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 x 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.

Keywords 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...
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 thermo-regulators, 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, Rodriguez 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 (Rodríguez 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 \( \Delta \text{AIC} \), the difference between the AIC of each model and the minimum AIC found. We also used \( \Delta \text{AIC} \) values to calculate the Akaike weighting of each model \( (\omega_i) \), 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
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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 ΔAIC ≤ 2 and explained similar proportions of variance (Table 2). However, Akaïke 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

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

<table>
<thead>
<tr>
<th>Variable</th>
<th>Size, anurans</th>
<th>Size, urodeles</th>
<th>Temp.</th>
<th>AET</th>
<th>PET</th>
<th>Range</th>
<th>Prec.</th>
<th>GVI</th>
<th>GSL</th>
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<tr>
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<tr>
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<tr>
<td>PET</td>
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<td>0.79*</td>
<td>0.67*</td>
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<td>−0.08</td>
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<td>0.30</td>
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<td>Prec.</td>
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<td>0.06</td>
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<td>0.17</td>
<td>0.41</td>
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<td>0.75**</td>
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<td>0.43</td>
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<td>0.23</td>
<td>0.69*</td>
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<table>
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<th>Variable</th>
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<th>Size, urodeles</th>
<th>Temp.</th>
<th>AET</th>
<th>PET</th>
<th>Range</th>
<th>Prec.</th>
<th>GVI</th>
<th>GSL</th>
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<tr>
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</table>

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.
Figure 1 Geographical patterns of amphibian mean body size in Europe and North America: (a) anurans in Europe \([S = 31]\); (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).
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 sizes that extends from south-central Canada throughout the Great Plains and eastern Rocky Mountains to the northern

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**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
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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 thermo-regulatory 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 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).
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 urodèles.

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 explicitly devise for ectotherms exhibiting a good control over heat exchanges (Olalla-Tárraga et al., 2006). 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 urodèles 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 urodèles. 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**


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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 urodèles 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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