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Broad-scale patterns of body size in squamate reptiles of Europe and North America

ORIGINAL ARTICLE

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ABSTRACT

Aim To document geographical interspecific patterns of body size of European and North American squamate reptile assemblages and explore the relationship between body size patterns and environmental gradients.

Location North America and western Europe.

Methods We processed distribution maps for native species of squamate reptiles to document interspecific spatial variation of body size at a grain size of 110×110 km. We also examined seven environmental variables linked to four hypotheses possibly influencing body size gradients. We used simple and multiple regression, evaluated using information theory, to identify the set of models best supported by the data.

Results Europe is characterized by clear latitudinal trends in body size, whereas geographical variation in body size in North America is complex. There is a consistent association of mean body size with measures of ambient energy in both regions, although lizards increase in size northwards whereas snakes show the opposite pattern. Our best models accounted for almost 60% of the variation in body size of lizards and snakes within Europe, but the proportions of variance explained in North America were less than 20%.

Main conclusions Although body size influences the energy balance of thermoregulating ectotherms, inconsistent biogeographical patterns and contrasting associations with energy in lizards and snakes suggest that no single mechanism can explain variation of reptile body size in the northern temperate zone.

Keywords

Bergmann's rule, body size gradients, Europe, macroecology, North America, squamate reptiles, thermoregulation.

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INTRODUCTION

Since Bergmann (1847) suggested that among closely related endothermic animals those living in colder environments tend to be larger than those in warmer environments, numerous studies have explored spatial variation in body size, resulting in a long and lively debate with respect to this ecogeographical rule. However, despite some doubts about its existence (Scholander, 1955; McNab, 1971; Geist, 1987), both the intraspecific and interspecific versions of Bergmann's rule have received broad support in mammals (Ashton *et al.*, 2000; Meiri & Dayan, 2003; Blackburn & Hawkins, 2004; Rodríguez *et al.*, 2006) and birds (James, 1970; Cousins, 1989; Blackburn

& Gaston, 1996; Ashton, 2002; Meiri & Dayan, 2003). Even so, two important basic issues remain. First, whereas intraspecific gradients in body size have been documented hundreds of times, tests for interspecific clines are scarcer. Second, the generalizability of geographical gradients in body size for ectotherms remains controversial. Lindsey (1966) demonstrated that the latitudinal variation in body size often documented for endotherms could also be extended to at least some ectothermic organisms. However, subsequent tests of body size gradients in ectotherms have found a range of patterns.

Among the seven interspecific analyses that have been conducted for invertebrates of which we are aware (Miller,

1991; Cushman *et al.*, 1993; Barlow, 1994; Hawkins, 1995; Hawkins & Lawton, 1995; Diniz-Filho & Fowler, 1998; Hausdorf, 2003), decreasing body size with decreasing latitude was found only for European ants (Cushman *et al.*, 1993), whereas for ectothermic vertebrates seven of eleven data sets were consistent with Bergmann's rule (Lindsey, 1966; McDowall, 1994; Cruz *et al.*, 2005). Four of the seven studies supporting the rule were for fish, and two were for amphibians; support for Bergmann's rule has only been documented once for reptiles (Cruz *et al.*, 2005), although there have been few studies (Lindsey, 1966; Reed, 2003).

An important challenge in macroecology is to identify and understand the large-scale variation of ecologically relevant characteristics of organisms, such as body size, along environmental gradients (Brown, 1995; Gaston & Blackburn, 2000). However, as recently noted by Reed (2003), reptiles have rarely been studied in the macro-ecological literature. Therefore, describing patterns of geographical variation in body size may generate insights into the evolutionary and ecological mechanisms structuring reptile assemblages while extending our understanding of macroecological patterns beyond the more intensely studied mammals and birds.

In this paper we test for the existence of broad-scale interspecific patterns of body size in European and North American lizards and snakes, using a grid approach. A comparison of patterns in two regions can help to evaluate the generalizability of the observed geographical trends and to find region-specific differences (Schall & Pianka, 1978; Murphy, 1985; Hawkins & Lawton, 1995). Our primary goal is to determine if the two most speciose reptile groups follow the pattern described by Bergmann's rule. Further, we explore the relationships between the observed patterns in body size and environmental gradients that might account for geographical patterns of mean body size for these ectotherms. Specifically, we focus the analysis on four relevant hypotheses likely to explain large-scale gradients in body size (see e.g. Cushman *et al.*, 1993; Blackburn *et al.*, 1999; Blackburn & Hawkins, 2004):

1. *Heat conservation*: This is the classic physiological explanation for Bergmann's rule for endotherms. According to this hypothesis large-bodied species can occupy northern latitudes due to their reduced surface-to-volume ratio. This has been considered unlikely to explain latitudinal clines in body size for ectotherms (Cushman *et al.*, 1993). However, reptiles actively thermoregulate by behavioural and physiological mechanisms, which can give them control over metabolic processes, and this hypothesis may apply to reptiles despite their being ectothermic.

2. *Migration abilities*: This hypothesis proposes that small species will be underrepresented at high latitudes because they have failed to fully colonize these regions following the retreat of the glaciers at the close of the Pleistocene. We are not aware of any data demonstrating that small-bodied reptiles have more limited dispersal abilities than large-bodied species, but it is plausible and deserves to be tested.

3. *Primary productivity*: Rosenzweig (1968a) argued that primary productivity could be an important selective pressure on body size since body mass must be maintained by a sufficient food supply. Therefore, this predicts that measures of plant productivity should best describe variation in body size.

4. *Starvation resistance*: This is also sometimes referred to as the *resource availability hypothesis*. It has been suggested that measures of seasonality best predict variation in body size (Boyce, 1978; Lindstedt & Boyce, 1985; Wigginton & Dobson, 1999; Ashton, 2001). This hypothesis assumes that larger body mass is advantageous where there is greater seasonality in resource abundance, because resistance to starvation increases with body size via allometric scaling of fat reserves (Cushman *et al.*, 1993; Blackburn *et al.*, 1999). This reasoning applies to endotherms, but in the case of ectotherms a more plausible mechanism relates the length of the growing season to the physiological time available for development (Mousseau, 1997). In seasonal environments resources are available for less time, and therefore animals have less time to grow. This will be less of a problem for small species, as they require fewer resources than larger species. Thus, small species can persist in more seasonal environments.

MATERIALS AND METHODS

Species data

Distribution maps for native squamate reptiles were obtained from Gasc *et al.* (1997) and two field guides to the North American herpetofauna (Conant & Collins, 1998; Stebbins, 2003). All islands, except Great Britain, were excluded. Data from Belarus, Russia and Ukraine in continental Europe were discarded because of incomplete sampling (Gasc *et al.*, 1997; Meliadou & Troumbis, 1997; Araújo *et al.*, 2001). Maps were digitized and processed using ArcGIS 8.3 in a grid comprising 110×110 km cells. Coastal cells containing less than 50% of the land mass of inland cells were excluded from the analysis. The mapped area included 386 cells in Europe and 1430 in North America.

After removing island endemics, exotic and extinct species, the reptile database comprised 71 species in Europe (28 snakes and 43 lizards) and 224 species in North America (124 snakes and 100 lizards). *Lacerta vivipara* in Europe and *Thamnopis sirtalis* in North America were also excluded from the analysis due to their extraordinary abilities to freeze and supercool. It is well known that these species are freeze-tolerant, a physiological trait that has been adduced to explain their presence in colder climates (Churchill & Storey, 1992; Costanzo *et al.*, 1995; Grenot *et al.*, 2000). Since our study seeks to establish the role of body size in determining reptile distributions, we excluded these species because it is already known that their distribution is associated with another trait. Also, these are the only reptiles found in central Canada or northern Scandinavia, so including them would have generated many cells with average body sizes due solely to their presence; thus it was deemed prudent to exclude them from the analysis.

Body sizes were extracted from field guides (Conant & Collins, 1998; Arnold, 2002; Stebbins, 2003). The masses of reptiles are rarely available in the literature, and previous studies used body length as a measure of body size (Boback & Guyer, 2003; Reed, 2003). Indeed, it has been suggested that both body length and body mass generate similar results in analyses of macroecological patterns (Brown, 1995). However, some authors have stressed the fact that mass represents the best estimate of body size (Hedges, 1985; Gaston & Blackburn, 2000), and it is especially important to use mass when making comparisons among organisms with different basic body shapes, as occurs in the case of lizards and snakes. Likewise, the occurrence of some serpentiform species among lizards may influence the overall patterns for this group if we had used body length as an estimate of body size. Therefore, we used the formulae proposed by Pough (1980) to convert length to mass for reptiles. These formulae represent the best models available for this conversion (F. H. Pough, pers. comm.). We used mass (g) $= 3.1 \times 10^{-2}$ length (cm)$^{2.98}$ for lizards, where length is measured snout-to-vent, and mass (g) $= 3.5 \times 10^{-4}$ length (cm)$^{3.02}$ for snakes, where length is snout-to-tail. The masses of serpentiform lizards were estimated from the equation for snakes (Pough, 1980). All members of the Anguidae (three species) and Scincidae (six species) in Europe, as well as *Anniella pulchra* (Anniellidae) and the four members within the genus *Ophisaurus* (Anguidae) in North America were considered serpentiform. We used maximum lengths for each species. In organisms with indeterminate growth maximum values are considered to be a reasonable estimate of the size potential for a species (Boback & Guyer, 2003; Reed, 2003). It should be noted that this analysis does not incorporate intraspecific variation in body size, since we assign the same value for body size to the whole geographical range occupied by a species. The inclusion of intraspecific variation in body size in our analyses could potentially reinforce or distort the observed interspecific patterns, depending on the size trends observed in each case. However, intraspecific data could not be included because such data exist only for a relatively small number species (see Electronic Appendix in Ashton & Feldman, 2003).

Body size was log$_{10}$ transformed, and we calculated average log mass (hereafter called the mean body size) in each grid cell separately for lizards and snakes occurring in each geographical region. Obviously, this does not reflect phylogeny because snakes developed from lizards and the latter are thus paraphyletic in relation to the former. Rather, it is intended to represent two functional groups that differ markedly in morphology and food habits (see e.g. Pough & Groves, 1983). Additionally, most lizard species (around 80%) weigh less than 20 g, while nearly 75% of snakes have adult body masses greater than 20 g (Pough, 1980; Pough & Groves, 1983).

Environmental variables

We generated seven environmental variables, selected because they can be related to four relevant hypotheses likely to explain large-scale gradients in body size (see e.g. Cushman *et al.*, 1993; Blackburn *et al.*, 1999; Blackburn & Hawkins, 2004). The variables (with their associated hypotheses) are as follows:

1. *Mean annual temperature, annual potential evapotranspiration and range in elevation (heat conservation)*: Mean annual temperature and annual potential evapotranspiration (PET) are both widely used as measures of ambient energy inputs (Schall & Pianka, 1978; Currie, 1991; Rodríguez *et al.*, 2005, 2006). PET is an estimate of the net atmospheric energy balance and is highly correlated with mean annual temperature and solar radiation (Currie, 1991). We used annual PET data calculated using the Priestley–Taylor formula, which are available at http://www.grid.unep.ch/data/summary.php?dataid=GNV183. Temperature data were taken from http://www.grid.unep.ch/data/summary.php?dataid=GNV15.We also used range in elevation as an estimate of mesoscale spatial climatic variation within the cells (Turner & Hawkins, 2004). This was calculated as the difference between maximum and minimum elevation within a grid cell from data available at http://www.ngdc.noaa.gov/seg/cdroms/ged_iia/datasets/a13/fnoc.htm.

2. *Time since glacial retreat (migration ability)*: We tested this in Europe using the time since the most recent glaciation when a cell became available for colonization (hereafter called the cell age). Age was estimated using changes in ice cover at 1 ka intervals from Peltier (1993). Cells that were not completely covered by ice during the most recent glacial maximum were assigned an arbitrary age of 20 ka (Hawkins, 2004; Rodríguez *et al.*, 2006), which represents the age corresponding to the time of maximum ice coverage in Europe. This hypothesis could not be tested in North America because most of Canada is without reptiles (see Fig. 1c,d), except for *T. sirtalis*, which we excluded because it can tolerate body freezing.

3. *Annual actual evapotranspiration, global vegetation index (primary productivity)*: Annual actual evapotranspiration (AET) measures water–energy balance, which drives plant growth. Because of the strong relationship between AET and plant productivity at large scales, this variable has been used as a proxy for productivity (Rosenzweig, 1968b; Lieth, 1975; Hawkins *et al.*, 2003; Hawkins, 2004). The global vegetation index (GVI) is derived from radiometer data from the NOAA Polar Orbiting Environmental Satellites (Kineman & Hastings, 1992) and measures standing crop and the greenness of the plant canopy. Therefore, it has been widely used as a proxy for plant productivity or standing crop (Hurlbert & Haskell, 2003; Hawkins, 2004; Rodríguez *et al.*, 2005). We generated annual data for both variables. AET (Thornthwaite formula) is available at http://www.grid.unep.ch/data/summary.php?dataid=GNV183 and GVI is available at http://www.ngdc.noaa.gov/seg/cdroms/ged_iia/datasets/a01/mgv.htm.

4. *Length of growing season (starvation resistance)*: We tested this hypothesis using the number of months available for plant growth in each grid cell. We followed the reasoning underlying Gaussen ombrothermic climatic diagrams to generate this variable (Gaussen, 1954). First, we calculated the xerothermic season length for each cell by noting the number of months
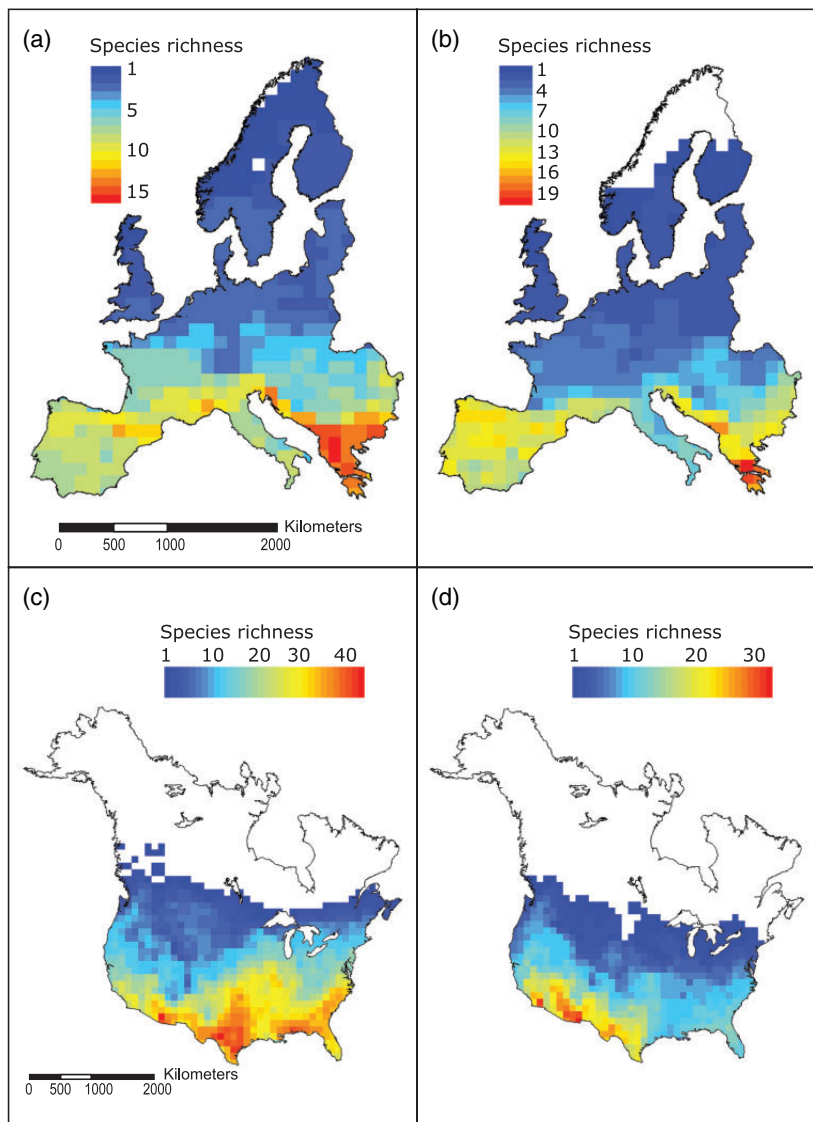
Figure 1 Geographical patterns of species richness at 110×110 km. (a) Snakes in Europe ($s = 28$ species). (b) Lizards in Europe ($s = 43$ species). (c) Snakes in North America ($s = 124$ species). (d) Lizards in North America ($s = 100$ species). These maps do not include *Lacerta vivipara* in Europe and *Thamnopis sirtalis* in North America which were excluded from the analysis (see Materials and methods).

when two times the mean monthly temperature was higher than mean monthly precipitation. We thus eliminated those summer months for which low precipitation limits plant productivity. For the remaining months, we calculated the number of months in which plant growth is limited by low temperatures. We plotted cell monthly values of GVI against mean monthly temperatures and used split-line regression to find the threshold temperature value above which plant growth occurs. We then counted the number of months having mean monthly temperatures greater than this value in each cell, and added this to the number of months with sufficient precipitation.

Statistical analyses

The data for lizards and snakes were analysed separately. Initially, we used simple regressions to test for relationships between mean body size and the seven explanatory variables. However, as is always the case with the grid approach, cells are not statistically independent, resulting in an underestimation of error variances. To obtain unbiased estimates of the significance of the simple regressions we used the modified *t*-test of Dutilleul (1993). This method corrects significance tests for spatial autocorrelation using correlograms to estimate the geographically effective degrees of freedom (see e.g. Legendre *et al.*, 2002).

We then used multiple regression to generate environmental models including multiple predictors, using a model selection approach based on information theory (see Burham & Anderson, 2002) to identify the set of models best supported by the data. The use of model selection, a statistical approach that is rapidly gaining support in ecology as an alternative to hypothesis testing (Johnson & Omland, 2004), allows us to evaluate the relative support for each hypothesis by comparing a complete set of competing models. Taking into account the strong collinearity among several of the predictors in our data set (Table 1), it is especially necessary to assess simultaneously the importance of all the various

Table 1 Correlation matrices for environmental variables. Significance levels are corrected for spatial autocorrelation using the modified *t*-test developed by Dutilleul (1993) (*$P < 0.05$; **$P < 0.01$): (a) North America and (b) Europe

Variable	Temp.	AET	PET	Range	GVI	GSL	
(a) North America							
Mean annual temperature	1						
Actual evapotranspiration	0.8*	1					
Potential evapotranspiration	0.94**	0.73	1				
Range in elevation	−0.04	0.30	0.02	1			
Global Vegetation Index	0.50*	0.62**	0.39	−0.03	1		
Length of growing season	0.69*	0.88**	0.61	0.33	0.58**	1	

Variable	Temp.	AET	PET	Range	GVI	GSL	Age
(b) Europe							
Mean annual temperature	1						
Actual evapotranspiration	0.44	1					
Potential evapotranspiration	0.79*	0.67*	1				
Range in elevation	−0.08	0.29	0.30	1			
Global Vegetation Index	0.60	0.74*	0.58	0.06	1		
Length of growing season	0.75**	0.37	0.43	−0.16	0.69*	1	
Cell age	0.76*	0.71	0.74	0.18	0.71	0.67	1

predictors included in the analysis. The Akaike information criterion (AIC) was used to rank competing models and weigh the relative support for each one. However, the presence of spatial autocorrelation in the residuals of all our models required us to correct the error variances before calculating the AICs. We accomplished this by calculating geographically effective sample sizes ($n^{\star}$), given by $n^{\star} = n/[(1 + p)/(1 − p)]$, where p is the first-order autoregressive parameter of the residuals, approximated by the standardized Moran's I in the first distance class (Cressie, 1993; Haining, 2003). Spatial correlograms of residuals were calculated using 17 distance classes in Europe and 19 in North America, and the first class ranged from 0 to 345 km and 0 to 451 km, respectively. Approximate unbiased variances were obtained dividing the residual sum of squares by $n^{\star}$, which were then used to calculate corrected AICs.

We compared the resulting AIC values of each model using ΔAIC, the difference between AICs of each model and the minimum AIC found. A value of ΔAIC higher than 10 represents a poor fit relative to the best model, whereas a value less than 2 indicates that a model is equivalent to the minimum AIC model.

These ΔAIC values were also used to calculate Akaike's weighting of each model (w_i), which can be interpreted as the probability that model i is actually the best explanatory model. The values of w_i are standardized across the candidate set of models.

Weightings also provide a way to define the relative importance of each predictor. This measure can be calculated as the sum of w_i values over all models that include the predictor of interest. However, it is virtually impossible to discern the relative influence of different predictors when all of them appear in the best set of models, so we used the standardized regression coefficients to rank the importance of the predictors in the best model (J. A. F. Diniz-Filho, pers. comm.).

Finally, we used the correlograms of the residuals of our best multiple-regression models to evaluate how these environmental models control spatial variation in body size across spatial scales (Diniz-Filho *et al.*, 2003). We restricted this analysis to Europe, where multiple-regression models had high explanatory power (see Results). To do this we generated spatial correlograms using Moran's I coefficients calculated for original mean body size data and residual mean body size after fitting each model at 17 distance classes. Thus, the lower the level of spatial autocorrelation for the residuals of the multiple-regression models at any distance class, the greater the capacity of the model to explain spatial structure in mean body size at that distance. On the contrary, remaining spatial autocorrelation at a distance class in the residuals of the fitted regression models indicates the inadequacy of the model to describe the body size pattern at that scale and, therefore, suggests that spatially patterned variables not included in the model are contributing to the spatial pattern.

All statistical analyses were performed using STATISTICA (StatSoft, Inc., 2003) and Spatial Analyses in Macroecology (SAM) (Rangel *et al.*, 2005).

RESULTS

Before describing the patterns in body size and their relationships with environmental variables, it should be noted that these patterns are potentially sensitive to spatial variation in species richness. Thus, the lower cell occupancies in species-poor areas may influence variation in mean body size because of the smaller range of sizes present in these cells, which should

be taken into account when interpreting trends in body size. Therefore, we also present maps of species richness for lizards and snakes on both continents (Fig. 1).

Bearing this in mind, Europe is characterized by clear latitudinal trends in body size for both snakes and lizards, although the gradients are in opposite directions (Fig. 2a,b), i.e. whereas mean body size for lizards increases northwards, snakes become larger towards the south. Patterns in North America are much more complex and reveal no consistent gradients in latitudinal space (Fig. 2c,d), although it is possible to pick out patterns in some parts of the continent (e.g. both snakes and lizards become larger towards the south in the east). There is also a marked longitudinal component within North America, with snakes being largest in the western half of the continent.

Within Europe, after correcting the probabilities of the simple regression coefficients between body size and the environmental predictors for spatial autocorrelation, only PET and mean annual temperature were significant for both groups

(Tables 2 and 3). Because the body size gradients were in opposite directions for the two groups, with snakes smaller and lizards larger in the north, the relationships with these two variables were also in opposite directions (Fig. 3). PET was the strongest predictor of mean log body size in Europe for lizards, with mean annual temperature ranking second (Table 2). Similarly, these two measures of energy availability were the best single predictors for the mean size of snakes in Europe. However, mean annual temperature accounted for 2% more variance than PET in this case (Table 3).

Even though mean annual temperature and PET are highly correlated (Table 1), both of them entered in all multiple-regression models with $\Delta AIC \leq 2$ for mean body size of snakes in Europe (Table 4). Based on this criterion alone we obtained a set of four equivalent models that accounted for the same amount of variance (59.4%). However, the Akaike weightings suggest that the first model, which includes mean annual temperature, PET and AET, is a better model ($w_i = 0.427$). The higher standardized coefficients of mean annual
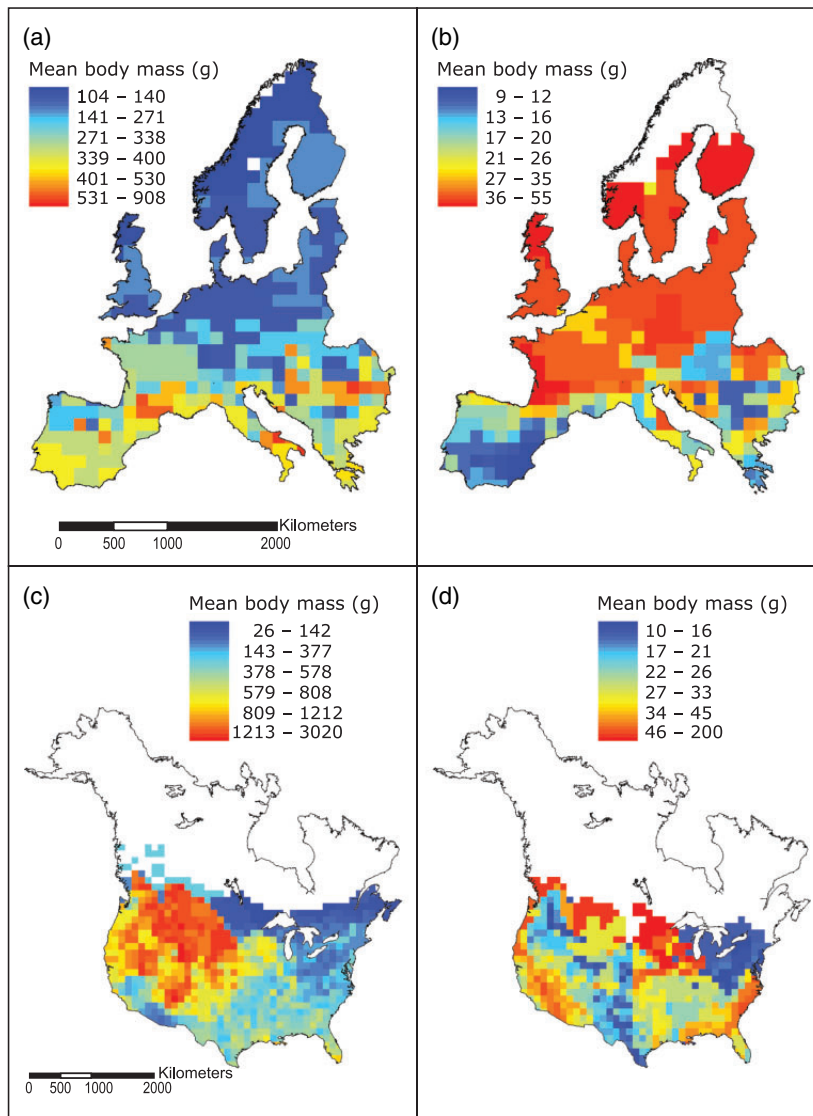

Figure 2 Geographical patterns of squamate reptile mean body size in Europe and North America. (a) Snakes in Europe ($s = 28$ species). (b) Lizards in Europe ($s = 43$ species). (c) Snakes in North America ($s = 124$ species). (d) Lizards in North America ($s = 100$ species). Numbers included in the legend of each map are back-transformed from average log-transformed mass values.

Table 2 Simple regressions of predictor variables against lizards mean body size in Europe. Predictors are ranked by their coefficient of determination. Corrected probabilities are based on the modified *t*-test developed by Dutilleul (1993)

Variable	r^2	Probabilities	
		Uncorrected	Corrected (d.f.)
−Potential evapotranspiration	0.586	< 0.0001	0.009 (8.0)
−Mean annual temperature	0.351	< 0.0001	0.049 (9.4)
−Age	0.310	< 0.0001	0.056 (10.2)
−Actual evapotranspiration	0.137	< 0.0001	0.070 (22.5)
−Range in elevation	0.076	< 0.0001	0.078 (39.6)
−Global Vegetation Index	0.050	< 0.0001	0.298 (21.5)
−Length of growing season	0.037	< 0.0001	0.388 (20.4)

d.f. = geographically effective degrees of freedom. Total number of analysed cells = 345.

Table 3 Simple regressions of predictor variables against snakes mean body size in Europe. Presentation as in Table 2. Total number of analysed cells = 382

Variable	r^2	Probabilities	
		Uncorrected	Corrected (d.f.)
+Mean annual temperature	0.522	< 0.0001	0.032 (6.7)
+Potential evapotranspiration	0.504	< 0.0001	0.043 (6.3)
+Age	0.458	< 0.0001	0.058 (6.3)
+Global Vegetation Index	0.286	< 0.0001	0.069 (10.2)
+Length of growing season	0.277	< 0.0001	0.051 (11.4)
+Actual evapotranspiration	0.275	< 0.0001	0.069 (10.7)
+Range in elevation	0.008	0.0399	0.541 (34.1)

Figure 3 The relationship between squamate reptile mean body size and potential evapotranspiration (PET) in 110×110 km cells for Europe. (a) Snakes ($s = 28$ species). (b) Lizards (43 species). Similar relationships were obtained for mean annual temperature.

temperature and PET provide strong evidence that these two variables are mainly driving broad-scale variation in body size of snakes in Europe.

The pattern of spatial autocorrelation for mean body size of snakes in Europe was representative of a cline, with positive autocorrelation at shorter distances and progressively becoming negative at larger distances (Fig. 4a). The model including mean annual temperature, PET and AET accounted for most of this pattern at all distance classes except for the shortest one. This indicates that a factor not included in the model influences body size patterns for snakes at more local scales in Europe.

Of the 128 possible multiple-regressions models for lizards in Europe, three had an $\Delta AIC \leq 2$ and explained similar proportions of variance (Table 4). Again, Akaike weightings indicate that the first model is the best model ($w_i = 0.576$). It included PET, cell age and GVI and explained 62.5% of the variance in mean body size. In this model, the standardized coefficients indicate that PET is consistently the strongest predictor, followed by age and GVI. Nonetheless, it should be noted that age and GVI together increase the variance explained by the model by less than 4%, which lead us to
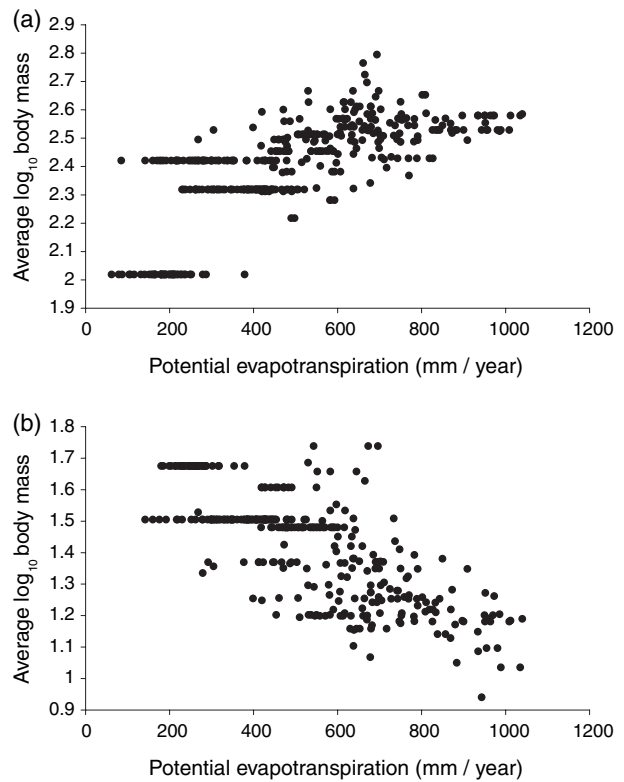
conclude that PET is the main driver of variation in body size of lizards in Europe.

Similar to the case of snakes, the spatial autocorrelation analysis shows a clinal pattern of variation of lizard body size (Fig. 4b). The regression model including PET, age and GVI accounted for most of this pattern at all distance classes except for the shortest one. Again, this suggests that additional factors not included in our analysis are necessary to fully explain variation in lizard body size at more local scales in Europe.

In North America, the simple regressions were much weaker than in Europe, and none of the environmental predictors remained significant after correcting for spatial autocorrelation in simple regressions (Tables 5 and 6). Energy variables (PET and mean annual temperature for lizards and range in elevation in the case of snakes) also represented the best single predictors of lizard body size in North America, and the signs of the regression coefficients were identical on both continents. However, none of the six variables (we did not test for the influence of cell age in this region) explained more than 10% of the variance in body size in either group, which might be expected given the complex spatial patterns found on this continent.

Of the 64 possible models for each group, the models with the lowest AIC included all variables except length of the growing season in the case of snakes and PET, AET and length of the growing season for lizards. Based on Akaike weightings

Table 4 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 auto-correlation in the model residuals. For each variable entering in the model we include their standardized coefficients to evaluate the relative importance of each one. In the case of North American lizards we only show the best of seven equivalent models, because none of them explained more than 6% of variance. Predictor variable codes are: Temp., mean annual temperature; PET, potential evapotranspiration; Elev., range in elevation; Age, time since glacial retreat; AET, actual evapotranspiration; GVI, Global Vegetation Index; GSL, length of growing season

| Group | Region | Predictors in model | | | | | | | AIC | ΔAIC | r^2 | w_i |
		Temp.	PET	Elev.	Age	AET	GVI	GSL				
Snakes	Europe	0.482	0.205			0.188			−659	0	0.594	0.427
		0.418	0.246			0.169		0.054	−658	1	0.594	0.259
		0.487	0.202			0.195	0.009		−657	2	0.594	0.157
		0.501	0.183	0.023		0.188			−657	2	0.594	0.157
	North America	0.451	−0.305	0.474		0.173	−0.331		−474	0	0.196	0.731
		0.451	−0.306	0.471		0.194	−0.328	−0.027	−472	2	0.196	0.269
Lizards	Europe		−0.708		−0.236		0.220		−608	0	0.625	0.576
			−0.713	0.013	−0.236		0.221		−606	2	0.625	0.212
			−0.721		−0.211		0.244	−0.051	−606	2	0.627	0.212
	North America		−0.232			0.236		−0.204	−743	0	0.050	0.234
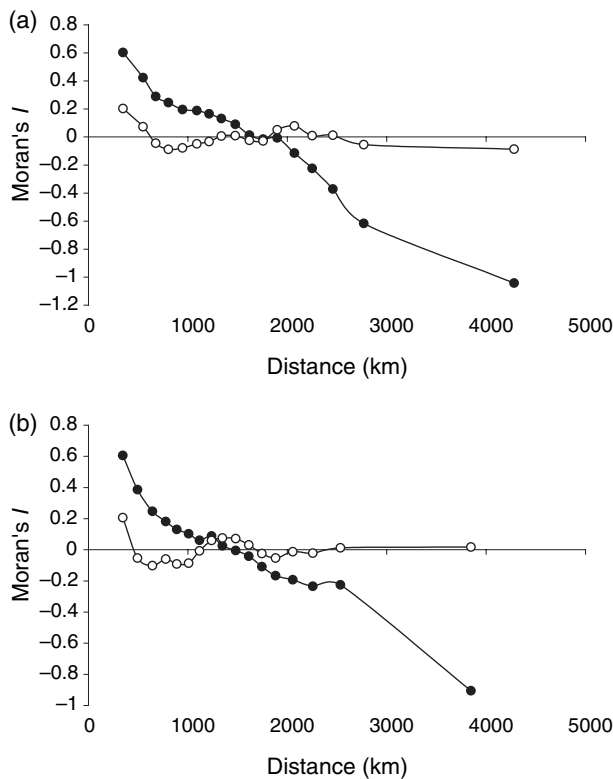
Figure 4 Spatial correlograms using Moran's *I* for mean body size (solid circles) and residuals of the best multiple-regression models in Europe (open circles): (a) snakes, (b) lizards.

Table 5 Simple regressions of predictor variables against mean body size of snakes in North America. Presentation as in Table 2. Total number of analysed cells = 788

| Variable | r^2 | Probabilities | |
		Uncorrected	Corrected (d.f.)
+Range in elevation	0.102	< 0.0001	0.262 (11.9)
−Global Vegetation Index	0.047	< 0.0001	0.288 (23.0)
−Length of growing season	0.035	< 0.0001	0.516 (11.9)
−Actual evapotranspiration	0.024	< 0.0001	0.626 (9.5)
+Potential evapotranspiration	0.023	< 0.0001	0.569 (14.6)
+Mean annual temperature	0.001	< 0.0001	0.729 (12.8)

Table 6 Simple regressions of predictor variables against mean body size of lizards in North America. Presentation as in Table 2. Total number of analysed cells = 658

| Variable | r^2 | Probabilities | |
		Uncorrected	Corrected (d.f.)
−Potential evapotranspiration	0.039	< 0.0001	0.220 (37.7)
−Mean annual temperature	0.036	< 0.0001	0.229 (38.6)
−Length of growing season	0.003	0.102	0.676 (43.3)
−Global Vegetation Index	0.001	0.211	0.719 (57.1)
−Actual evapotranspiration	0.001	0.336	0.804 (44.7)
−Range in elevation	0.001	0.950	0.985 (62.2)

DISCUSSION

Our results reveal clear, albeit group-specific, patterns of interspecific body size variation in squamate reptiles throughout Europe. In contrast, patterns are more complex and patchier in North America. Despite this, associations of mean body size with measures of ambient energy are similar in sign

both models were the best among equivalent models ($w_i = 0.731$ and $w_i = 0.576$, respectively). However, the former explained only 19.6% of variance, whereas the latter accounted for 5% of the variance.

in both regions. Specifically, PET was the best predictor of mean body size for lizards in both continents, whereas mean annual temperature, together with range in elevation in North America, is the strongest predictor of size variation in snakes. Moreover, the slope of the relationship between energy variables and mean body size was positive for snakes and negative for lizards in both regions. The proportions of variance described by these variables were notably larger in Europe in both cases (Europe > 57% and North America < 10%).

The importance of energy in explaining the observed gradients in body size was also indicated within our multiple-regression models; in all cases, the addition of extra explanatory variables only increased slightly the amount of variance explained by energy alone. However, our finding of strong trends in body size in Europe and weak patterns in North America is particularly intriguing and limits a general explanation. Indeed, the very low explanatory power of our models to describe variation in body size for both reptile groups in North America strongly suggests that factors as yet unknown account for the existence of complex spatial patterns in this region. As a consequence, it is impossible to derive a single explanation for such patterns of variation in body size.

A second limitation in interpreting these results is the paucity of studies that have examined interspecific biogeographical patterns of body size in reptiles. In a pioneering study, Lindsey (1966) tested for Bergmann's rule across 1222 snake species and 935 lizard species throughout the world. He found no latitudinal trends, although he reported that some snake families weakly followed Bergmann's rule. In spite of the taxonomic breadth of his analysis, the results are difficult to compare directly with ours because he did not include complete regional faunas (Lindsey, 1966; Currie & Fritz, 1993; McDowall, 1994), and the data were binned into three broad latitudinal bands (i.e. cool temperate, warm temperate and tropical) without differentiating between biogeographical regions. Indeed, the region-specific differences we find for Europe and North America suggest that broad-scale patterns in body size may be confounded when biogeographical regions are pooled. Similarly, Hawkins & Lawton (1995) found opposing patterns of variation in body size of butterflies between continents, and concluded that evaluations of Bergmann's rule based on a single region may not be generalizable to other regions.

Lizards

Lizards follow Bergmann's rule in Europe. Moreover, mean body size is negatively correlated with energy variables in both Europe and North America, consistent with the heat conservation hypothesis. However, heat balance in ectotherms depends on both heat gain and heat conservation, which means that the explanation proposed by Bergmann (1847) for endotherms can only partially account for the observed gradients. So, what is the relationship between body size and heating rates? Cowles (1945) and Bogert (1949) (cited in

Ashton & Feldman, 2003) hypothesized that smaller squamate reptiles are favoured in colder environments because their increased surface to volume ratio allows them to heat more rapidly. If true, we are confronted with two opposing forces in cold climates, one that favours larger sizes (i.e. Bergmann's explanation to conserve internal temperature), and the other favouring smaller sizes to gain heat. To further complicate matters, it is well established that heat balance in reptiles can also be strongly affected by physiological and behavioural adjustments (Cowles & Bogert, 1944; Bartholomew, 1982; Huey, 1982). For example, in a study of eight lacertid lizards in Europe, Díaz et al. (1996) found that the four species living in the north reduced their heating times as a result of both changes in heating rates (a physiological trait) and selection of basking sites matching their preferred body temperature (a behavioural trait). Consequently, northern species can warm at faster mass-specific rates than those living in Mediterranean areas and are able to reduce basking time by 17%. Lacertids represent 28 of the 43 lizard species in Europe. Therefore, if the abilities observed by Díaz et al. (1996) in the northern lacertids they studied are common, this could account for the pattern of variation in body size on this continent. In other words, heat gain may not be as strongly dependent on lizard body size as it is on behavioural and physiological traits.

Lacertidae do not occur in North America, which has twice as many lizard species as Europe. Another major difference between the lizard fauna of both continents is the number of families (6 in Europe and 11 in North America). The broader taxonomic breadth in North America might be responsible for the more complex pattern of body size on this continent, particularly bearing in mind that both Bergmann's rule and the converse have been reported in intraspecific studies of lizards (Ashton & Feldman, 2003) and between congenerics (Angilletta et al., 2004; Sears & Angilleta, 2004). Although not strictly comparable to our analysis, the variable intraspecific patterns suggest that individual lizard species respond idiosyncratically to environmental variation. If so, greater spatial heterogeneity of mean body sizes in the richer lizard fauna of North America is not surprising. Additionally, North America is larger and more environmentally complex and has habitats that are not present in Europe, including deserts and subtropical forests. This wide environmental variation might also contribute to the patchwork pattern in North America. However, in spite of these complexities, energy variables remain the best predictors of body size patterns in this continent, which suggests that similar mechanisms to those described for Europe might still play a role in constraining variation in body size of North American lizards, albeit not the dominant one.

Recently, Cruz et al. (2005) tested for interspecific body trends within the lizard genus Liolaemus of South America and found evidence for Bergmann's rule for the 34 species they analysed. Also, they observed a strong negative relationship between latitudinal variation in body size and thermal variables, which led them to favour heat conservation as the

most plausible explanation. They suggested that both the slower rate of cooling associated with larger sizes and the increased rate of heat gain as a result of physiological and anatomical mechanisms may explain why lizard species from cold climates tend to be larger. This concurs with our results for European lizards and the explanation for the pattern is similar in both cases. Furthermore, Cruz *et al.* (2005) found that variation in the strength of this pattern strongly depended on the phylogenetic scale of the analysis. Thus, when they analysed all species within the subgenera *Liolaemus* and *Eulaemus* the relationship between body size and latitude was weaker. Therefore, they concluded that although macroecological patterns in body size for these lizards are more likely to be the result of ecological factors related to heat conservation, these patterns are sensitive to phylogenetic scale. A similar result has been found for different clades of snakes (Ashton, 2001; see below) and this may at least partially account for the marked differences in strength of the gradients when comparing Europe and North America.

Another explanation for a negative relationship between body size and energy in lizards is the temperature–size rule (Atkinson, 1996), which describes a trend amongst ectotherms to grow faster and to reach smaller adult sizes at higher temperatures. Although much of the evidence for this comes from laboratory experiments (see Atkinson, 1994), it has also been observed in natural conditions (Angilletta *et al.*, 2004). Angilletta *et al.* (2004) compiled data on maturation time from 18 studies of the eastern fence lizard (*Sceloporus undulatus*) at different latitudes and found that lizards from colder environments reach larger adult sizes by delaying maturity, a characteristic they linked to lower levels of competition and/or predation, and, hence, juvenile mortality. Again, extending intraspecific observations to interspecific biogeographical patterns can only be speculative, but if further research confirms that lizard species from high latitudes reach larger adult sizes through delayed maturation, the mechanisms underlying the temperature–size rule would represent an additional explanation for the increased size in lizard faunas living in colder areas.

Snakes

As with lizards, body size in snakes shows a clear latitudinal gradient in Europe, with snakes being larger southwards, but with a patchwork distribution in North America. Mean annual temperature and PET, together with range in elevation in the case of North America, which are linked to the heat conservation hypothesis, were the best descriptors of snake body size in both continents, albeit the influence of these variables is much stronger in Europe. These findings give fuel to the hypothesis that energy availability influences body size in squamate reptiles; although other factors must be important in North America as well. Indeed, it is noteworthy that there is a cluster of the largest snake species in the western half of North America, which results in a longitudinal size cline. Like latitude, longitude *per se* provides no biological or ecological information about spatial

gradients (Hawkins & Diniz-Filho, 2004), and whatever generates this gradient appears to be largely statistically independent of all of our environmental variables. The observation that range in elevation, a measure of altitudinally driven climatic variation within an area, influences variation in body size of snakes suggests that these organisms are responding to local effects of cold, with the largest species occurring in higher, colder spots located in the western half of North America. However, this explains only 10% of the variance in body size, and the causes for this pattern remain unclear.

Although most European and North American snakes belong to the Viperidae and Colubridae, North America has more than four times more species of snakes than Europe (124 and 28, respectively). Ashton (2001) observed that sister species of rattlesnakes (*Crotalus viridis* and *Crotalus oreganus*) had opposite latitudinal clines of body size and concluded that mixing data from separate clades may obscure biogeographical patterns of body size. This suggests that larger numbers of species in interspecific studies probably result in noisier data, as more responses to environmental variation are possible. Accordingly, the complex patterns of body size in snakes in North America may reflect the greater variety of biologies presumably present within the richer snake fauna of this continent.

Although body size patterns of both lizards and snakes in Europe are mainly explained by measures of energy availability, there are obvious differences between them (snakes become larger southwards) and we can only speculate on the mechanisms, since no previous interspecific studies have explored them. In a meta-analysis of intraspecific studies, Ashton & Feldman (2003) reported that the most common trend of body size variation within squamate species is an increase with increasing environmental energy, consistent with what we find interspecifically. But the question remains of why mean body sizes of snakes and lizards show opposite relationships with energy. Based on the available evidence, this discrepancy does not exist at an intraspecific level (Ashton & Feldman, 2003). One possibility is the differences in body mass of these groups. Pough (1980) and Pough & Groves (1983) found that nearly 80% of living species of lizards weigh less than 20 g, whereas 73% of snakes are larger than this. Similarly, 75% of the lizards in our data sets weigh ≤ 50 g, whereas the same proportion of snakes weigh ≥ 80 g. Zug *et al.* (2001) suggested that the behavioural control of thermal interactions is particularly important for small lizards, whereas other mechanisms are more important for the heat balance of larger species. Implicit in this is that large ectotherms might not be able to warm their bodies rapidly enough to meet their needs in the narrow activity windows available in cold environments. Willemsen & Hailey (1999) argued that a converse Bergmann's rule pattern is more likely to occur in large thermoregulating ectotherms since they have less time available after thermoregulation and lower food intake in colder latitudes (see also Avery, 1976, 1978). This suggests the existence of a body size threshold below which body size increases with decreasing environmental energy (as in lizards) and above which the reverse occurs (as in snakes). Again, this

appears not to be an adequate explanation at an intraspecific level, since size–latitude trends do not differ among large and small species (Ashton, 2004).

To evaluate this hypothesis at an interspecific level we combined lizard and snake data in North America and analysed small and large species (defined as those below and above the mean in the approximately log-normal body size distribution) against PET. We found no support for a threshold in North America (slopes were negative in sign in both cases), which might be expected given the complex spatial variation in body size for both groups on this continent. Thus, we cannot conclude that interspecific trends in variation in body size are size-dependent in squamate reptiles everywhere. However, there is a body size threshold in Europe (see Fig. 3), which suggests that this could still be a cause for the contrasting gradients found in this region. Clearly, analyses in other biogeographical regions are necessary to assess whether absolute organism size is driving interspecific body size patterns of reptiles.

In sum, in North America and Europe lizards tend to be larger and snakes smaller in low-energy regions, indicating that Bergmann's mechanism is insufficient to explain the body size patterns of these groups. But this mechanism was proposed for endotherms and does not explain how body size influences heat gain. Our results for Europe suggest that squamates shift from Bergmann's rule patterns to the converse as body size increases, reflecting the transition from a positive influence of increasing size on heat conservation for small squamate groups (lizards), to a negative influence when animals are too large for efficient heat gain in cold environments (snakes). However, our results for North America suggest that body size plays a secondary role in determining thermoregulation in some areas, and that complex body size patterns can be expected when physiological and behavioural thermoregulatory mechanisms prevail in a regional fauna. This in turn emphasizes that there may be no simple answer, so we need to document the patterns in other areas of the world if we are to understand the importance of body size in determining the biogeographical distribution of squamate species.

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BIOSKETCHES

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