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RESEARCH PAPER

Energy and interspecific body size patterns of amphibian faunas in Europe and North America: anurans follow Bergmann's rule, urodeles its converse

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ABSTRACT

Aim To describe broad-scale geographical patterns of body size for European and North American amphibian faunas and to explore possible processes underlying these patterns. Specifically, we propose a heat balance hypothesis, as both heat conservation and heat gain determine the heat balance of ectotherms, and test it along with five other hypotheses that have a possible influence on body size gradients: size dependence, migration ability, primary productivity, seasonality and water availability.

Location Western Europe and North America north of Mexico.

Methods We processed distribution maps for native amphibian species to estimate the mean body size in 110 × 110 km cells and calculated eight environmental predictors to explore the relationship between environmental gradients and the observed patterns. We used least squares regression modelling and model selection approaches based on information theory to evaluate the relative support for each hypothesis.

Results We found consistent body size gradients and similar relationships to environmental variables within each amphibian group in Europe and North America. Annual potential evapotranspiration, a measure of environmental energy, was the strongest predictor of mean body size in both regions. However, the contrasting responses to ambient energy in each group resulted in opposite geographical patterns, i.e. anurans increased in size from high- to low-energy areas in both continents and urodeles showed the opposite pattern.

Main conclusions Our results support the heat balance hypothesis, suggesting that the thermoregulatory abilities of anurans would allow them to reach larger sizes in colder climates by optimizing the trade-off between heating and cooling rates, whereas a lack of such strategies among urodele faunas would explain why these organisms tend to be smaller in cooler areas. These findings may also have implications for the role of climate warming on the global decline of amphibians.

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Amphibians, bauplans, Bergmann's rule, body size gradients, Europe, heat balance hypothesis, macroecology, North America.

INTRODUCTION

The reduced surface area to volume ratios, and hence greater heat conservation potential, of large-bodied animals led Bergmann (1847) to predict that, within groups of closely related endotherms, larger species would abound in colder climates and smaller species in warmer areas. Following the same logic, Rensch (1938) elaborated an intraspecific version of this rule, stating that, within a particular species, larger individuals should be more frequent in cold climates. Since then, the variation of animal body sizes at broad scales has become of central interest for biogeographers and ecologists (Mayr, 1956; Rosenzweig, 1968; McNab, 1971; Ashton *et al.*, 2000; Meiri & Dayan, 2003, Blackburn & Hawkins, 2004; Rodríguez *et al.*, 2006), although both the generality of the patterns and possible causal mechanisms are still debated (Blackburn *et al.*, 1999).

Bergmann's gradients and their converse have been observed in ectotherms, both at the intraspecific (Mousseau, 1997; Ashton, 2002; Belk & Houston, 2002; Ashton & Feldman, 2003; Angilletta *et al.*, 2004; Blanckenhorn & Demont, 2004) and interspecific

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levels (Lindsey, 1966; Cushman *et al*., 1993; Barlow, 1994; McDowall, 1994; Hawkins & Lawton, 1995; Diniz-Filho & Fowler, 1998; Cruz *et al*., 2005, Olalla-Tárraga *et al*., 2006). These findings not only suggest that climate might be a key determinant of body size distributions within cold-blooded animals, but also emphasize the need for hypotheses that are specifically tailored for animals with limited capability to thermoregulate, and whose body temperature depends on heat conservation as well as on heat gain. Accordingly, we propose here the heat balance hypothesis to account for the patterns exhibited by thermoregulators (i.e. animals with good thermoregulating abilities) and thermoconformers (animals with body temperatures fluctuating more closely to ambient temperature). For thermoregulators, this hypothesis states that larger animals would be favoured in cold environments due to their reduced surface to volume ratios and greater heat conservation potentials. Conversely, among thermoconformers, smaller organisms would be favoured in cold areas as their greater surface to volume ratios allow them to have shorter heating times. The first part of this hypothesis coincides with the heat conservation mechanism proposed by Bergmann for endotherms, and can also be extended to ectotherms that are able to control body temperature effectively through physiological and/or behavioural adjustments (see, e.g., Bartholomew, 1982; Huey, 1982; Hutchinson & Dupré, 1992). For example, the few species of anurans (frogs and toads) in which these issues have been investigated do exhibit thermoregulatory abilities to enhance heat gain and heat conservation (e.g. basking or selecting temperatures in available microhabitats) (Brattstrom, 1963; Hutchinson & Dupré, 1992; Stebbins & Cohen, 1995). However, since similar thermoregulating activities are believed to be uncommon amongst urodeles (newts and salamanders) (Brattstrom, 1963; Hutchinson & Dupré, 1992; Stebbins & Cohen, 1995), the second part of the hypothesis would be applicable for them. This indeed generates two predictions. First, that body size would increase towards colder areas in the case of anurans and towards warm territories in that of urodeles and, second, that these patterns should be inversely related to those climatic factors more directly conditioning amphibian thermoregulation, that is, heat and sunlight (Hutchinson & Dupré, 1992).

Along with this hypothesis, we also investigate five other explanations for body size gradients in ectotherms. First, the size dependence hypothesis (Olalla-Tárraga *et al*., 2006) suggests that below a certain body size threshold heat conservation leads to an increase in size towards cold environments, whereas beyond this threshold the trend reverses due to the longer heating times of larger animals and the narrow activity windows available at high latitudes that leave the animals with no time to meet other needs. Second, the migration ability hypothesis, which assumes that large-bodied species disperse better and have been more able to recolonize far northern territories after the retreat of the late Pleistocene ice sheets (Cushman *et al*., 1993; Blackburn *et al*., 1999). Third, the primary productivity hypothesis, which assumes that body mass must be maintained by a sufficient food supply and predicts greater body sizes in more productive areas (Rosenzweig, 1968). Fourth, the seasonality hypothesis (also known as the starvation resistance hypothesis), which, in the case of amphibians, relates growing season length and the time available for physiological development, and predicts small-bodied species to be more frequent in more seasonal environments where animals have less time to grow (Mousseau, 1997). Finally, the water availability hypothesis, which assumes a greater desiccation tolerance for larger amphibians due to their reduced surface to volume ratio, and predicts them to be more frequent than smaller species in areas with lower water availability (Ashton, 2002).

To describe amphibian body size patterns and to test these hypotheses, 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 × 110 km each (see also Olalla-Tárraga *et al*., 2006, Rodríguez *et al*., 2006). We analyse separately the two major orders of living amphibians, i.e. anurans (order Anura) and urodeles (order Caudata).

MATERIALS AND METHODS

Species data

Distribution maps for native amphibian species of western Europe and North America were obtained from the same sources used in a previous investigation of reptile body size gradients in these territories (Olalla-Tárraga *et al*., 2006), that is, Gasc *et al*. (1997), Conant and Collins (1998) and Stebbins (2003). The methodology used for map processing was described in detail in Olalla-Tárraga *et al*. (2006), and rendered 386 cells in Europe and 1430 in North America, all of them having an equal area of 110 × 110 km. Additionally, this grain size overrode all slight discrepancies existing between different sources (Conant & Collins 1998; Stebbins 2003) in the mapped range distributions of species present in eastern and western North America (1 salamander and 15 anurans).

The amphibian data base comprised 49 species in Europe (31 anurans and 18 urodeles) and 216 species in North America (81 anurans and 135 urodeles). This data base does not include five small North American frogs living in the far north (*Rana sylvatica*, *Pseudacris crucifer*, *Pseudacris triseriata*, *Hyla versicolor* and *Hyla chrysoscelis*). These species are known to be tolerant of freezing, a physiological trait believed to explain their presence in colder territories (Storey & Storey, 1996). Since our study seeks to establish the role of body size in determining amphibian distribution, we excluded these species because it is already known that their distribution is associated with other traits (see Appendix S1 in Supplementary Material).

Body size data were extracted from field guides (Behler & King, 1994; Conant & Collins, 1998; Arnold, 2002; Stebbins, 2003, see Appendix S2 in Supplementary Material). We used maximum snout-to-vent length (SVL) for anurans, and maximum total length (TL) for urodeles. The latter were the only size estimates available for all species and, in the case of North America, the only ones that were comparable between the various field guides that provided these data (Behler & King, 1994; Conant & Collins, 1998; Stebbins, 2003). For those species in which length measurements were provided for males and females or for different subspecies, we averaged the values to obtain a single estimate of body size. On the other hand, in order to assess the indicative value of TL, we also extracted the SVL of the urodele species for which these data were available (42 species from western North America) and correlated both size estimates. This correlation was very high ($r = 0.92$), thus indicating that both measurements are likely to generate similar results. In addition, maximum length values are believed to be reasonable indicators of the size potential of organisms with indeterminate growth such as amphibians, and have been used in previous studies of macroecological patterns in ectothermic vertebrates (Boback & Guyer, 2003; Reed, 2003).

With regard to our response variables, we took into account that the frequency distribution of animal body sizes is often right skewed on large geographical scales (Brown, 1995). This indeed makes it inadvisable to use arithmetic means as those might be strongly influenced by the presence of large-sized species. Blackburn and Hawkins (2004) have already tackled this problem in a similar interspecific study of the mean body sizes of northern North American mammals, and their solution consisted of $\log_{10}$-transforming the body size values of the species before averaging them (see also Olalla-Tárraga *et al*., 2006; Rodríguez *et al*., 2006). Following the same protocol, we calculated the average $\log_{10}$ body length (hereafter called mean body size) for anurans and urodeles for each grid cell in each biogeographical region.

Environmental predictors

We included eight potential explanatory variables, selected because they can be related to the six following hypotheses (see Olalla-Tárraga *et al*., 2006, for further details on data definition and sources). (1) *Heat balance*: to account for thigmothermy and heliothermy; i.e. the two mechanisms involved in heat gain in amphibians (Hutchinson & Dupré, 1992), mean annual temperature and the Priestley–Taylor annual potential evapotranspiration (PET; see Lu *et al*., 2005) were used as indicators of heat, and heat and light inputs in the environment, respectively (Rodríguez *et al*., 2005). Range in elevation within each cell was also used as an estimate of mesoscale spatial climatic variation (Turner & Hawkins, 2004). (2) *Size dependence*: the analyses were based on the same variables, complemented with visual inspections of their relationships with amphibian body size to look for body size thresholds. (3) *Migration ability*: time since glacial retreat (cell age) was estimated by mapped changes in ice coverage at specific intervals since the last glacial maximum (e.g. Rodríguez *et al*. 2006) in Europe (Peltier, 1993) and North America (Dyke *et al*., 2003). (4) *Primary productivity*: the global vegetation index (GVI) was utilized as a proxy for plant productivity. (5) *Seasonality*: the number of months available for plant growth in each grid cell was estimated to measure the length of the growing season. (6) *Water availability*: annual precipitation and Thornthwaite's annual actual evapotranspiration (AET) were used as indicators of water and water–energy balance, respectively. Whereas annual precipitation reflects the limits of water stress to amphibian body size, AET indicates the need for animals to have access to water as well as to tolerable temperatures (Rodriguez *et al*., 2005).

Statistical analyses

Statistical analyses were run separately for anurans and urodeles in each biogeographical region. We first used Pearson correlations to evaluate the relationships between mean body size and the eight explanatory variables. To control for spatial autocorrelation in the body size and environmental data, we used a modified *t*-test (Dutilleul, 1993) to obtain unbiased estimates of the significance of the correlation coefficients.

We also used ordinary least squares multiple regression to generate environmental models including multiple predictors. For this we took into account the strong collinearity among several of the variables in our data set (Table 1), which makes the use of common model simplification procedures, such as step-wise regression methods, inadvisable. Instead, we used the Akaike information criterion (AIC) to evaluate the relative support for each hypothesis by comparing the models resulting from combinations of the environmental variables. Due to the presence of spatial autocorrelation in the data, we calculated AICs using corrected error variances according to methods described in Hawkins and Diniz-Filho (2006) (see also Olalla-Tárraga *et al*., 2006 for additional details). We compared the resulting AIC values of each model using ΔAIC, the difference between the AIC of each model and the minimum AIC found. We also used ΔAIC values to calculate the Akaike weighting of each model (w_i), which is standardized across the candidate set of models and can be interpreted as the probability that model i is actually the best explanatory model.

Additionally, we used the standardized regression coefficients of the models as indicators of the relative importance of each variable for mean body size (Neter *et al*., 1996). Because the value of these coefficients is sensitive to collinearity (Neter *et al*., 1996), we did not include highly correlated variables in the analyses. Thus, due to the high correlation between PET and mean annual temperature in both continents (Table 1), we performed a separate modelling exercise with either variable. The results were equivalent (which was expected due to the similar biological meaning of these variables) and we only included here those obtained with PET, while the models generated using temperature are provided as supplementary material (see Appendix S3 in Supplementary Material).

Because only the migration ability hypothesis is associated with past climatic conditions, whereas the rest are linked to current climatic variables, and present and past climates are spatially correlated, we used the following procedure to disentangle current and historical effects on variation in amphibian body size. We first evaluated the relative support for each of the hypotheses related to present climates by including only current variables in the model selection process. Then, once we had identified the best environmental model based on present climatic conditions, we conducted partial regression analyses to partition the variance explained by present climate vs. cell age. This allowed us to test the extent that the historical effect is independent of the

Table 1 Pearson correlation coefficients of environmental variables and mean body size. Significance levels are corrected for spatial autocorrelation using the modified *t*-test developed by Dutilleul (1993): (a) Europe; (b) North America

(a)

Variable	Size, anurans	Size, urodeles	Temp.	AET	PET	Range	Prec.	GVI	GSL
Temp.	–0.67	0.56	1						
AET	–0.66*	0.46*	0.44	1					
PET	–0.77*	0.73*	0.79*	0.67*	1				
Range	–0.11	0.21	–0.08	0.29	0.30	1			
Prec.	–0.17	0.07	0.06	0.47	0.17	0.41	1		
GVI	–0.61	0.27	0.60	0.74*	0.58	0.06	0.46	1	
GSL	–0.42	0.21	0.75**	0.37	0.43	–0.16	0.23	0.69*	1
Cell age	–0.75	0.56	0.76*	0.71	0.74	0.18	0.33	0.71	0.67

(b)

Variable	Size, anurans	Size, urodeles	Temp.	AET	PET	Range	Prec.	GVI	GSL
Temp.	–0.66**	0.63	1						
AET	–0.61**	0.62	0.8*	1					
PET	–0.62**	0.65*	0.94**	0.73	1				
Range	0.21	–0.36	–0.04	0.30	0.02	1			
Prec.	–0.24	0.43	0.44	0.65**	0.33	–0.03	1		
GVI	–0.27	0.15	0.50*	0.62**	0.39	–0.03	0.43**	1	
GSL	–0.54**	0.54	0.69*	0.88**	0.61	0.33	0.62**	0.58**	1
Cell age	–0.44	0.62	0.65	0.46	0.64	0.29	0.12	0.37	0.38

Temp., mean annual temperature; AET, actual evapotranspiration; PET, potential evapotranspiration; Range, range in elevation; Prec., annual precipitation; GVI, global vegetation index; GSL, growing season length.

$^*P < 0.05$; $^{**}P < 0.01$.

explanation provided by measures of current climatic conditions (Hawkins & Porter, 2003). We used simple and multiple regressions to calculate separately the coefficients of determination for the best current climatic model, cell age and climate and cell age combined. Then we used these three coefficients of determination to partition the independent effects of present climates, cell age and the overlap between them.

Finally, we compared spatial autocorrelation patterns in mean body size with those of the residuals of our multiple regression models to evaluate how these models explain spatial variation in body size (Diniz-Filho *et al*., 2003, see also Olalla-Tárraga *et al*., 2006, for further details).

All statistical analyses were performed with STATISTICA (StatSoft, Inc. 2003) and SAM 1.1 (Spatial Analysis in Macroecology; Rangel *et al*., 2006).

RESULTS

Anuran body size and current climate

Mean body size of the European anuran fauna increases towards the north, exhibiting a marked Bergmann's rule pattern (Fig. 1a), with the smallest animals occurring in the Iberian and Italian peninsulas, and the largest in Great Britain and eastern Scandinavia. Mean body size was negatively correlated with all of the environmental variables, but only significantly with PET and AET (Table 1a). Of 64 multiple regressions models, two had a $\Delta\text{AIC} \leq 2$ and explained similar proportions of variance (Table 2). However, Akaike weightings indicated that the model including PET, elevation range, AET, GVI and growing season length was the best model. This model explained 6.8% more variance of anuran body size than PET alone, (66.2% vs. 59.4%, respectively) and its standardized coefficients identified PET as the strongest predictor (Table 2). Moreover, these relationships remained robust after accounting for the effects of variation in species richness across cells with weighted least squares regression (the results are included in Appendix S4 in Supplementary Material).The relationship of anuran mean body size with PET in Europe is shown in Fig. 2(a).

Spatial variation of anuran mean body size also follows Bergmann's rule in North America, although the pattern is patchier than in Europe (Fig. 1b). Indeed, although the smallest sizes appear in the south (especially in the south-east) and the largest ones occur in the north in general, northern areas are not uniformly occupied by large animals. Instead, they are characterized by a large area occupied by intermediate sizes, in which three major patches of large mean body sizes occur (in western and central Canada, and from the Great Lakes to the west coast).

Anuran mean body size was significantly negatively correlated with four variables in North America (Table 1b), and the best

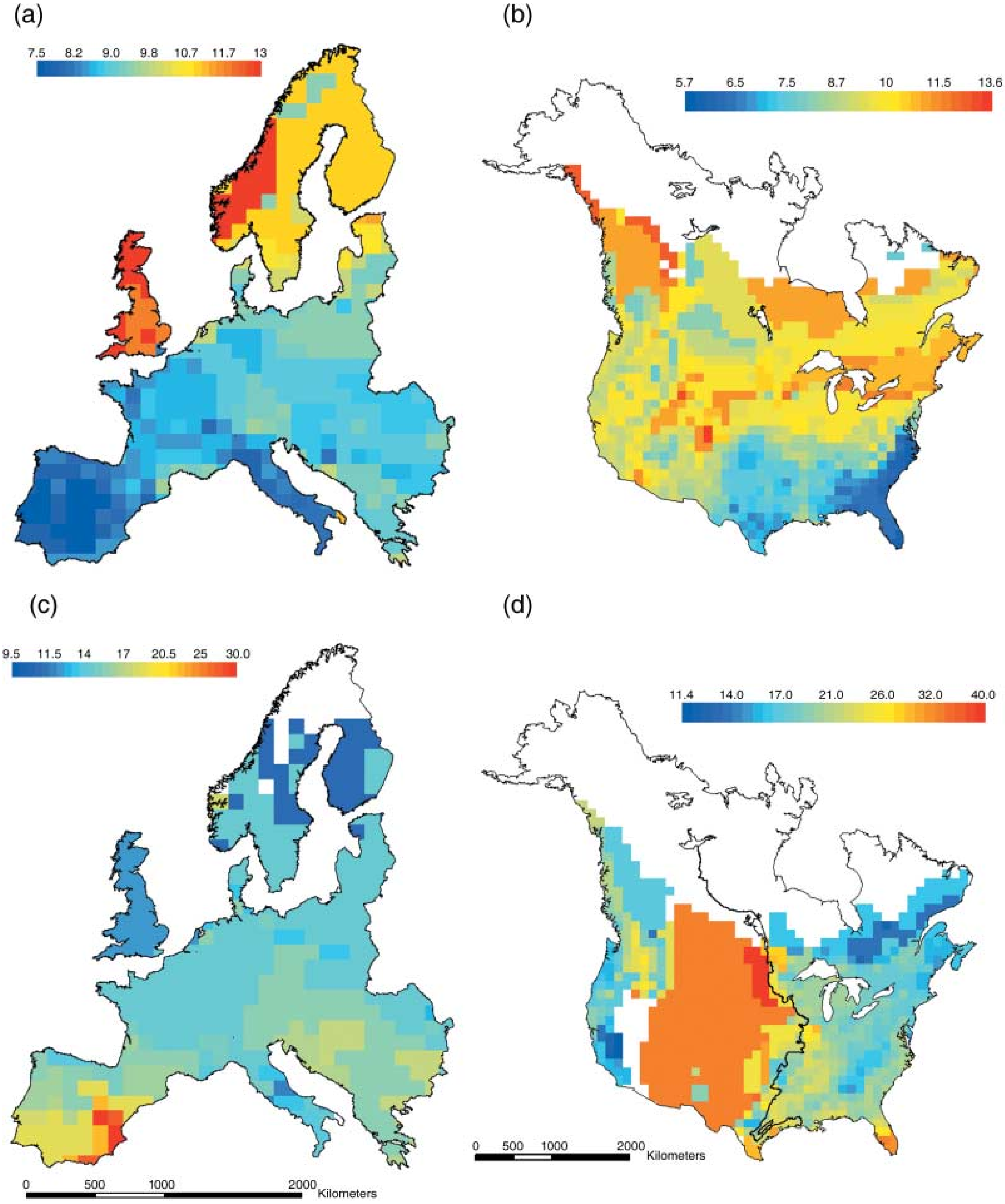

Figure 1 Geographical patterns of amphibian mean body size in Europe and North America: (a) anurans in Europe [number of species (S) = 31]; (b) anurans in North America ($S = 81$); (c) urodeles in Europe ($S = 18$); (d) urodeles in North America ($S = 135$). The maps were built using cell averages of $\log_{10}$-transformed length values. Numbers included in the legend of each map are length values in centimetres obtained after antilog transformation. The black line in (d) represents the eastern border of the Great Plains used to conduct separate analyses for eastern North America (see text).

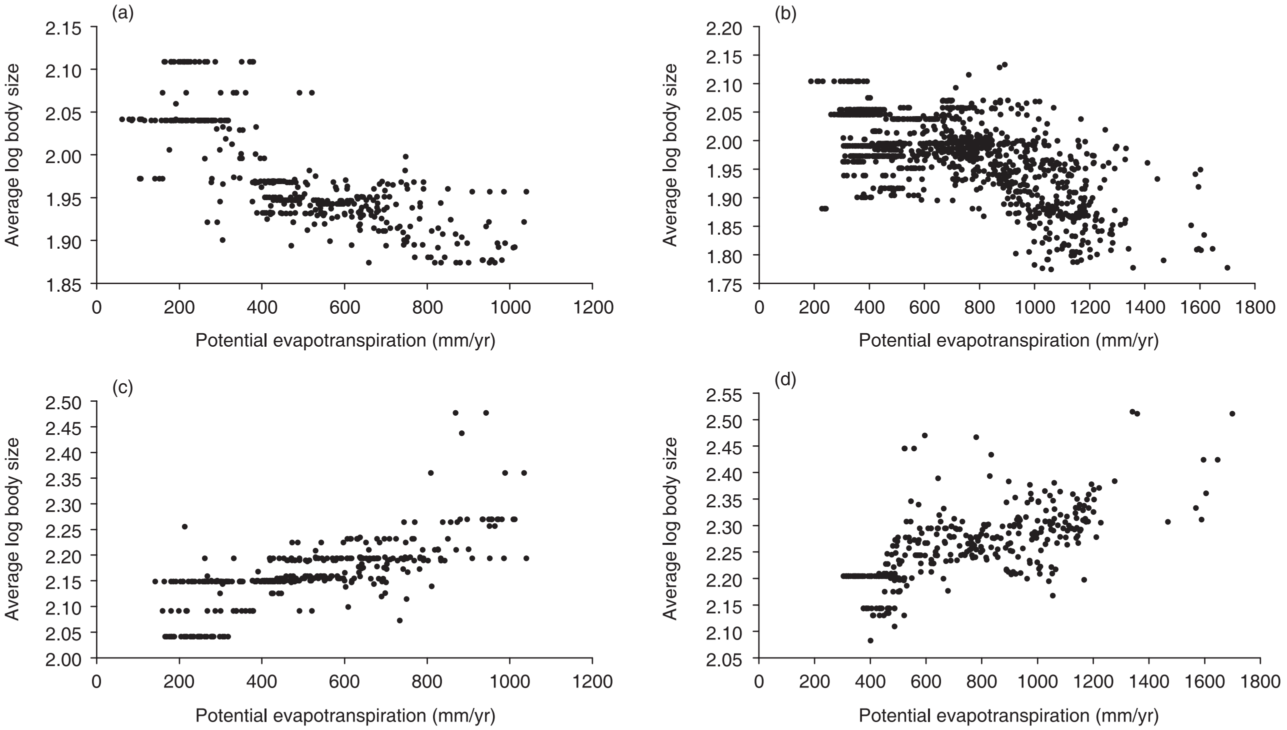

Figure 2 The relationships between amphibian mean body size and potential evapotranspiration (PET) in 110 × 110 km cells for Europe and North America: (a) anurans in Europe; (b) anurans in North America; (c) urodeles in Europe; (d) urodeles in eastern North America. Similar relationships were obtained for mean annual temperature. Note that although urodeles appear to be larger than anurans, the difference arises because the tail is included for urodeles. Overall, anurans cannot be considered as small-sized amphibians when compared with urodeles (Lindsey, 1966; Pough, 1980).

Table 2 Multiple regression models for mean body size (data resolved to 110 × 110 km). Models are ranked in each case by AIC from best- to worst-fitting model, and only the models with ΔAIC < 2 are presented. AICs have been corrected for the presence of spatial autocorrelation in the model residuals. For each variable entering in the model we include their standardized coefficients to evaluate the relative importance of each one. Predictor variable codes are: PET, annual potential evapotranspiration; Range, range in elevation; AET, annual actual evapotranspiration; Prec., annual precipitation; GVI, global vegetation index; GSL, growing season length. See Appendix S2 in Supplementary Material for models including mean annual temperature instead of PET

		Predictors in model									
Group	Region	PET	Range	AET	Prec.	GVI	GSL	AIC	ΔAIC	w_i	R^2
Anurans	Europe	−0.628	0.155	−0.171		−0.168	0.063	−980	0	0.509	0.662
		−0.612	0.143	−0.201		−0.117		−979	1	0.291	0.660
	North America	−0.475					−0.321	−2483	0	0.347	0.469
		−0.480				−0.044	−0.296	−2482	1	0.235	0.471
		−0.473			0.011		−0.329	−2482	1	0.221	0.461
		−0.478			0.017	−0.046	−0.306	−2481	2	0.157	0.471
Urodeles	Europe	0.757	−0.092	0.205	0.057	−0.320	0.103	−919	0	0.428	0.567
		0.783	−0.118	0.164	0.068	−0.243		−918	1	0.343	0.562
	Eastern North America	0.692	−0.192		−0.106			−828	0	0.510	0.475

multiple regression model included PET and growing season length and explained 46.9% of variance (Table 2). On the other hand, the standardized coefficient for PET indicated that this variable is the main driver of variation in anuran body size in North America, even after accounting for species richness patterns with weighted least squares regression (see Appendix S4).

It is worth noting that although we excluded five anuran species known to be freeze-tolerant from the analyses, the patchier patterns detected in northern North America may still be influenced by the occurrence of species with similar but yet unknown capabilities to tolerate cold via physiological mechanisms independent of body size. As might be expected, the results obtained after including these five species support this idea, considering that we found similar but noisier patterns of body size variation (map included in Appendix S1) and our best model (i.e. with PET and length of the growing season) only explained 21.1% of the variance. Moreover, a full model involving all six predictors only raised this amount to 37.4% (also included in Appendix S1); that is, 10% less than the proportion of variance described by the best model when excluding such species (see above).

Urodele body size and current climate

In contrast to anurans, urodele mean body size clearly tends to increase southwards in Europe (Fig. 1c), whereas in North America the most conspicuous feature is a broad patch of larger sizes that extends from south-central Canada throughout the Great Plains and eastern Rocky Mountains to the northern Chihuahuan Desert (Fig. 1d). Most of this patch was made up by a single species, the big tiger salamander (*Ambystoma tigrinum*), a widely distributed species that also appears, albeit more spottily, in the eastern United States (from the Ohio Valley to the Atlantic seaboard), the south-eastern states, and in northern Mexico (see Conant & Collins, 1998; Stebbins, 2003). Besides this feature, there is also a body size gradient similar to that observed in Europe (i.e. mean body size tends to increase southwards) occurring between the eastern border of the Great Plains (we followed the ecoregions division of the Commission for Environmental Cooperation, 1997) and the east coast (Fig. 1d). This part of North America, and particularly the Appalachian Mountains, has the highest urodele richness in the Nearctic and represents a global hotspot of salamander biodiversity (Duellman & Trueb, 1986) (see richness map included in Appendix S4). In fact, as Darlington (1957) has already noted, we found two well-differentiated urodele faunas in North America, one occupying the western half of the continent with no obvious geographical trends in body size, and the other occurring in the east. Such dissimilarities in faunal composition suggest not only that the western mountains and deserts may have impeded faunal exchanges between western and eastern subfaunas, but also that they might impose different constraints on body size variation. Taking this into account, as well as the existence of only one species (*Ambystoma tigrinum*) in most cells to the west of the Great Plains, we decided to concentrate our analysis in the eastern region.

Urodele mean body size was significantly positively correlated with PET and AET in Europe, and with PET in eastern North America (Table 1). The best multiple-regression models for both regions described 56.7% and 47.5% of the variation in mean body size, respectively (Table 2). The standardized coefficients also identified PET as the strongest predictor of body size in both cases (see Fig. 2c,d). Again, weighted least squares regression analyses indicated that these results were not affected by the geographical variation of species richness in either continent (the results are included in Appendix S4).

Spatial analysis

In all cases the pattern of spatial autocorrelation for mean body size was representative of a cline, with positive autocorrelation at shorter distances progressively becoming negative at larger distances (Fig. 3a,c,e,g). The best multiple regression models reduced the spatial autocorrelation in all distance classes, although less strongly in the shortest one, which suggests that factors not included in our analysis are needed to account for the spatial variation in body size at more local scales (see below).

We also mapped the residuals of these models to explore where the unexplained variation occurs. For European anurans, we found three clusters of positive values, in Great Britain, eastern Scandinavia and the Balkan Peninsula, indicating that body sizes are larger than predicted there (Fig. 3b). Similarly, the map for North American anurans revealed four major clusters of large residuals, three located in areas covered by the Laurentide ice sheet in the Pleistocene (two of negative residuals and one of positive values), and the other one in the south-east (negative residuals) (Fig. 3d). In the case of urodeles, larger residuals were mainly found in European peninsulas, especially in Italy (negative residuals) and Scandinavia (positive and negative residuals), and in the region bordering the Great Plains in eastern North America (positive residuals). On the whole, these maps reinforced the suggestion that factors not included in our analyses (e.g. peninsular effects in Europe, and 'contagion' effects of the western urodele fauna in eastern North America) are needed to account for the variation in mean body size in these areas.

Body size and post-Pleistocene climatic change

Strong correlations between cell age and most current climate variables (see Table 1) explain why large amounts of the spatial variation in mean body size of anurans and urodeles are described by the overlap between past and present climates (Fig. 4). Despite this, the proportion of variance that can be independently attributed to cell age is much lower than that corresponding to present climatic factors in all cases. In fact, the addition of cell age to the models only improved their explanatory power by between 1.5 and 4.8%, whereas current variables independently described between 13.2 and 28.3% of the variance. This indicates that historical effects, as measured by the pattern of glacial retreat, on amphibian body size gradients are weak. Further, when we added cell age to the best climatic models, the resulting AIC values were higher than those of the original models, thus reinforcing the idea that cell age has little or no effect on body size variation. Consequently, we conclude that the broad-scale body size patterns of the amphibian faunas of both continents are mainly driven by present climate, with PET being the strongest descriptor.

DISCUSSION

The two major orders of living amphibians — anurans and urodeles — show clear biogeographical patterns of mean body size variation

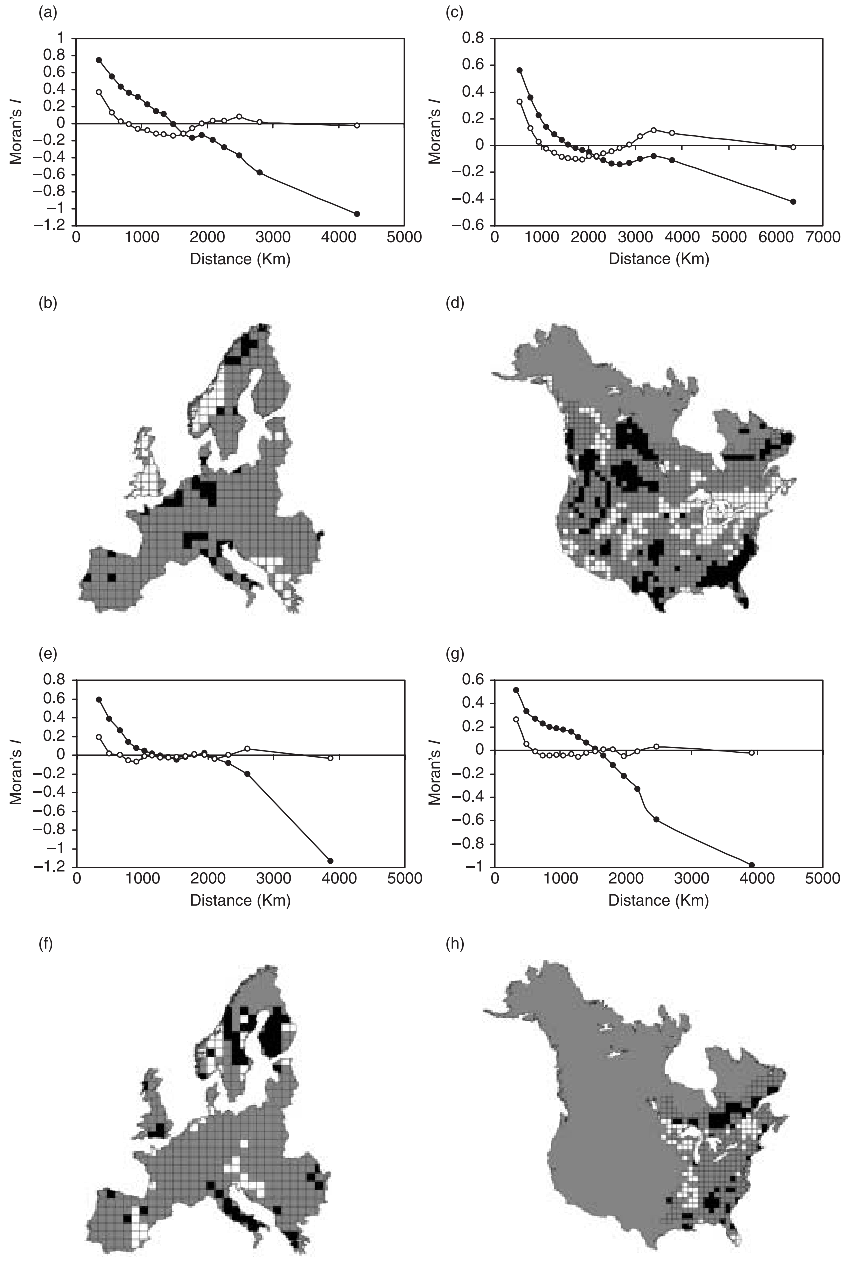

Figure 3 Spatial correlograms using Moran's *I* for mean body size (solid circles) and residuals of the best environmental model (open circles) for: (a) anurans in Europe; (c) anurans in North America; (e) urodeles in Europe; (g) urodeles in eastern North America. Maps below the correlograms show the geographical distribution of the higher positive (> 0.04) (white) and lower negative (< −0.04) (black) residuals of the corresponding model (b, d, f, h).

in North America and, especially, in Europe. Following a clear Bergmann's rule gradient, anurans increase their body size northwards in both regions. In contrast, urodeles exhibit the reverse trend, becoming larger towards southern latitudes in Europe and eastern North America, whereas in the western part of this continent the patterns are patchier. On the other hand, our data also indicate a leading role of current climate in driving these patterns. Specifically, we found a strong association between geographical gradients in body size and the spatial variation of PET, a direct measure of ambient energy (heat and light) which is highly correlated with temperature. However, in accordance with the contrasting patterns we detect for both amphibian groups, the relationships of PET with anuran and urodele body sizes are opposite in sign, so that anurans tend to be larger and urodeles smaller towards low-energy areas.

Of the six explanations for amphibian body size patterns we have examined, the best support is for the heat balance hypothesis. This takes into account that ectotherm body temperature is limited by heat gain as well as heat conservation, and proposes that geographical body size gradients in cold-blooded animals are influenced by the interplay between heating and cooling rates. An essential constraint for larger-sized ectotherms in colder environments has to do with the fact that their low surface to volume ratio confers upon them a reduced capability to gain heat. This is likely to be critical for animals with low thermoregulatory potential (thermoconformers), which are virtually unable to accelerate the heating process, mainly because the difficulties these animals have in reaching active body temperatures might leave them with insufficient time for foraging or reproduction in the short activity windows available in cold

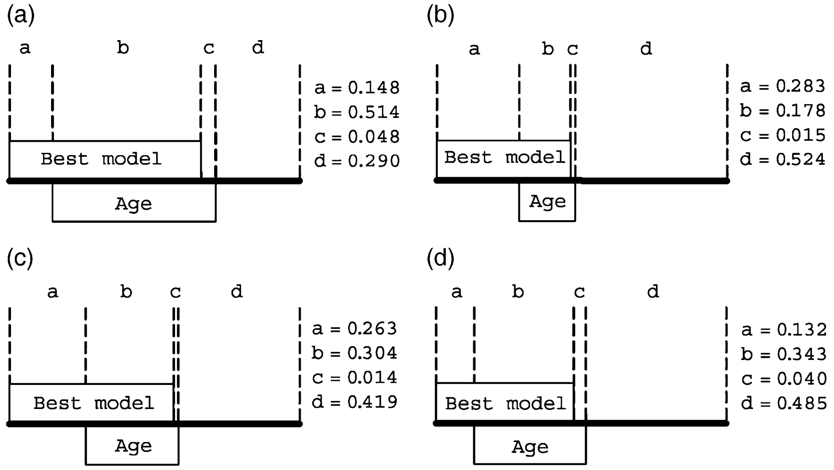

Figure 4 Results of partial regression analyses using the best multiple regression model and cell age as predictors of mean body size: for (a) anurans in Europe; (b) anurans in North America; (c) urodeles in Europe; (d) urodeles in North America. In each case (a) represents the independent proportion of variation in mean body size explained by the best environmental model only; (b) indicates the overlap between the best environmental model and cell age; (c) the variation added by cell age; (d) is the unexplained variance.

regions (cf. Olalla-Tárraga *et al.*, 2006). In contrast, smaller sizes would favour a rapid heating, thus allowing the animals to take advantage of these short time segments in which benign environmental conditions allow them to be active. Urodeles are believed to have low thermoregulatory abilities (Brattstrom, 1963; Hutchinson & Dupré, 1992; Stebbins & Cohen, 1995; but see Spotila, 1972), which agrees with the northwards decrease in mean body size we observe in this group.

In contrast, the ability of some ectotherms to make physiological and/or behavioural adjustments to obtain heat (thermoregulators) could overcome the constraints imposed by large sizes, while these sizes would become advantageous due to the positive influences that their corresponding low surface to volume ratios confer on maintaining body temperature excesses (e.g. Digby, 1955). Accordingly, the heat balance hypothesis predicts Bergmann's patterns when ectothermic organisms are able to achieve some control over heat exchange, a characteristic that has been shown by the anuran species for which thermoregulatory capabilities have been documented (Brattstrom, 1963; Hutchinson & Dupré, 1992; Stebbins & Cohen, 1995). This indeed suggests that heat balance also lies behind the body size trends we observe in this group.

The different bauplans of both amphibian groups might also have played a role in determining their mean body size patterns. Anurans are tailless and squat while, in general, urodeles are more elongated. This affects heat gain since, for the same body mass, the anuran bauplan renders a lower surface to volume ratio and, hence, a lower capability of obtaining heat compared with urodeles. However, as stated before, anurans appear to be able to actively generate body temperature excesses by performing physiological and/or behavioural adjustments that enhance heat gain. Such capabilities not only help to minimize their design limitations for obtaining heat, but might also convert their bauplan into an advantage in low-energy areas because a round body shape is better at conserving animal temperatures. Urodeles, on the other hand, benefit from having an elongated body that allows a better heat acquisition. However, it appears unlikely that, by itself, this design will be able to generate body temperature excesses comparable to those that might be attained through basking, and accordingly we do not observe an increase in mean body size with cold for this group, but the converse pattern.

On the other hand, although body size trends found at the interspecific level have not necessarily been reproduced intraspecifically by all species, the reasoning underlying the heat balance hypothesis could also be extended to explain intraspecific gradients. However, available intraspecific studies reveal Bergmann's trends to be the most frequent ones not only for anuran species, but also for urodeles (reviewed by Ashton, 2002; Morrison & Hero, 2003). This indeed concords with the interspecific patterns we found for anurans, but contrasts with the counter Bergmann's ones shown by urodeles. Bearing this in mind, as well as the reduced number of urodele species that have been analysed intraspecifically to date [e.g. only 18 species were included in Ashton's (2002) review], any conclusions regarding the extension of the heat balance hypothesis to this level will have to wait until more investigations have been performed.

Besides the heat balance hypothesis, environmental energy also constitutes the basis of other explanations for body size gradients. Amongst them, the size dependence hypothesis, which was specifically thought to account for interspecific patterns of thermoregulating ectotherms (Olalla-Tárraga *et al.*, 2006), and similar explanations specifically tailored to the intraspecific level (Blanckenhorn & Demont, 2004; Walters & Hassall, 2006) both predict Bergmann's clines below a certain body size threshold and the converse clines beyond it. However, we can discard the size dependence hypothesis as an explanation for the disparate interspecific patterns between the two amphibian groups because there are no differences in absolute body size between anurans and urodeles (Fig. 2; Lindsey, 1966; Pough, 1980). Likewise, the hypothesis is also refuted at the intragroup level, since we found no size thresholds in the relationships of body size with energy variables within either anurans or urodeles. For anurans, it might be the case that the species present in the studied territories were all below the size threshold marking the transition between Bergmann's clines and the converse ones. This would indeed explain why we only observed Bergmann's trends. For urodeles, this lack of support might be related to their reduced thermoregulatory abilities, while the size dependence hypothesis was explicitly devised for ectotherms exhibiting a good control over heat exchanges (Olalla-Tárraga *et al*., 2006).

An additional intraspecific explanation relating variations in body size with the energy available in the environment is the temperature–size rule. According to this, cold temperatures result in increased adult body sizes by delaying maturity through decreasing rates of growth and development (Atkinson, 1996). This has been experimentally observed among the majority of ectotherm species studied to date (reviewed by Atkinson, 1994), including amphibian species (see Ashton, 2002, and references therein). Consequently, constraints on the rates of growth and development have frequently been proposed to explain intraspecific Bergmann's clines in cold-blooded animals (see e.g. Ray, 1960; Van Voorhies, 1996). However, extrapolation from laboratory responses to geographical gradients entails the risk of elucidating possible mechanisms before actually knowing what the patterns look like in nature (Belk & Houston, 2002; see also Mousseau, 1997). For instance, whereas all amphibian species reared at lower temperatures reached larger adult sizes in controlled laboratory settings (see references in Ashton, 2002), some species studied in natural conditions did not exhibit these patterns (see references in Morrison & Hero, 2003). In the latter review, these exceptions were said to be explained by the effects of factors such as habitat quality or predation pressure. This, along with the reduced number of intraspecific investigations on variation in amphibian body size (Ashton, 2002; Morrison & Hero, 2003), limits the generality of the explanation involving constraints on rates of growth and development. On the other hand, even though this mechanism may still play a role in determining the interspecific patterns displayed by anurans, it cannot account for the converse Bergmann's rule gradients we found for urodeles.

Besides, it is worthwhile noting that the patterns observed are potentially sensitive to phylogenetic autocorrelation effects (i.e. closely related species tend to have similar body sizes and are not statistically independent). Usually, phylogenetic comparative methods have been used in cross-species analyses to control for phylogenetic structure in the data. However, our study does not fit into this category since we conducted a spatial grid-based analysis in which we calculated average body sizes within each cell instead of analysing species values. This prevents the use of traditional phylogenetic comparative methods, and emphasizes the need for developing techniques that allow the incorporation of phylogenetic components in community approaches (see also Ruggiero & Hawkins, 2006). Future studies should address this question.

Our data are also potentially relevant for an understanding of the mechanisms behind the global decline of amphibian populations (Alford & Richards, 1999; Houlahan *et al*., 2000). Increased heat and sunlight (particularly in the ultraviolet spectrum) have been hypothesized to drive amphibian declines (Carey & Alexander, 2003), and we found that the main predictor of body size gradients for both anurans and urodeles is PET, a measure combining the availability of these two variables in the environment. This suggests that the geography of amphibian body size might be particularly sensitive to climate change, a process that involves dramatic changes of temperature and radiation across the planet (Houghton *et al*., 2001).

In sum, our results best support the heat balance hypothesis as an adaptive explanation for the observed body size patterns in anurans and urodeles. We propose that greater thermoregulatory abilities among anurans allow them to reach larger sizes in low-energy areas by actively optimizing the trade-off between heating and cooling rates. In contrast, the lack of such strategies among urodele faunas can explain why their mean body sizes are smaller in the same territories. Although this hypothesis requires further testing, it does not alter the fact that the body size patterns and their associations with PET are highly consistent in two continents, suggesting that the patterns are not regional idiosyncrasies but general trends.

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REFERENCES

Alford, R.A. & Richards, S.J. (1999) Global amphibian declines: a problem in applied ecology. *Annual Review of Ecology and Systematics*, **30**, 133–165.

Angilletta, M.J., Niewiarowski, H.P., Dunham, A.E., Leaché, A.D. & Porter, W.P. (2004) Bergmann's clines in ectotherms: Illustrating a life-history perspective with sceloporine lizards. *The American Naturalist*, **164**, 168–183.

Arnold, E.N. (2002) *A field guide to the reptiles and amphibians of Britain and Europe*. HarperCollins, London.

Ashton, K.G. (2002) Do amphibians follow Bergmann's rule? *Canadian Journal of Zoology*, **80**, 708–716.

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? *The American Naturalist*, **156**, 390–415.

Atkinson, D. (1994) Temperature and organism size — a biological law for ectotherms? *Advances in Ecological Research*, **25**, 1–58.

Atkinson, D. (1996) Ectotherm life history responses to developmental temperature. *Animals and temperature: phenotypic and evolutionary adaptation* (ed. by I.A. Johnston and A.F. Bennett), pp. 183–204. Cambridge University Press, Cambridge.

Barlow, N.D. (1994) Size distributions of butterfly species and the effect of latitude on species sizes. *Oikos*, **71**, 326–332.

Bartholomew, G.A. (1982) Physiological control of body temperature. *Biology of the Reptilia*, Volume 12 (ed. by C. Gans and F.H. Pough), pp. 167–213. Academic Press, New York.

Behler, J.L. & King, F.W. (1994) *National Audubon Society field guide to North American reptiles and amphibians*, 12th edn. Alfred A. Knopf, Inc., New York.

Belk, M.C. & Houston, D.D. (2002) Bergmann's rule in ectotherms: a test using freshwater fishes. *The American Naturalist*, **160**, 803–808.

Bergmann, C. (1847) Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Gottinger Studien*, **3**, 595–708.

Blackburn, T.M. & Hawkins, B.A. (2004) Bergmann's rule and the mammal fauna of northern North America. *Ecography*, **27**, 715–724.

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

Blanckenhorn, W.U. & Demont, M. (2004) Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum? *Integrative and Comparative Biology*, **44**, 413–424.

Boback, S.M. & Guyer, C. (2003) Empirical evidence for an optimal body size in snakes. *Evolution*, **57**, 345–351.

Brattstrom, B.H. (1963) Preliminary review of the thermal requirements of amphibians. *Ecology*, **44**, 238–255.

Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago, IL.

Carey, C. & Alexander, M.A. (2003) Climate change and amphibian declines: is there a link? *Diversity and Distributions*, **9**, 111–121.

Commission for Environmental Cooperation (1997) *Ecological regions of North America: toward a common perspective*. Department of Communications and Public Outreach of the CEC Secretariat, Montreal, Canada (http://www.epa.gov/wed/pages/ecoregions/na_eco.htm).

Conant, R. & Collins, J.T. (1998) *A field guide to reptiles and amphibians of eastern and central North America*, 3rd edn. Houghton Mifflin, Boston, MA.

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

Cushman, J.H., Lawton, J.H. & Manly, B.F.J. (1993) Latitudinal patterns in European ant assemblages: variation in species richness and body size. *Oecologia*, **95**, 30–37.

Darlington, P.J. (1957) *Zoogeography: the geographical distribution of animals*. John Wiley & Sons, New York.

Digby, P.S.B. (1955) Factors affecting the temperature excess of insects in sunshine. *Journal of Experimental Biology*, **32**, 279–298.

Diniz-Filho, J.A.F. & Fowler, H.G. (1998) Honey ants (genus *Myrmecocystus*) macroecology: effect of spatial patterns on the relationship between worker body size and geographic range size. *Environmental Entomology*, **27**, 1094–1101.

Diniz-Filho, J.A.F., Bini, L.M. & Hawkins, B.A. (2003) Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography*, **12**, 53–64.

Duellman, W.E. & Trueb, L. (1986) *Biology of amphibians*. McGraw-Hill, New York.

Dutilleul, P. (1993) Modifying the *t*-test for assessing the correlation between two spatial processes. *Biometrics*, **49**, 305–314.

Dyke, A.S., Moore, A. & Robertson, L. (2003) *Deglaciation of North America*, Geological Survey of Canada (open file 1574). Natural Resources Canada, Ottawa.

Gasc, J.P., Cabela, A., Crnobrnja-Isailovic, J., Dolmen, D., Grossenbacher, K., Haffner, P., Lescure, J., Martens, H., Martínez Rica, J.P., Maurin, H., Oliveira, M.E., Sofianidou, T.S., Veith, M. & Zuiderwijk, A. (eds) (1997). *Atlas of amphibians and reptiles in Europe*, Collection Patrimoines Naturels, 29. Societas Europaea Herpetologica, Muséum National d'Histoire Naturelle & Service du Petrimone Naturel, Paris.

Hawkins, B.A. & Diniz-Filho, J.A.F. (2006) Beyond Rapoport's rule: evaluating range size patterns of New World birds in a two-dimensional framework. *Global Ecology and Biogeography*, **15**, 461–469.

Hawkins, B.A. & Lawton, J.H. (1995) Latitudinal gradients in butterfly body sizes: is there a general pattern? *Oecologia*, **102**, 31–36.

Hawkins, B.A. & Porter, E.E. (2003) Relative influences of current and historical factors on mammal and bird diversity patterns in deglaciated North America. *Global Ecology and Biogeography*, **12**, 475–481.

Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K. & Johnson, C.A. (2001) *Climate change 2001: the scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.

Houlahan, J.E., Findley, C.S., Schmidy, B.R., Meyer, A.H. & Kuzmin, S.L. (2000) Quantitative evidence for global amphibian declines. *Nature*, **404**, 752–755.

Huey, R.B. (1982) Temperature, physiology, and the ecology of reptiles. *Biology of the Reptilia*, Volume 12 (ed. by C. Gans and F.H. Pough), pp. 25–67. Academic Press, New York.

Hutchinson, V.H. & Dupré, R.K. (1992) Thermoregulation. *Environmental physiology of the amphibians* (ed. by M.E. Feder and W.W. Burggren), pp. 206–249. University of Chicago Press, Chicago.

Lindsey, C.C. (1966) Body sizes of poikilotherm vertebrates at different latitudes. *Evolution*, **20**, 456–465.

Lu, J., Sun, G., McNulty, S.G. & Amatya, D.M. (2005) Comparison of six potential evapotranspiration methods for regional use in the southeastern United States. *Journal of the American Water Resources Association*, **41**, 621–633.

Mayr, E. (1956) Geographical character gradients and climatic adaptation. *Evolution*, **10**, 105–108.

McDowall, R.M. (1994) On size and growth in freshwater fish. *Ecology of Freshwater Fish*, **3**, 67–79.

McNab, B.K. (1971) On the ecological significance of Bergmann's rule. *Ecology*, **52**, 845–854.

Meiri, S. & Dayan, T. (2003) On the validity of Bergmann's rule. *Journal of Biogeography*, **30**, 331–351.

Morrison, C. & Hero, J.M. (2003) Geographic variation in life-history characteristics of amphibians: a review. *Journal of Animal Ecology*, **72**, 270–279.

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

Neter, J., Kutner, M.H., Nachtsheim, C.J. & Wasserman, W. (1996) *Applied linear statistical models*. Irwin, Chicago.

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. *Journal of Biogeography*, **33**, 781–793.

Peltier, W. (1993) *Time dependent topography through the glacial cycle*, IGBP PAGES/World Data Center-A for Paleoclimatology Data Contribution Series no. 93-015. NOAA/NGDC Paleoclimatology Program, Boulder, CO.

Pough, F.H. (1980) The advantages of ectothermy for tetrapods. *The American Naturalist*, **115**, 92–112.

Rangel, T.F.L.V.B., Diniz-Filho, J.A.F. & Bini, L.M. (2006) Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Global Ecology and Biogeography*, **15**, 321–327.

Ray, C. (1960) The application of Bergmann's and Allen's rule to the poikilotherms. *Journal of Morphology*, **106**, 85–108.

Reed, R.N. (2003) Interspecific patterns of species richness, geographic range size, and body size among New World venomous snakes. *Ecography*, **26**, 107–117.

Rensch, B. (1938) Some problems of geographical variation and species-formation. *Proceedings of the Linnean Society of London*, **150**, 275–285.

Rodríguez, M.Á., Belmontes, J.A. & Hawkins, B.A. (2005) Energy, water and large-scale patterns of reptile and amphibian species richness in Europe. *Acta Oecologica*, **28**, 65–70.

Rodríguez, M.Á., López-Sañudo, I.L. & Hawkins, B.A. (2006) The geographic distribution of mammal body size in Europe. *Global Ecology and Biogeography*, **15**, 173–181.

Rosenzweig, M.L. (1968) The strategy of body size in mammalian carnivores. *American Midland Naturalist*, **80**, 299–315.

Ruggiero, A. & Hawkins, B.A. (2006) Mapping macroecology. *Global Ecology and Biogeography*, **15**, 433–437.

Spotila, J.R. (1972) Role of temperature and water in the ecology of lungless salamanders. *Ecological Monographs*, **42**, 95–125.

StatSoft Inc. (2003) *STATISTICA (data analysis software system), version 6* (http://www.statsoft.com).

Stebbins, R.C. (2003) *A field guide to western reptiles and amphibians*, 3rd edn. Houghton Mifflin, Boston, MA.

Stebbins, R.C. & Cohen, N.W. (1995) *A natural history of amphibians*. Princeton University Press, Princeton, NJ.

Storey, K.B. & Storey, J.M. (1996) Natural freezing survival in animals. *Annual Review of Ecology and Systematics*, **27**, 365–386.

Turner, J.R.G. & Hawkins, B.A. (2004) The global diversity gradient. *Frontiers of biogeography: new directions in the geography of nature* (ed. M.V. Lomolino and L.R. Heaney), pp. 171–190. Sinauer, Sunderland, MA.

Van Voorhies, W.A. (1996) Bergmann size clines: a simple explanation for their occurrence in ectotherms. *Evolution*, **50**, 1259–1264.

Walters, R.J. & Hassall, M. (2006) The temperature-size rule in ectotherms: may a general explanation exist after all? *The American Naturalist*, **167**, 510–523.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Geographical patterns of anuran mean body size in North America at 110 × 110 km including the five species with freezing abilities (see main text) and corresponding multiple regression models

Appendix S2 Species list and body size data

Appendix S3 Multiple regression models for mean body size using mean annual temperature as a predictor instead of PET

Appendix S4 Geographical patterns of species richness at 110 × 110 km for anurans and urodeles in Europe and North America (Figure S4) and multiple regression results using species richness values (S) and $[1 - \log_{10}(1/S^2)]$ as weighting factors (Table S4).

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