broad geographical scales, because they found that the association between mammal body size and temperature was strong in northern Europe, whereas it virtually disappeared in the south. Although the geographical scope of Blackburn & Hawkins (2004) did not extend into areas with warm climates, they also reported evidence of a nonlinear relationship between mean body size and temperature. Thus, both studies suggest that broad-scale gradients of mammal body size are more influenced by temperature in colder climates than in warmer ones; this is not unexpected under the heat conservation mechanism.

To explore this issue further, we examine geographical variation in mean body size of the non-volant terrestrial mammal faunas of the Western Hemisphere. Based on the previous analyses, we expect mean body size to exhibit a negative relationship with temperature in the far north and south, but this relationship should weaken or disappear in more temperate and tropical areas. In addition to the heat conservation hypothesis, we also evaluate three other explanations for variation in body size within the constraints imposed by a correlative approach: (1) the heat dissipation hypothesis, which states that the higher rates of heat loss of small-bodied species should favour them in warm, moist climates, where evaporative cooling is more difficult (Brown & Lee, 1969; James, 1970); (2) the resource availability hypothesis, which proposes that large-bodied species are favoured in areas with seasonal shortages in resources because they metabolize fat stores at lower weight-specific rates than smaller species (Lindstedt & Boyce, 1985; Dunbrack & Ramsay, 1993); and (3) the habitat availability hypothesis, developed to explain geographical range size variation in the Western Hemisphere avifauna (Hawkins & Diniz-Filho, 2006), which suggests that the greater habitat zonation associated with stronger mesoscale climatic gradients in tropical mountainous areas would limit the occurrence of large-sized mammal species. A fifth possible explanation emphasizes dispersal differences between large- and small-bodied animals and the colonization of the new habitats created during the retreat of the late Pleistocene ice sheets (e.g. Olalla-Tárraga *et al*., 2006; Olalla-Tárraga & Rodríguez, 2007). However, we excluded this hypothesis because it has been shown to be an unlikely explanation for the mean body size patterns of the Holarctic mammal fauna (see Blackburn & Hawkins, 2004; and Rodríguez *et al*., 2006) and because only 1.2% of the Neotropics were covered by ice during the late Pleistocene (Adams & Faure, 1997).

MATERIALS AND METHODS

Mammal species data

Digital range maps for the 1328 non-volant terrestrial mammal species native to the Western Hemisphere were obtained from Patterson *et al.* (2005). The maps were rasterized in ArcGIS 9.2 using separate 110 × 110 km grids for North and South America. We excluded all islands except Tierra del Fuego. We also excluded all coastal cells containing < 50% of the land mass of inland cells and used the mammal zoogeographical regions in Cox (2001) to differentiate the Nearctic and Neotropics.

Average body mass (in grams) for each of 1082 species was taken from Smith *et al.* (2003). For the remaining species, we searched the literature for body mass measurements of individuals of each species distributed across the species' range, and then averaged them. We found body mass or length estimates for 47 and 6 species, respectively (see Appendix S1 in Supplementary Material). We transformed lengths into body masses using the equations by Silva & Downing (1995). For 111 additional species, we determined that they have been sometimes considered subspecies, synonyms, or conspecifics of species of known mass, and assigned these masses to them (see Appendix S2). For 61 species cited as 'being similar in size to', or as 'belonging to the group of' species of known body masses, we assigned these masses to them (see Appendix S3). We were unable to find direct or indirect measures of size for 21 species, and we assigned the average mass of its genus in these cases (see Appendix S4). All body masses were $\log_{10}$-transformed for analysis.

Environmental variables

We selected five variables to evaluate four hypotheses for body size gradients, as follows.

Heat conservation

We used mean annual temperature as our indicator of heat. The data were obtained from http://www.grid.unep.ch/data/summary.php?dataid=GNV15. Potential evapotranspiration has also frequently been used as an indicator of ambient energy inputs (reviewed by Hawkins *et al*., 2003). However, this variable (the Priestley–Taylor equation) is highly correlated with mean annual temperature in the Western Hemisphere ($r = 0.907$, $n = 3111$), so we did not use it.

Heat dissipation

We used cell averages of annual actual evapotranspiration (AET) as our water-energy measure. Evaporative cooling should be more difficult in areas with high AET. These data are available at http://www.grid.unep.ch/data/summary.php?dataid=GNV183.

Resource availability

Following Blackburn & Hawkins (2004), we used the mean monthly global vegetation index (GVI) and its temporal coefficient of variation across the year (GVIcv) to test for effects of plant production and seasonality on mammal body mass. These variables were estimated from monthly values from April 1985 to December 1988, available at http://www.ngdc.noaa.gov/seg/cdroms/ged_iia/datasets/a01/mgv.htm.

Habitat availability

We followed the logic and procedures used by Hawkins & Diniz-Filho (2006) to investigate potential indirect effects of mesoscale climatic gradients on mean body size variation occurring through the effects of mesoclimate on habitat variability. Thus, we used range in elevation (i.e. the difference between maximum and minimum elevations within each grid cell) as our indicator of variation in mesoclimate, and we combined this variable with its interaction with mean annual temperature in multi-factor models to account for potential differential trends of body size variation in mountains of cold and warm areas (see Hawkins & Diniz-Filho, 2006). Elevation data were obtained at http://www.ngdc.noaa.gov/seg/cdroms/ged_iia/datasets/a13/fnoc.htm.

Statistical analyses

Because of regional differences in the body size gradients that were obvious when we mapped the data (Fig. 1), the Nearctic and Neotropical data sets were analysed separately. First, we used simple correlation to explore associations among response and explanatory variables. We then used least-squares multiple regression to identify the models best supported by the data. For this we applied model selection techniques based on information theory which we preferred over stepwise regression because it is well known that the results of the latter analysis are highly dependent on the strategy chosen for model simplification, i.e. forward and backward strategies and their combinations (Whittingham *et al.*, 2006). Further, the use of model selection techniques as an alternative to hypothesis testing is becoming increasingly common in ecology (Johnson & Omland, 2004), as these techniques allow the relative support for each hypothesis to be evaluated by comparing a complete set of competing models. Moreover, in our case, given the strong collinearity among several of the predictors in our data set (Table 1), it was imperative to assess simultaneously the importance of all the various predictors included in the analysis. Specifically, we used the Akaike information criterion (AIC), which we computed for all possible models for each region using geographically effective sample sizes (n^*), given by $n^* = n/[(1 + p)/(1 - p)]$ where p is the first-order autoregressive parameter of the residuals, approximated by the standardized Moran's I in the first distance class (Cressie, 1993; Haining, 2003). We also computed the ΔAIC of each model (i.e. $\Delta AIC_i = AIC_i - \text{minAIC}$; where $\Delta AIC > 10$ represent poor fits and $\Delta AIC \leq 2$ correspond to models equivalent to the best model) (Burnham & Anderson, 2001), as well as its Akaike weighting (w_i), a value that can be interpreted as the probability that model i is actually the best explanatory model among those evaluated. We used the 25 models with the lowest AICs for each analysed region (and subregion, see below) to calculate w_i. In addition, we used the standardized regression coefficient of the variables included in each model to rank the importance of each variable in determining mean body size variation.

In order to investigate whether environmental influences on mammal mean body size differ in warm and cold macroclimates

Table 1 Correlations among response (mammal mean body size) and explanatory variables (environmental predictors) in the Nearctic and Neotropics.

Variable	Mean size	Temp.	R. Elev	AET	GVI	GVIcv
(a) Nearctic (n = 1529)						
Mean body size	1					
Mean annual temperature	−0.746	1				
Range in elevation	−0.061	−0.010	1			
Annual evapotranspiration	−0.568	0.703	−0.292	1		
Global vegetation index (GVI)	−0.552	0.632	−0.148	0.848	1	
Coefficient of variation of GVI	0.263	−0.445	−0.307	−0.052	0.106	1
(b) Neotropics (n = 1582)						
Mean body size	1					
Mean annual temperature	0.508	1				
Range in elevation	−0.578	−0.574	1			
Annual evapotranspiration	0.413	0.719	−0.406	1		
Global vegetation index (GVI)	0.407	0.717	−0.528	0.822	1	
Coefficient of variation of GVI	−0.113	−0.118	−0.013	−0.336	−0.129	1

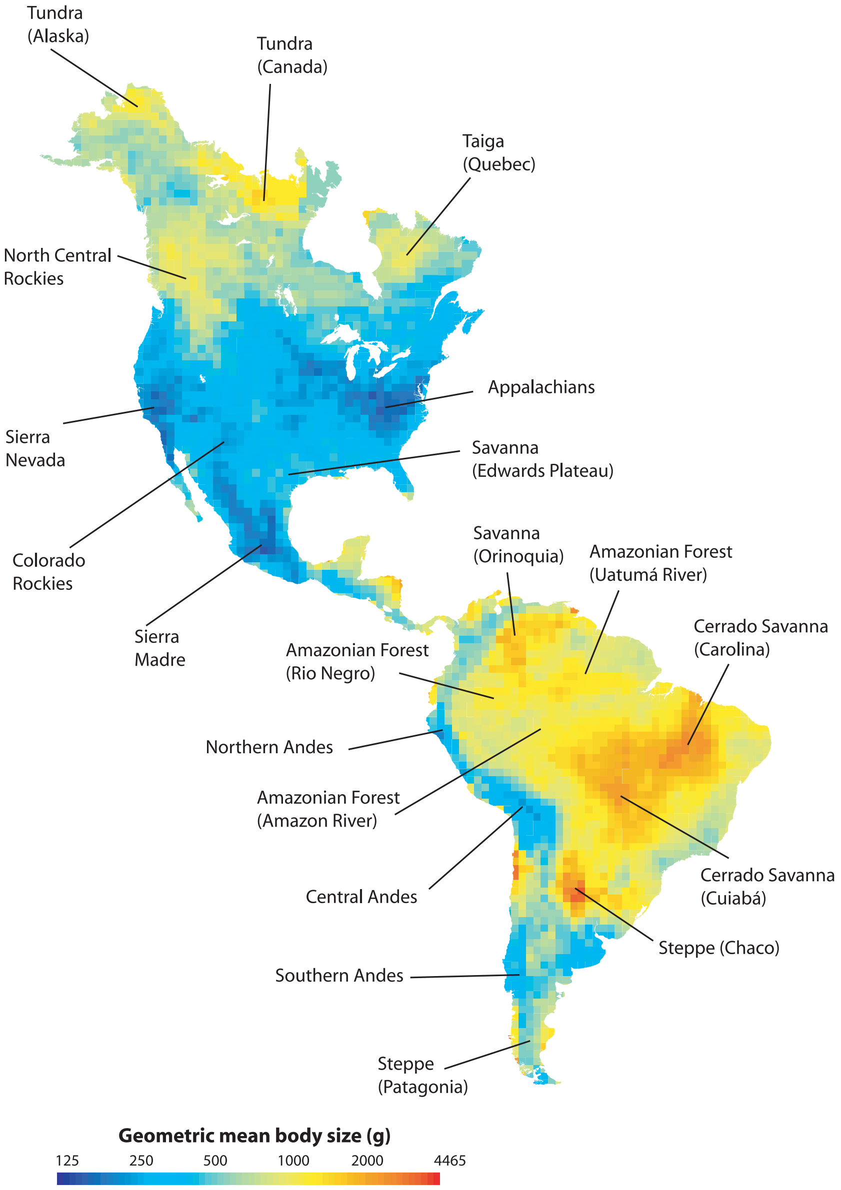

Figure 1 Mean $\log_{10}$-transformed body sizes of non-volant mammals in the Western Hemisphere. Numbers included in the legend are mass values (in g) generated after antilog transformation. Labelled sites are midpoints of 110 × 110 km cells selected to examine the body size distributions on which the means are based (see Figs 2 & 3).

(Rodríguez *et al*., 2006), we used split-line regression (Schmid *et al*., 1994) to look for potential breakpoints in the relationship of temperature with mammal mean body size in the Nearctic and the Neotropics. For this, we developed a two-step procedure. First, we utilized the quasi-Newton routine of STATISTICA (see StatSoft, Inc., 2003) to obtain an initial approximation to the breakpoint in each region. Second, we checked all potential breakpoints within a temperature range of 5 °C below and above this approximated value (considering increments of 0.1 °C) and retained that which maximized the coefficient of determination as the most likely temperature breakpoint. Finally, for each region, we performed the model selection protocol described above for the areas above and below the breakpoint.

We performed two additional sets of analyses to investigate the robustness of the relationships we found. First, we generated correlograms (not shown) of the residuals of the best multiple-regression models to evaluate how well they described spatial variation in body size across spatial scales (Diniz-Filho *et al*., 2003). These correlograms were calculated across complete regions (i.e. the Nearctic and Neotropics) as well as to the areas above and below the temperature threshold found for each region. In all instances we found that our models explained mean body size patterns at all scales except the smallest distance classes. This result is common in map-based data, and indicates either that variables not included in our models may be needed to account for the spatial pattern of mean body size at smaller scales, or that the use of range map data has made closely spaced cells more similar than they should be. Second, because patterns of mean body size variation are potentially sensitive to the uneven distribution of species richness across geographical spaces, which in turn may affect statistical analysis, we used weighted least squares regression techniques to recalculate the standardized regression coefficients of the variables included in our best models, as well as the coefficient of determination of each model (R^2) (Olalla-Tárraga & Rodríguez, 2007). For all regions, the results of these analyses (not shown) were similar to those generated with ordinary least squares regression, thus indicating that they were not affected by spatial variation in species richness.

All statistical analyses were performed with STATISTICA (StatSoft, Inc., 2003) and SAM 2.0 (Spatial Analysis in Macroecology; Rangel *et al.*, 2006).

RESULTS

The geography of mammal mean body size

Mean body size exhibits a clear Bergmann-like pattern of spatial variation in the Nearctic, with the largest sizes found in the far north (e.g. the arctic tundra of Alaska and Canada, and the taiga of Quebec) and in the northern Rocky Mountains, whereas the smallest sizes are found in the south, particularly in mountain ranges such as the Appalachians, the Colorado Rockies, the Sierra Nevada and the Sierra Madre (Fig. 1). Intermediate mean body sizes, on the other hand, are particularly found in the lowlands of the southern half of the region. Histograms of the frequency of body sizes in 12 size classes (Fig. 2) allow a comparison of the body size distributions of representative cells of these zones. The southern cells show right-skewed distributions and generally lack species of the two larger size classes. In contrast, the northern cells exhibit multimodal distributions with a noticeable representation of species with intermediate to large sizes. Therefore, the northward increase in mean body sizes observed in the Nearctic is mainly due to a higher proportion of small-sized species occurring in the south, coupled with an increase in the proportion of species with intermediate to large sizes in the north.

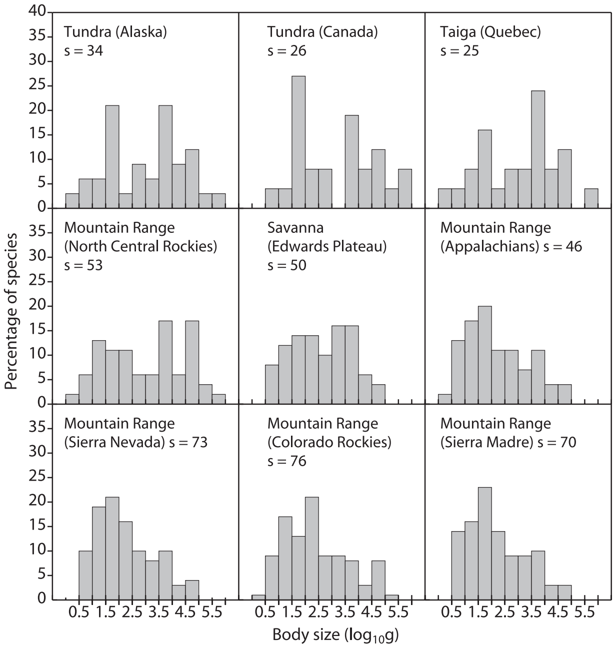

Figure 2 Histograms of mammal body sizes of species occurring in nine 110 × 110 km Nearctic cells. Species richness values (s) are provided for each cell. See Fig. 1 for cell locations.

The pattern of body size variation is reversed in the Neotropics. The smallest sizes are distributed across the high Andes (Fig. 1); whereas the largest sizes cover the tropical lowlands, particularly in the savannas of Brazil (the cerrado) and Venezuela and the steppes of Paraguay and northern Argentina (the chacos). There are also small clusters of larger mean body sizes in the Atacama Desert and in the eastern half of Nicaragua. The small mean body sizes in the Neotropical mountains are due to a high proportion of species having small sizes (i.e. right-skewed body size distributions), whereas the larger mean sizes of the tropical lowlands are associated with a high proportion of intermediate-sized species, particularly of those belonging to the size class of 3.5–4 $\log_{10}$ g (i.e. with a body size between 3.2 and 10 kg) (Fig. 3).

In sum, mountain ranges in both the southern half of the Nearctic and throughout the Neotropics support small-bodied species, but the largest mammals occur in areas with very different climates in each region, that is, throughout the cold, northern Nearctic and in the warm lowlands of the central Neotropics.

Mean body size was strongly negatively correlated with mean annual temperature and, to a lesser extent, with AET and GVI in the Nearctic (Table 1a), which is consistent with the observed increase in body size towards the cold, low-productive areas of the north. Similarly, a strong negative correlation between mean

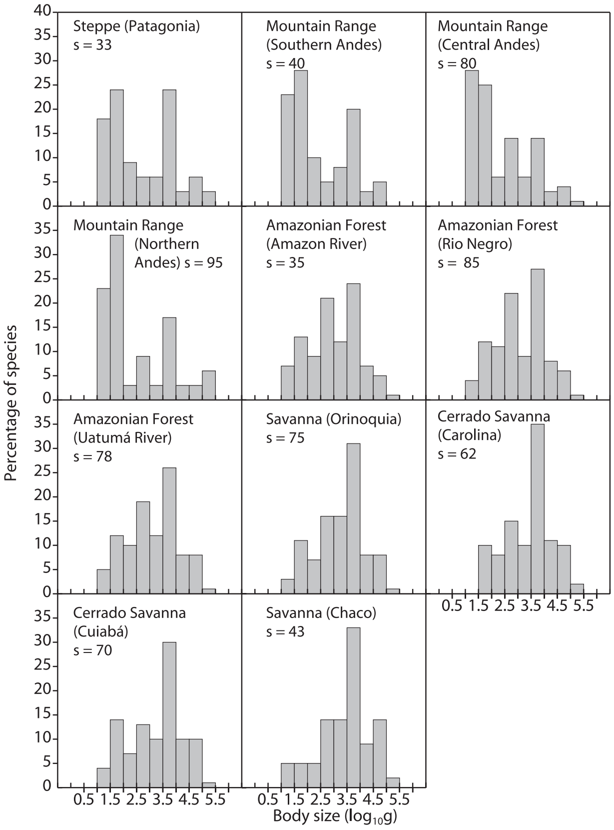

Figure 3 Histograms of mammal body sizes of species occurring in 11 110 × 110 km Neotropical cells. Species richness values (s) are provided for each cell. See Fig. 1 for cell locations.

Table 2 Environmental multiple regression models for mammal mean body size in the Nearctic, the Neotropics, and the areas of each region on each side of the break points identified by split-line regression (see text). The standardized regression coefficients of the predictors included in the 'best' models (i.e. with $\Delta AIC \leq 2$; see methods) are provided, along with the coefficient of determination (R^2), AIC and the Akaike weighting of each model (w_i). These information theory indices were calculated correcting for the presence of spatial autocorrelation in the model residuals. Predictor variables are: Temp., mean annual temperature; R. Elev., range in elevation; AET, annual actual evapotranspiration; GVI, mean monthly global vegetation index; and GVIcv, temporal coefficient of variation of GVI.

Predictors in model									
	Temp.	R. Elev	Temp. × R. Elev.	AET	GVI	GVIcv	R^2	AIC	w_i
(a) Nearctic									
	−0.519	0.134	−0.345	−0.203		−0.104	0.589	−5265	0.949
(b) Nearctic (Temp. ≤ 10.9 °C)									
	−0.657	−0.149	0.195	−0.251		0.194	0.612	−4108	0.497
	−0.661	−0.146	0.185	−0.266	0.029	0.185	0.612	−4108	0.495
(c) Nearctic (Temp. > 10.9 °C)									
	0.394	−0.523		−0.144		−0.369	0.539	−1846	0.470
(d) Neotropics									
	0.688	0.871	−1.163		−0.054		0.459	−4817	0.913
(e) Neotropics (Temp. ≤ 12.6 °C)									
				−0.156	−0.365		0.236	−577	0.282
			0.044	−0.176	−0.357		0.238	−576	0.165
				−0.175	−0.306	−0.078	0.240	−575	0.131
		0.001		−0.156	−0.365		0.236	−575	0.109
(f) Neotropics (Temp. > 12.6 °C)									
	0.367	0.570	−1.006	0.124	−0.032	0.100	0.430	−4235	0.995

body size and range in elevation in the Neotropics (Table 1b) reflects the small mean body sizes in the Andes and the large sizes in the tropical lowlands. Temperature has the second strongest correlation with mean body size among our environmental variables in this region, but this correlation is positive.

Multiple regression models of mean body size

The Nearctic

Our multimodel selection protocol found one good model in the Nearctic, which described 59% of mean body size variance and was strongly favoured as the best model according to its *w* value (Table 2a). Even so, collinearity among the model's variables (see Table 1) means that its interpretation must be cautious, so we focused on variables with either higher standardized regression coefficients – that is, mean annual temperature and its interaction with topography, both with a negative sign – or low correlation with the rest of the predictors, i.e. range in elevation which had a positive sign (see Table 2a). The negative relationship with temperature is what would be expected from the heat conservation hypothesis, as would also be the positive correlation with range in elevation, which reflects a general tendency for body sizes to increase in mountainous areas. However, the low standardized coefficient of range in elevation reflects that its association with body size is found only in the northern Rockies, whereas in more southern mountains this relationship disappears, or reverses (see Fig. 1). This was captured by the interaction between macroclimate (measured by temperature) and range in elevation, thus accounting for the aforementioned shift from larger mammals in mountains in cold climates to smaller mammals in mountains in warmer climates.

We further explored these patterns by plotting the relationship between mean body size and temperature, and found it to be U-shaped (Fig. 4), which led us to investigate both sides of the temperature gradient. First, we used split-line regression in order to find the most likely temperature breakpoint in the relationship of this variable with mammal mean body size. This breakpoint was found at 10.9 °C. Then, we built environmental models for the areas below and above this threshold temperature (covering 86% and 14% of the region, respectively). In the cold Nearctic (Table 2b), we obtained two equally likely models that described similar proportions of variance (61%) and were overwhelmingly dominated by a negative relationship of body size with temperature, as indicated by the higher standardized regression coefficient of this variable. Moreover, simple regression analysis revealed that temperature alone described much of the variance of mean body size in this region (57%). This suggests a pre-eminent role for the heat conservation mechanism in the cold Nearctic. In contrast, in the warmer Nearctic (Table 2c), we found only a single 'best' model which described 54% of variance (Table 2c). In this case, temperature had a positive sign but was of secondary importance compared to range in elevation, which had the highest standardized coefficient and a negative association with body size. This indicated a trend for animals to be smaller in mountain ranges than in the plains, consistent with the habitat availability hypothesis for the warmer part of the Nearctic.

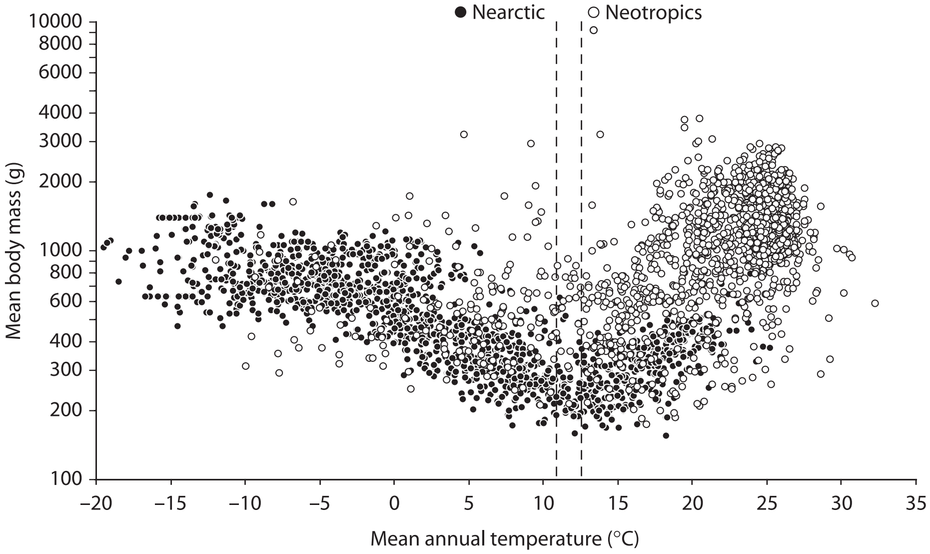

Figure 4 Mean body mass (in g) as a function of mean annual temperature in the Nearctic and Neotropics. The dashed lines are threshold temperatures marking a shift in the relationships with mean body size in each region (Nearctic 10.9 °C; Neotropics 12.6 °C) identified by split-line linear regressions (see text). The below-threshold (cooler) Nearctic area is larger and colder (1144 cells; regional average temperature ± 1 SD, –1.3 ± 7.1 °C; minimum, –19.4 °C) than its Neotropical equivalent (192 cells; regional average temperature 4.6 ± 6.9 °C; minimum –11.9 °C). In contrast, the warmer part of the Nearctic to the right of the threshold is also colder but smaller (385 cells; regional average temperature 16.5 ± 3.2 °C; maximum 35.3 °C) than the Neotropical area (1390 cells; regional average temperature 22.9 ± 3.4 °C; maximum 32.3 °C).

Finally, our models also captured secondary relationships of mean body size with actual evapotranspiration (AET) and seasonal variability in vegetation (GVIcv) in all Nearctic areas. However, it is unclear what these relationships mean, given the low standardized coefficients of AET and GVIcv, as well as their collinearity with temperature (Table 1a).

The Neotropics

The single best model for this region described 46% of the variance in mean body size, and had a 91% probability of being the best model (Table 2d). This model included mean annual temperature, range in elevation, the interaction term between these variables, and GVI, although the standardized regression coefficients identified the interaction between temperature and topography as having the strongest relationship with body size. Additionally, the negative sign of this interaction term reflects that mean body sizes tend to decrease towards mountainous areas with warm macroclimates (e.g. in the tropical Andes), which is again consistent with the habitat availability hypothesis. Range in elevation ranked second and had a positive coefficient, in contrast to both the negative simple correlation between mean body size and range in elevation in this region (see Table 1b) and to the concentration of small-sized mammals in the mountains and of large-sized mammals in the tropical lowlands (see Fig. 1). A possible explanation would be that mean body sizes are relatively larger in the mountains when controlling for the other environmental variables. However, strong collinearity between range in elevation and its interaction with temperature ($r = 0.930$, $n = 1582$) cast doubts about any biological interpretation. The standardized regression coefficient for temperature was even lower and positive, in clear contrast to the model for the whole Nearctic (see Table 2a). The best model also included GVI, but with a low standardized coefficient, thus suggesting that the independent effect of plant production is marginal in this region.

Similar to the Nearctic, the relationship between body size and temperature was U-shaped in the Neotropics (Fig. 4), although split-line regression analysis found that the threshold temperature marking the shift in the relationship was slightly higher in this case (12.6 °C). The below-threshold domain included a low number of cells (192, representing 22% of the region) that comprised a nearly continuous strip covering the Andes south to the equator (171 cells), southern Patagonia, and Tierra de Fuego (not shown). Notably, temperature was not included in any of the four best models found for this area (Table 2e), which might be related to the reduced extent of the temperature gradient found there (see Fig. 4). Yet, all the models did include GVI and AET, both with negative coefficients, but this was difficult to interpret as all models explained body size poorly ($R^2 = 24\%$ in all cases). This low explanatory power might be another consequence of the narrow climatic gradient in this area. As for the above-threshold Neotropics (1390 cells), only one model was selected, with a 99.5% chance of being the best model (Table 2f). According to its standardized coefficients, this model was clearly dominated by the interaction between temperature and topography, which had a negative sign, while range in elevation and temperature rated second and third, both with positive signs. This matches the model found for the whole Neotropics (see Table 2c), which is not unexpected given that 78% of the Neotropical cells had above-threshold temperatures (see Fig. 4). Our interpretation of this result was therefore the same as that made above for the entire region.

DISCUSSION

Our clearest result at the level of a biogeographical region is the strong difference between the Nearctic and the Neotropics with respect to patterns of mammal mean body size. Whereas temperature is the strongest predictor of body size in the Nearctic, with the animals becoming larger towards colder latitudes, Bergmann's rule is not observed in the Neotropics, where mean body sizes increase towards the warmer tropical areas (Fig. 1). Blackburn and Hawkins (2004) found strong support for Bergmann's rule in their interspecific analysis of the mammal fauna of northern North America, but their study did not include warm regions. However, in a study involving a larger latitudinal span in the Western Palaearctic, Rodríguez *et al.* (2006) found nonlinear relationships between mammal mean body size and temperature, with a clear Bergmann's trend occurring in the northern, colder half of this region, but not in the south. They proposed that the Bergmann's heat-conservation mechanism should generate gradients of increasing mean body size with decreasing temperature only in areas with cold climates. Bearing in mind that the Nearctic is a much colder biogeographical region than the Neotropics (average temperatures 3.2 °C and 20.7 °C, respectively), this is supported by our data.

This said, our results also suggest that the different body size trends of the Nearctic and Neotropics have more to do with the particular environmental characteristics of each region than with their dissimilar faunas (e.g. the presence of primates in the Neotropics and the absence of them from the Nearctic), or with their evolutionary histories before or after the late Cenozoic, i.e. when the Great American Biotic Interchange occurred (Marshall *et al.*, 1982; Croft, 2001). For example, in the Nearctic, the data indicate that mean body sizes do not display uniform trends across the region that can be linked to regional evolutionary history. Instead, we found a clear temperature threshold (10.9 °C) that divides the Nearctic into two areas with opposing relationships between mean body size and the environment. Thus, whereas in the northern part of the region mean body sizes increase with cold, in the warmer south topography is the strongest predictor, just as the habitat availability hypothesis predicts (see below). Moreover, temperature is positively related to mean body size in the models generated for the warmer area, likely reflecting a spurious side-effect of the influence of topography on body size gradients, as within the same macroclimate mountains are typically cooler than lowlands. Interestingly, relationships with topography resemble the dominant trend in the Neotropics, where the effects of this factor were even stronger, possibly because the Neotropics are warmer and have stronger elevational gradients (see below).

We also found nonlinear relationships between body size and temperature in the Neotropics, which again were characterized by a temperature threshold (12.6 °C) below and above which the association of body size with the environment differs. Yet it should be noted that, compared with its equivalent in the Nearctic, the colder part of the Neotropics is much smaller and comprises a narrower and warmer temperature gradient (see Fig. 4) mostly represented by cells in the Andes (89%). These characteristics, either individually or in concert, might have obscured Bergmann's trends at the scale of our study, or even precluded them entirely (see Medina *et al.*, 2007). Since all environmental models for the cooler part of the Neotropics performed poorly, we cannot discriminate between these possibilities. Irrespective of this, the existence of similar temperature thresholds, as well as the leading role of topography in the Neotropics and in the warmer part of the Nearctic, both suggest that body size gradients are controlled by similar environmentally driven mechanisms (chiefly associated with combinations of temperature and topography) across the Western Hemisphere.

The nonlinear relationships of body size with temperature reported by Rodríguez *et al.* (2006) for the mammal fauna of the Western Palaearctic suggest that the same environmental controls might be operating in other regions of the world (see their Fig. 3). To explore this further, we applied split-line regression to the Palaearctic data set (for details see Rodríguez *et al.*, 2006) and found a temperature threshold very similar to those found in the Western Hemisphere (10.0 °C). Below this threshold, the mean body size–temperature relationship was very strong and negative ($r = -0.830$, $n = 287$) while the relationship was very weak above the threshold ($r = 0.199$, $n = 99$). Thus, Rodríguez *et al.*'s (2006) supposition that the heat conservation mechanism proposed by Bergmann operates only in cold climates is supported in both the Old and New Worlds.

In contrast to the patterns in lowlands, body size gradients are reversed moving into mountains. The likely explanation is that mountains, especially in the tropics, support large numbers of small-ranged species (Hawkins & Diniz-Filho, 2006). The reasons for this seem straightforward: stronger climatic gradients generate greater habitat zonation which means more, but smaller, habitats that accumulate large numbers of habitat specialists. However, as the macroclimate cools moving away from the tropics, there is less habitat zonation and montane habitats become more similar to lowland habitats, thus allowing more broadly distributed species to inhabit both mountains and lowlands. Because larger-sized species tend to have larger geographical range sizes (see, e.g., Hernández-Fernández & Vrba, 2005), it is likely that mammal mean body sizes are smaller in the mountains of the warmer Nearctic and the Neotropics because habitats are not large enough for many larger species. The right-skewed body size distributions observed in the mountain ranges of these areas (see Figs 2 and 3) are consistent with this explanation. Moreover, if reduced habitat areas lead to the prevalence of small body sizes in warm mountains, then the greater importance of topography for mean body size variation in the Neotropics might be associated with the greater habitat zonation and, hence, smaller habitats found in the Andes (Janzen, 1967; see also Ghalambor *et al.*, 2006). This can also account for the increase of mean body size with increasing temperature across South America, as it suggests that temperature does not directly influence body size in warm climates but acts indirectly via effects on habitat size and structure. Interestingly, Medina *et al.* (2007) recently found reversed Bergmann's trends at the inter- and intraspecific levels in a genus of rodents (*Ctenomys*) in the southern Neotropics. Although they did not consider range in elevation, they found strong positive associations between body size and ambient temperature variables, which they interpreted to be effects of factors not included in their study. It is possible that topographical variability was such a missing factor.

In conclusion, the complex geographical distribution of the mean body size of the Western Hemisphere mammal fauna supports previous findings in the Palaearctic reporting Bergmann's trends in cold macroclimates but not in warmer macroclimates (Rodríguez *et al.*, 2006). Moreover, in both the Western Hemisphere and the Western Palaearctic we found similar temperature thresholds (between 10 and 12.5 °C) marking the transition between Bergmann-like patterns (the heat conservation hypothesis) and no direct relationship between temperature and average body sizes. And even in regions where temperature and body size are not directly linked, there may still be indirect relationships due to the influences of climate on habitat structure (the habitat availability hypothesis). Thus, we propose that there are at least two environmental drivers of body size gradients across broad latitudinal extents, with their relative influence being dependent on macroclimate; temperature influences body size in cold regions whereas topographically driven habitat variation influences patterns in warm areas.

ACKNOWLEDGEMENTS

This study was supported by the Spanish Ministry of Education and Science (grants REN2003-03989/GLO and CGL2006-03000/BOS to M.Á.R.; FPU fellowship: AP2005-0636 to M.A.O.-T.; and sabbatical grant: SAB2003-0213 to B.A.H.). We also thank M. Hernández Fernández and A. G. Boyer for valuable suggestions and comments.

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BIOSKETCHES

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Editor: Tim Blackburn

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Species with body mass or body length data found in the literature. Body masses are provided for all species.

Appendix S2 Species considered as synonyms, subspecies or conspecifics of species with known body masses (see column labelled 'Equivalent weighted species').

Appendix S3 Species considered 'similar to' or 'belonging to the group' of species with known body masses (see column labelled 'Equivalent weighted species').

Appendix S4 Species for which we were unable to find any direct or indirect indication of species' size.

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