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PAPER



# The geographic distribution of mammal body size in Europe

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## ABSTRACT

**Aims** To describe the pattern of mean body size of native mammals in Europe, and to investigate its relationships with environmental predictors related to four hypotheses: (1) dispersal; (2) heat conservation; (3) heat dissipation; and (4) resource availability.

**Location** Continental western Europe and Great Britain.

**Methods** We used range maps to estimate the mean body size (average log mass) of mammals in 386 cells of 12,100 km<sup>2</sup> each. Environmental conditions in each cell were quantified using nine historical, climatic and primary production variables. We attempted to tease apart the effects of these variables using correlation, multiple regression and spatial autocorrelation analyses.

**Results** In the part of the continent covered by ice during the Pleistocene, body mass decreases southwards, and annual average temperature explains 73% of the variance in body size, consistent with the heat-conservation hypothesis. However, in warmer, non-glaciated areas the best predictor is an estimate of seasonality in plant production, but it explains only 18% of the variance. Carnivores, omnivores and herbivores show similar relationships, but the pattern for herbivores is substantially weaker than for the other groups.

**Main conclusions** Overall, the relationship between mean body size and temperature is non-linear, being strong in cold environments but virtually disappearing above a temperature threshold.

## Keywords

Bergmann's rule, body size gradients, climate, heat tolerance, macroecology, mammals, spatial autocorrelation.

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## INTRODUCTION

Body size is a fundamental trait of an organism (McNab, 1971; Lindstedt & Boyce, 1985; Cushman *et al.*, 1993), and identifying the forces influencing the spatial distribution of body sizes may have implications for understanding the organization of ecological communities (Lawton, 1990; Brown & Nicoletto, 1991). Research related to the geography of body size is usually formulated around Bergmann's rule, which states that the body sizes of endothermic animals increase from warm to cold parts of the world (Bergmann, 1847). Bergmann conceived this as an interspecific pattern, but Rensch (1938) reformulated it to describe geographic variation of body size within species (Blackburn *et al.*, 1999). This later version of the rule has received the most

attention, although the processes underlying it, and even its very existence, are still debated (Ashton *et al.*, 2000; Meiri & Dayan, 2003; Meiri *et al.*, 2004). In contrast, the interspecific pattern has been less studied and only a handful of studies have focused on endotherms (mammals: Zaveloff & Boyce, 1988; Cotgreave & Stockley, 1994; Blackburn & Hawkins, 2004; birds: Cousins, 1989; Blackburn & Gaston, 1996; Gaston & Blackburn, 2000). Consequently, we still do not know the patterns of interspecific body size variation for mammal or bird faunas in most parts of the world, much less what factors drive them.

In this paper, we first describe the pattern of mean body size of native mammals in Europe, and then investigate its relationships with environmental predictors. We use a 'community' approach (*sensu* Blackburn & Hawkins, 2004) by examining the mean

body size of species occurring in equal-area grid cells of  $110 \times 110$  km each. We also compare the mean body sizes of all mammal species with the separate patterns for carnivores, omnivores and herbivores. We focus the analysis on four hypotheses that have been proposed to explain broad-scale body size gradients of endotherms: (1) dispersal, which assumes that large-bodied species have been more able to recolonize far northern Europe following the retreat of the Pleistocene ice sheet (Blackburn & Hawkins, 2004); (2) heat conservation, which assumes that large-bodied species tolerate cold climates better due to the reduction of the surface area to volume ratio (Bergmann, 1847) and/or thicker insulation layers (Blackburn *et al.*, 1999); (3) heat dissipation, which assumes that evaporative cooling is more difficult in warm, moist climates and small-bodied species will have higher rates of heat loss (Brown & Lee, 1969; James, 1970); and (4) resource availability, which assumes that large animals metabolize fat stores at a lower weight-specific rate, and therefore large-bodied species should be more frequent as seasonal shortages in resource availability increase (Lindstedt & Boyce, 1985; Dunbrack & Ramsay, 1993).

## MATERIALS AND METHODS

### Mammal species data

Range maps for 142 non-marine mammal species native to Europe were obtained from an atlas by Mitchell-Jones *et al.* (1999). This atlas covers all of Europe except European Turkey, Belarus, Russia and the Ukraine (see Fig. 1). The maps were digitized into ArcGIS 8.3 and rasterized at  $110 \times 110$  km grain size. We used this cell size instead of the smaller original one provided in the atlas (i.e. UTM cells with an average size of  $50 \times 50$  km) to minimize the potential effects of insufficient sampling in some territories (see Mitchell-Jones *et al.*, 1999). We excluded all islands except Great Britain, which we believe has enough extension and proximity to the mainland to warrant that body size patterns are not affected by island effects. We also excluded all coastal cells containing < 50% of the land mass of inland cells, resulting in 386 cells for analysis. Because we included all mammal species present in the study territory, we avoided potential bias occurring when analysing partial data sets (see Meiri *et al.*, 2004).

Body mass (in grams) and diet data were obtained from field guides (primarily Schilling *et al.*, 1987; supplemented with Burton, 1978; Nowak, 1991; Palomo & Gisbert, 2002). When a range of body masses was provided for a species, we assigned the midpoint. Also, when male and female masses were provided, we averaged the midpoints of both measurements. Data for two eastern European species (*Microtus rossiaemeridionalis* and *Mus macedonicus*) were provided by Kostadin Valchev, who extracted them from an unpublished atlas of the mammals of Bulgaria. Average  $\log_{10}$ -transformed mass (hereafter called mean body size) was calculated in each grid cell for four mammal species groupings: namely, all species, carnivores, omnivores and herbivores. It is well documented that, on large geographical scales, the frequency distribution of mammal body sizes is skewed to the right (see Kozłowski & Gawelczyk, 2002), so following Blackburn

and Hawkins (2004) we used averages of  $\log_{10}$ -transformed mass values to minimize the influence of large species in the calculation of mean body sizes.

### Environmental variables

We selected eight variables that can be related to four hypotheses that we considered the most plausible explanations for body size gradients. The hypotheses and their associated variables are as follows:

1 Dispersal — we used time since glacial retreat (cell age), estimated by mapped changes in ice coverage at 1-Kyr intervals since the last glacial maximum (Peltier, 1993). This variable measures the time an area has been available to be occupied by animals after the retreat of the late Pleistocene ice sheets. Therefore, for those grid cells that remained unglaciated (i.e. available) during this period we assigned an age of 20,000 years; that is, the age corresponding to the time of maximum ice coverage in Europe. The data are available at: [ftp://ftp.ncdc.noaa.gov/pub/data/palaeo/ice\\_topo](ftp://ftp.ncdc.noaa.gov/pub/data/palaeo/ice_topo).

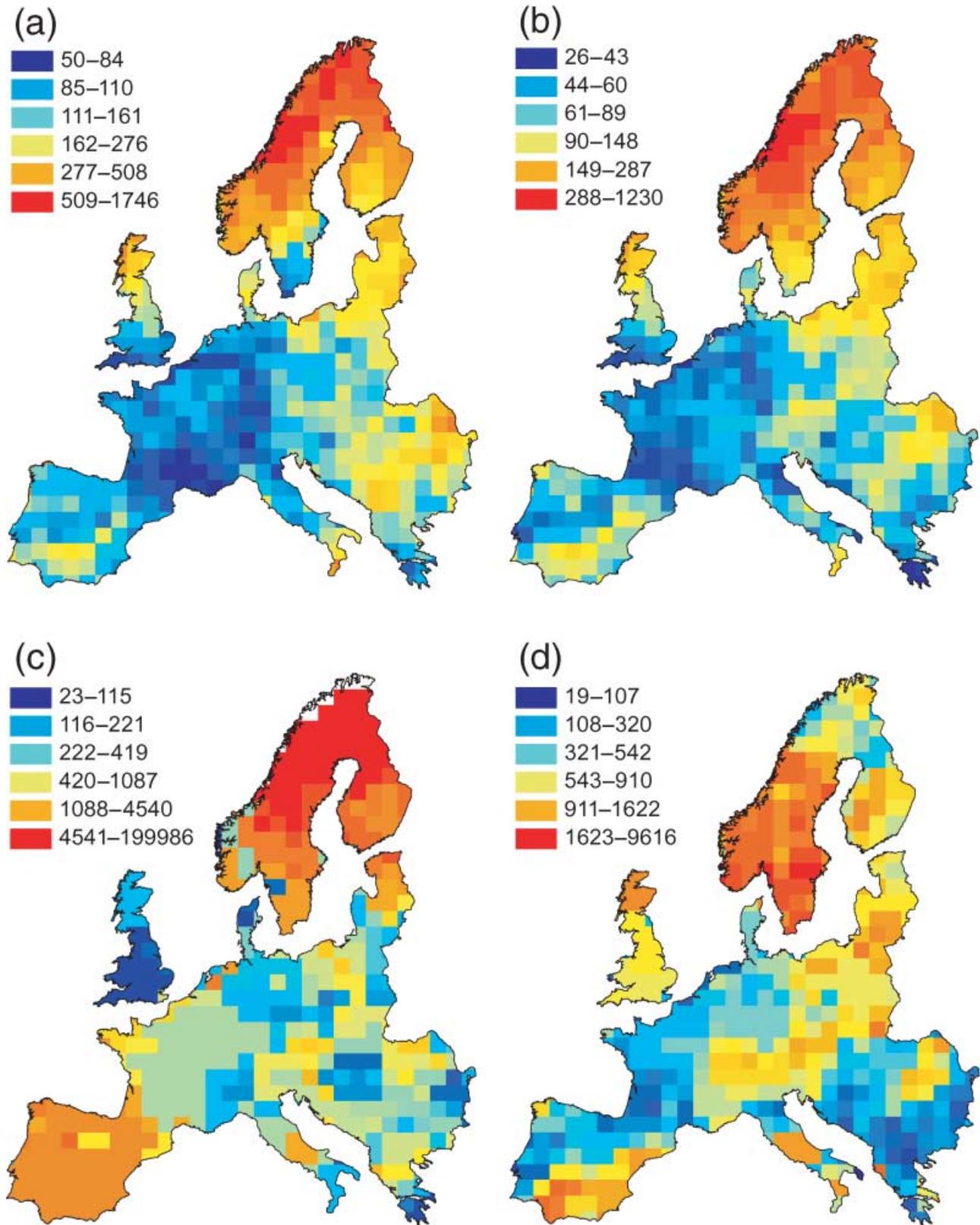
2 Heat conservation — grid cell averages of mean annual temperature, mean January temperature and potential annual evapotranspiration (PET) were used as measures of heat and ambient energy. Mean annual and January temperatures were highly correlated with each other ( $r_{\text{Pearson}} = 0.948$ ,  $P < 10^{-17}$ ) for which we only kept mean annual temperature for analyses. Temperature data were obtained at: <http://www.grid.unep.ch/data/summary.php?dataid=GNV15>, and PET at: <http://www.grid.unep.ch/data/summary.php?dataid=GNV183>. We also used range in elevation to measure mesoscale climatic variation within the cells (Turner & Hawkins, 2004). Range in elevation was estimated as the difference between maximum and minimum elevation within a grid cell from data available at: [http://www.ngdc.noaa.gov/seg/cdroms/ged\\_iiia/datasets/a13/fnoc.htm](http://www.ngdc.noaa.gov/seg/cdroms/ged_iiia/datasets/a13/fnoc.htm).

3 Heat dissipation — we averaged annual precipitation and actual evapotranspiration (AET) for each cell as water and water–energy measures. Precipitation data are available at: <http://www.grid.unep.ch/data/summary.php?dataid=GNV174>, and AET data at: <http://www.grid.unep.ch/data/summary.php?dataid=GNV183>.

4 Resource availability — we used the coefficient of variation of the Global Vegetation Index ( $GVI_{cv}$ ) as a measure of seasonality in plant production. We also used annual GVI to test for the effects of total annual plant production on mammal body mass. GVI is derived from radiometer data from the NOAA Polar Orbiting Environmental Satellites (NCDC Satellite Data Services Division, 1985–88) and is associated with the density and greenness of the plant canopy, total standing biomass, green leaf–area index (LAI) and percentage vegetation cover. Annual GVI and  $GVI_{cv}$  were estimated from monthly values from April 1985 to December 1988. The data are available at: [http://www.ngdc.noaa.gov/seg/cdroms/ged\\_iiia/datasets/a01/mgv.htm](http://www.ngdc.noaa.gov/seg/cdroms/ged_iiia/datasets/a01/mgv.htm).

### Data analyses

We used simple correlation/regression and stepwise multiple regression to identify minimally adequate explanatory models.



**Figure 1** Variation of mammal mean body size in Europe for (a) all species ( $n = 142$ ); (b) carnivores ( $n = 72$ ); (c) omnivores ( $n = 19$ ); and (d) herbivores ( $n = 51$ ). The maps were elaborated using cell averages of  $\log_{10}$ -transformed mass values. Numbers included in the legend of each map are mass values in grams obtained after antilog transformation.

We checked for non-linearities in the relationships between response and explanatory variables by adding quadratic terms to the linear models when necessary. Because of spatial autocorrelation in the data, non-significant variables can appear significant in correlation and regression analyses. Thus, we used a modified *t*-test (Dutilleul, 1993) to obtain unbiased estimates of the significance of simple correlations. This test cannot be applied to non-linear or multiple regression models, so it was not possible to generate the corrected significance levels in all cases. Even so, we are more interested in the explanatory power of the variables rather than in probability levels. When generating multiple regression models, we evaluated each variable based on the coefficient of determination and stopped when the addition of a variable (including a quadratic term if the relationship was nonlinear) did not improve the model  $R^2$  by at least 5%. We also used the technique described by Diniz-Filho *et al.* (2003) to evaluate the sources of spatial autocorrelation in the data. We used the Spatial Autocorrelation Analysis Program (SAAP) 4.3 (Wartenberg, 1989) to generate correlograms of the raw body size data at 6–12 distance classes (depending on the size of the territory being analysed). We then recalculated Moran's *I* on the residuals after fitting the multiple regression model. If no detectable spatial autocorrelation remains in a distance class, then the spatial pattern of mean body size can be explained by environmentally-driven spatial autocorrelation across that distance. In contrast, spatial autocorrelation remaining at any distance class among the residuals indicates that the environmental model does not adequately describe the pattern in mean body size at that scale, and spatially patterned variables not included in the model are contributing to the body size pattern.

Finally, mean body size in a grid cell may be sensitive to richness in that cell because, as richness increases, the mean body size must shift towards the overall mean of body size of all species in the continent. In this case, the relationship between body size and any environmental variable could be an artefact of the random loss of species in cells of low species richness. So, following Hawkins *et al.* (2005), we used a randomization procedure to obtain the expected mean body size in each cell by sampling without replacement the species in the overall species pool according to the species richness. The procedure was repeated 10,000 times, creating a statistical distribution of null body sizes for each cell. A normalized *Z*-score for each cell was calculated by subtracting observed and expected body sizes, divided by its standard error. Thus, *Z*-scores higher than 1.96 indicate that there is a 95% chance that the body size in the cell is higher than would be expected if species found there were a random sample of the overall species pool in Europe.

## RESULTS

Mean body size for all species shows a clear Bergmann's rule-like pattern from intermediate to high latitudes, and a more heterogeneous distribution at lower latitudes (Fig. 1a). There is also a west to east trend of increasing mean body size in central Europe, although this gradient is weaker. Similar patterns were found for carnivores (Fig. 1b), omnivores (Fig. 1c) and, to a lesser extent, herbivores (Fig. 1d).

**Table 1** Simple regressions of predictor variables against mammal mean body size. The coefficients of determination and significance levels are provided. Variables are ranked by their coefficient of determination, and non-linear models are indicated by the inclusion of squared terms. Corrected probabilities are based on the modified *t*-test developed by Dutilleul (1993). Grid-based data sets are frequently spatially autocorrelated, so that adjacent cells are pseudo-replicated units in space, and regression analyses need to be tested with a reduced number of degrees of freedom (see Diniz-Filho *et al.*, 2003). This test defines analytically the correct number of degrees of freedom (in brackets) based on the spatial autocorrelation structure in the data, and provides corrected probabilities. This test cannot be used for polynomial regression models

Variable	$r^2$	Probabilities	
		Uncorrected	Corrected (d.f.)
Age	0.776	< 0.0001	0.031 (3.5)
Mean annual temperature + temp <sup>2</sup>	0.689	< 0.0001	—
Potential evapotranspiration + PET <sup>2</sup>	0.657	< 0.0001	—
Global vegetation index	0.540	< 0.0001	0.044 (5.7)
Actual evapotranspiration	0.378	< 0.0001	0.117 (5.6)
GVI <sub>cv</sub> + GVI <sub>cv</sub> <sup>2</sup>	0.076	< 0.0001	—
Annual precipitation	0.069	< 0.0001	0.267 (17.2)
Range in elevation	0.005	0.082	0.672 (23.3)

Age is an estimate of the number of years before present when an area became available to animals as the ice sheets retreated during the late Pleistocene climate warming. GVI<sub>cv</sub> is the coefficient of variation of the Global Vegetation Index, and measures seasonality in plant production.

Mean body size for all species was significantly correlated with seven of the eight environmental variables (Table 1). However, after correcting for spatial autocorrelation (in those cases in which it was possible), variables describing less than 50% of the variance became non-significant. Four variables explained  $\geq 54\%$  of the variance in mean body size when analysed individually: age, mean annual temperature, potential evapotranspiration and GVI. In the multiple regression, age was the primary explanatory variable with mean annual temperature having a secondary role (Table 2). The pattern of spatial autocorrelation for the mean body sizes for all species was characteristic of a cline, with positive autocorrelation at shorter distances and gradually becoming negative at larger distances (Fig. 2a). The two-factor environmental model reduced the spatial autocorrelation in all distance classes, especially at moderate to long distances. The largest amounts of residual positive and negative spatial autocorrelation remained in short and intermediate distance classes, respectively. Mapping these residuals (Fig. 2b) revealed a large cluster of negative residuals in central Europe, suggesting that a factor not included in our analysis is needed to account for the spatial variation in body size in this area. The analyses of carnivore, omnivore and herbivore mean body sizes generated similar regression models (Table 2) and patterns of residual autocorrelation (not shown).

Cell age measures the time when Pleistocene glaciers retreated from an area, making it available to be occupied by plants and

**Table 2** Minimally adequate regression models of predictor variables against mean body size values for different mammal groups and areas of Europe. The numbers are coefficients of determination indicating the increment of variance described by the model after adding each variable. Only variables explaining  $\geq 5\%$  of the variance have been included (see text). The first variable entering into the model is indicated in bold type. The sign of the relationships are indicated parenthetically. Quadratic relationships have two signs: the first corresponding to the linear term, and the second to the quadratic term. Conventions as in Table 1

Region and mammal group	Variables in the model (sign)			Elevation range
	Age	Temperature	PET	
Europe				
All species	<b>77.6</b> (-)	5.0 (-, +)		
Carnivores	<b>63.1</b> (-)	9.3 (-, +)		
Omnivores	<b>64.5</b> (-, +)	8.8 (-, +)		
Herbivores	<b>29.1</b> (-)			
Glaciated areas				
All species		<b>72.5</b> (-)		
Carnivores		<b>72.2</b> (-)		
Omnivores		<b>67.9</b> (-)		6.2 (-)
Herbivores		<b>13.0</b> (+, -)		9.4 (+)
Non-glaciated areas				
All species				<b>18.0</b> (-, +)
Carnivores			6.6 (+)	<b>27.2</b> (-, +)
Omnivores				<b>33.3</b> (-)
Herbivores		<b>8.7</b> (-, +)		5.0 (-, +)

animals. However, age is highly significantly correlated with other strong predictors of mean body size (Table 3), so it is possible that the association between age and body size does not reflect the direct effects of time passed since the ice retreated, but the combined effects of other factors. To examine this issue, we conducted separate analyses for areas that were covered by ice and non-glaciated areas. If age indeed explains the pattern of recolonization, it should be most obvious in the glaciated region.

Annual average temperature explained 16.1% more variance in mean body size than cell age in the formerly glaciated part of the continent (72.5% vs. 56.4%; see Fig. 3a). Further, temperature entered the multiple regression models for all mammal groups (Table 2). All these regression models have high explanatory power except, again, that for herbivores. Age, on the other hand, did not enter into any model. Finally, autocorrelation analyses revealed similar results as for the entire continent (Fig. 2c). These results taken together suggest that temperature is the primary driver of mean body size in the formerly glaciated regions rather than cell age, with mammal species being larger in colder climates.

Temperature performed poorly in the non-glaciated areas, where the range variation in mean body size is much lower than in the glaciated region, and the coldest areas (e.g. the Alps) do not differ in mean body size from the flatter, warmer parts of the

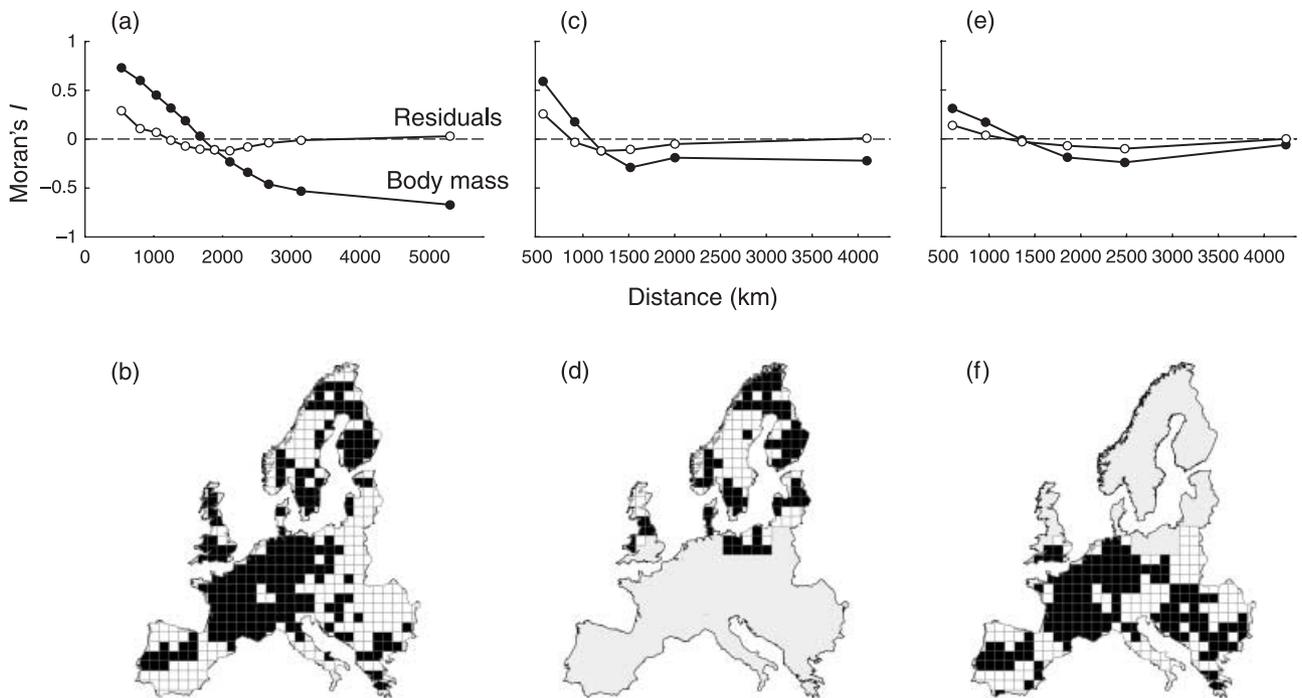
region (see Fig. 3a). Therefore, the data indicate that the relationship between mean body size and mean annual temperature across Europe is non-linear. The Z-scores for Scandinavia are also significantly greater than expected if the lower species richness found in this territory was a random sample of European species (Fig. 3b), confirming the existence of Bergmann's rule in northern Europe.

Seasonality in plant production ( $GVI_{cv}$ ) accounted for most of the variance explained by the minimum adequate models in the non-glaciated region, with energy variables playing a secondary role in the case of carnivores and herbivores (Table 2). However, all these models have low explanatory power. Autocorrelation analyses also indicate that the spatial pattern in the body size data was fairly weak to begin with (Fig. 2e), which explains why the spatially patterned environmental variables included in the multiple regression models have low explanatory power. Also, the Z-scores provide no evidence for Bergmann's rule in the south. Even so, as in the analysis of the entire continent, negative residuals remain clustered in central Europe (Fig. 2f). In sum, seasonality in plant production may have some influence on mammal body size in the non-glaciated region, but the relationship is much weaker than that of temperature farther north, and there is little spatial pattern in body size within the warmer parts of the continent.

## DISCUSSION

Bergmann's rule is clearly evident at high latitudes. These results are similar to those in the northern Nearctic (Blackburn & Hawkins, 2004). Further, our approach is conservative; the pattern would be even more pronounced if we had been able to include data incorporating intraspecific variation in body sizes instead of assuming that each species is the same size everywhere. Because individual mammal species also tend to follow Bergmann's rule (Ashton *et al.*, 2000; Freckleton *et al.*, 2003; Meiri & Dayan, 2003; Meiri *et al.*, 2004), there seems little doubt that in the far north the average body size of mammals increases towards the pole.

Of the four hypotheses we examine the best support is for the heat-conservation hypothesis, at least in the far north. When we analyse the entire region, cell age is the best descriptor of mean body size with mean annual temperature rating second, implicating dispersal limitation as being important. However, when we analysed the glaciated region separately, age was not as good as temperature at predicting body size variation. Moreover, temperature alone (for all species and carnivores), or together with range in elevation (omnivores and herbivores) are the only variables remaining in the minimum regression models (Table 2). Range in elevation probably represents altitudinally driven climatic variation within an area, with mountains having more cold spots than flatter areas of similar macroclimate. Therefore, the small but significant proportion of variance explained by range in elevation in the cases of omnivores and herbivores may reflect local effects of cold on their respective mean body sizes, with larger species becoming more frequent in higher, colder spots. Thus, in general, our data support the heat-conservation hypothesis for the cold parts of Europe once covered by ice,



**Figure 2** Correlograms for all-species mean body size and for residuals after fitting the significant variables in the models shown in Table 2. Maps below the correlograms indicate the geographic distribution of the positive (white) and negative (black) residuals after fitting the models. (a, b) All of Europe; (c, d) glaciated region; and (e, f) nonglaciated region.

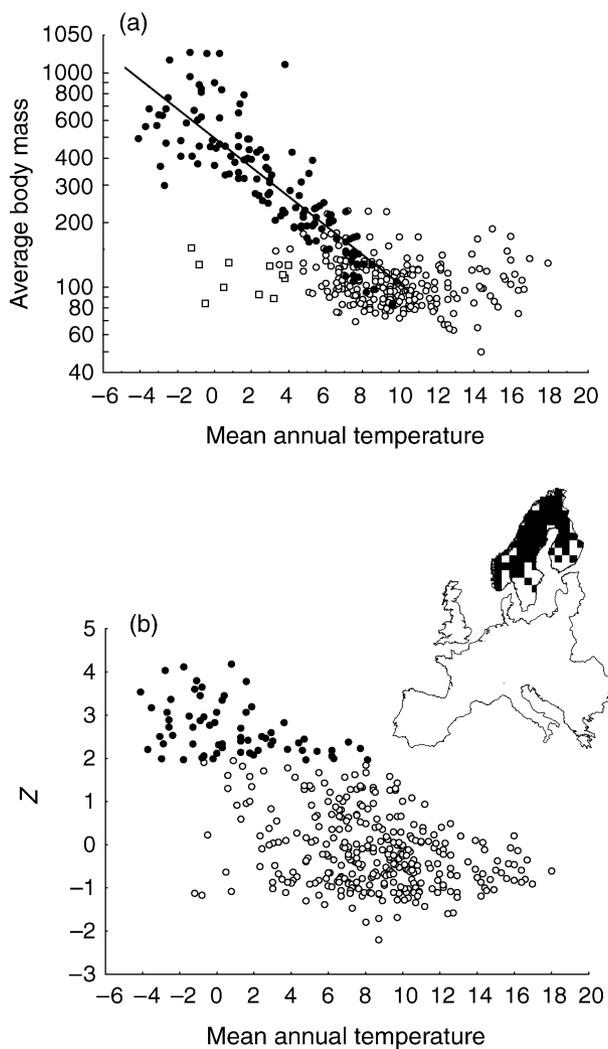
**Table 3** Correlation matrix for predictor variables. High correlations ( $r > 0.55$ ) are indicated in bold type;  $n = 386$  in all cases. Conventions as in Table 1

Variable	Age	Temp	PET	Precip	AET	GVI	GVI <sub>cv</sub>	R. Elev
Age	1							
Mean annual temperature	<b>-0.559</b>	1						
Potential evapotranspiration	<b>-0.675</b>	<b>0.793</b>	1					
Annual precipitation	-0.301	0.055	0.168	1				
Actual evapotranspiration	<b>-0.636</b>	0.436	<b>0.672</b>	0.474	1			
Global vegetation index	<b>-0.581</b>	<b>0.603</b>	<b>0.581</b>	0.457	<b>0.741</b>	1		
GVI <sub>cv</sub>	0.168	-0.221	-0.174	0.242	0.410	0.231	1	
Range in elevation	-0.256	-0.080	0.302	0.410	0.295	0.061	-0.115	1

although strong collinearity between cell age and current temperatures makes it difficult to disentangle their independent effects.

Blackburn and Hawkins (2004) found similarly that annual average temperature was the best predictor of mammal average log mass in the glaciated Nearctic. Further, annual average temperature explained 69% of the variance in body size, closely matching the variance explained by temperature in the glaciated part of Europe (72.5%), whereas cell age was a poor predictor in Canada (explaining 20% of the variance). The similarity of the results in the two regions suggests that the strong, negative dependencies of mean body size on temperature are not idiosyncrasies of their mammal faunas, but reflect general patterns.

There is a clear non-linearity in the relationship between mammal body size and temperature (Fig. 3a), suggesting that this variable becomes a key determinant of body size below a certain temperature threshold. McNab (1971) also reported that, in intraspecific comparisons, positive associations of mammal body sizes with latitude are more common at higher latitudes. However, this author argued that this trend was not temperature related but an artefact of competitive release at the northern parts of the range of a species. In contrast, Ashton *et al.* (2000) detected no significant trend and Geist (1987) reported the reverse; that is, that the trend of individuals of mammal species towards greater sizes reverses between 60 and 65° N parallel. Our study is interspecific, for which our results cannot be compared



**Figure 3** (a) Relationship of mammal mean body size (in grams) with annual average temperature ( $^{\circ}\text{C}$ ) in the areas of Europe covered by ice in the last glaciation (black symbols) and in the non-glaciated areas (white symbols). The vertical axis is in  $\log_{10}$ -scale. The regression line was generated using the glaciated data only. The overall relationship is non-linear, with mean body size being associated with mean annual temperature in the glaciated region but not in the rest of the continent. Cells comprising the Alps (squares) form a clear cluster in the bottom left and have been differentiated from the rest. (b) Relationship between mean annual temperature and the normalized difference ( $Z$ -scores) comparing the observed body size of resident species against the expected body size from a random selection of species. Significant scores ( $P < 0.05$ ) are designated by black symbols, and the geographical locations of the significant cells are indicated in black on the map.

directly with these former findings, and we are not aware of any interspecific studies reporting changes of the nature of the relationship between average body size and temperature (or latitude) at continental scales. Even so, our results and their apparent contrast with former findings in intraspecific studies make the question of whether temperature influences mammal body size only below certain temperature levels worthy of further attention.

In conjunction with the shift from a strong relationship between temperature and body size to a very weak one, the body-size pattern is much noisier in non-glaciated areas (see Fig. 1). There is an association of body size with plant production seasonality (as measured by  $\text{GVI}_{\text{c}}$ ) in all mammal groups, but it does not run in the direction predicted by the resource availability hypothesis (animals should be larger in more variable habitats, but we found the converse over most of the range of variation of plant production). More importantly, the regression models have low explanatory power ( $\leq 34\%$ ), suggesting that none of the hypotheses we examine explain the body size pattern well in central and southern Europe. We believe it is significant that the cells with the smallest mean body sizes for both all mammals and carnivores are primarily in southern Britain, France, Germany and the Low Countries (see Fig. 1). This also corresponds with the densest human populations in Europe and, possibly, with the areas most strongly modified by humans (see Araújo, 2003). This also merits more attention.

Herbivores appear to be a special case among mammals. Their mean body size patterns are broadly consistent with those exhibited by other groups, but are less clear. Similarly, the regression models are qualitatively similar to those for other groups, but are much weaker, particularly in the formerly glaciated region (see Table 2). Thus, the processes influencing body size in other mammal groups also affect herbivores, but to a lesser extent. We suspect that this may be due to the specific biological traits of the herbivores occupying northern Europe. Along these lines, Meiri and Dayan (2003) found that Rodentia was the only order that failed consistently to conform to Bergmann's rule in their meta-analysis of intraspecific studies of body size. They suggested that the fact that most rodents burrow account for this, because burrows allow these species to remain in more favourable microclimates most of the time. There are 21 herbivore species in the formerly glaciated region of Europe, 14 of which create complete or partial burrows (12 rodent + two lagomorph species; van den Brink, 1968; Corbet & Ovenden, 1980). In contrast, the proportion of burrowing non-herbivore species in the same area is significantly lower (17 of 44 carnivore and omnivore species;  $P < 0.032$ , Fisher's exact test). Therefore, it could be that the noisier spatial patterns and weaker dependence on temperature by herbivores in the glaciated areas are due to the burrowing capabilities that permit many of them to escape from extremely cold winter temperatures.

In conclusion, most studies of Bergmann's rule for endotherms have been at the intraspecific level, and many have simply tested for the existence of the rule. Consequently, there has been a great deal of debate fuelled by the fact that, although the rule applies to many endothermic species, some species do not follow it (Ashton *et al.*, 2000; Meiri & Dayan, 2003; Meiri *et al.*, 2004). The European mammals provide three reasons for understanding this. First, the mechanism conceived by Bergmann (1847) implied a simple, linear relationship between body size and climate. However, the relationship between mean body size and temperature is probably nonlinear, at least over very large scales. The fact that Europe comprises a broad range of climates (from Mediterranean to Arctic) makes it possible to see this. On the other hand, studies concentrated in either cold or warm areas

only may give contradictory results, hence fuelling the debate on the existence of the Bergmann's rule. We think it may be necessary to reformulate the rule to admit nonlinear relationships.

Secondly, if body size is in fact constrained primarily by the tolerance of endothermic animals to temperature, strong associations between these variables should exist, as shown by many studies. However, temperature tolerance depends on multiple factors (see Gaston & Blackburn, 2000), and there may be species and even higher taxa with strategies to cope with cold other than growing large. The weak relationship of herbivore body size with temperature suggests this; so, a lack of fit with Bergmann's rule is possible, even at the levels of Order (e.g. Rodentia) or trophic group (e.g. herbivores).

Finally, humans have modified nature to the point that pristine habitats probably no longer exist in the world (Vitousek, 1994), and many large mammals have been driven extinct since the Pleistocene (see, e.g. Barnosky *et al.*, 2004; Lyons *et al.*, 2004). Such modifications are particularly intense in central Europe, perhaps strong enough to alter biogeographic patterns of body size (e.g. Schmidt & Jensen, 2003). Our study was not designed to examine this issue, but we believe it likely, given the absence of large mammals in this area, especially carnivores. If true, this has obvious potential implications for biodiversity conservation and, in particular, for evaluation of the human footprint on nature.

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## BIOSKETCHES

**Miguel Á. Rodríguez's** main interests include the study of factors and processes conditioning patterns of biodiversity at local, regional and global scales. Recent research involves investigating the effects of habitat destruction and fragmentation on aggregate properties of faunas at broad scales.

**Irene L. López-Sañudo** is a graduate student at the University of Alcalá. Her PhD thesis focuses on the impacts of Mediterranean forest fragmentation on mammal diversity.

**Bradford A. Hawkins** is interested in large-scale patterns in ecology, primarily the latitudinal diversity gradient. Recent projects involve attempts to narrow the set of the most plausible hypotheses and to reconcile points of view focusing on processes operating contemporaneously vs. those operating over evolutionary time. He also is interested in the biology and ecology of insect parasitoids.

Editor: Tim Blackburn