Body size variation across climatic gradients and sexual size dimorphism in Tropidurinae lizards

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Abstract

In certain lineages of tetrapods, latitude and climate relate to body size in agreement with Bergmann's rule. Trends for squamates are ambiguous, even between genders within a species. Therefore, additional studies are required before generalizations can be made, and attention is needed to the possibility that male and female experience distinct selective pressures and display different patterns. We examine body size in male and female Tropidurinae lizard species and test both Bergmann's and Rensch's rule, using phylogenetic comparative methods. We also analyze whether trends are better explained by latitude or climatic conditions. In Tropidurinae lizards, body size does not vary in accordance with Bergmann's rule within the range of latitudes studied. Therefore, within this range, tropidurines seem not to experience thermal constraints limiting activity time, and therefore growth and body size. Yet, female body size relates to rain patterns, expectedly linked to productivity, suggesting that this gender experiences a stronger tradeoff between energy allocated to growth and to reproduction. In Tropidurinae, males tend to be larger than females and sexual dimorphism is male biased, with an isometric relationship between both sexes that does not support Rensch's rule.

Introduction

One long-standing question in the evolutionary literature is how the size of organisms varies along macrogeographic gradients. For example, several species of birds and mammals display larger body size at higher latitudes, a trend known as Bergmann's rule honoring the author who first noticed it (Bergmann, 1847). Bergmann's rule usually applies to species across macrogeographical gradients involving changes in thermal regime (Blackburn, Gaston & Loder, 1999 and references therein), thus favoring the view of climate as a causal factor. However, whether Bergmann's rule applies to ectothermic tetrapods is a complex question given the enormous diversity in natural history (Shine, 2005), and the role of ontogenetic phenotypic plasticity (Ledon-Rettig & Pfennig, 2011 and references therein) that distinguishes some lineages. To date, the relationship between body size and climate in ectothermic tetrapods remains ambiguous, even within squamates (Ashton & Feldman, 2003; Cruz et al., 2005; Olalla-Tarraga, Rodriguez & Hawkins, 2006; Pincheira-Donoso, Tregenza & Hodgson, 2007; Pincheira-Donoso, Hodgson & Tregenza, 2008). For example, some lineages of European lizards follow

Bergmann's rule, whereas snakes follow its inverse, and in North America complex patterns exist, probably in association with a broader taxonomic breadth (Olalla-Tarraga et al., 2006). Therefore, valid generalizations across lineages cannot be proposed at this time and lineage-specific questions are valuable.

Assuming no trophic constraints, larger body sizes are attained by faster growth rates, extended growth periods or both (Adolph & Porter, 1993). However, within a lineage of ectothermic tetrapods adapted to a similar thermal range, lower growth rates are expected in populations from colder climates (Adolph & Porter, 1993). This premise assumes covariation between body temperature and environmental temperature, and may be questionable in lineages able to thermoregulate behaviorally, especially under low predation risk. In heliothermic lizards, for example, environmental temperature may not be the best proxy for body temperature (Huey, Hertz & Sinervo, 2003) and comparable activity temperatures may characterize populations along geographical clines. For example, small heliothermic lizards at various elevations up to 3500 m may exhibit activity temperature near or above 30°C (reviewed by Navas, 2002). However, the buffering capacity of behavioral thermoregulation may have limits

and species from very high latitudes may experience body temperatures lower than expected (Medina *et al*., 2012). In addition, climate may affect productivity and other factors also relevant to body size (Dunham, 1978). Indeed, seasonality may be a better predictor of body size than environmental temperature (e.g. in rattlesnakes, see Ashton, 2001) and precipitation, a factor assumed to affect productivity, relates positively to body size in lizards (Brandt & Navas, 2011).

In some contexts, Bergmann's rule can be considered as a reaction norm of phenotype (body size) to a change in the environment (temperature). If so, patterns result from effects of temperature on individuals, but the norms themselves result from evolutionary adjustment (Angilletta, 2009). For example, the body size of one anuran species across an altitudinal range includes both acute and adaptive effects (Berven, 1982), and in general, individual and evolutionary adjustments are expected to co-occur in an observed Bergmann's rule pattern. In this case, common garden experiments are required to distinguish mechanisms (Garland & Adolph, 1991) and the evolutionary plasticity of such reaction norms can be studied with phylogenetic approaches (Felsenstein, 1985; Blackburn *et al*., 1999). However, different patterns of natural selection on males and females may lead to gender-specific thermal reaction norms of body size (Bolnick & Doebeli, 2003; Losos, Butler & Schoener, 2003) and to sexual size dimorphism (SSD). In animals, SSD is usually associated to sexual selection driving the evolution of size, and is commonly allometric (Abouheif & Fairbairn, 1997). The allometry of SSD is known as Rensch's rule (Rensch, 1950). This pattern when applied to taxa characterized by larger males, predicts that an evolutionary increase in the body size of individuals (i.e. male-biased SSD) would be paralleled by enhanced SSD (Abouheif & Fairbairn, 1997). This would be plausible because, in the context of sexual selection, males are expected to be more evolutionary plastic than females (Fairbairn, 1997). SSD and pressures associated to it may obscure a Bergmann pattern if male and female body size are averaged and is a strong argument in favor of independent analyses of such pattern in male and female data sets.

In lizards, environmental temperature along macrogeographic ranges may influence body size if thermoregulation cannot compensate for thermal variation, as discussed earlier, and patterns can be tested through empirical work (Underwood, Chapman & Connell, 2000). This paper aims to analyze the patterns of variation of body size in Tropidurinae lizard species across climates and latitudes. In this context, we ask if (1) latitude is a good proxy for climate (2), latitude or climate predict the average body size of species and predictions are similar for males and females, and (3) tropidurines exhibit SSD consistent with Rensch's rule. Tropidurines are good systems to test for such associations because they are widespread over a broad geographic range in South America (Frost, 1992), they occupy diverse habitats and are exposed to a wide range of climates. Furthermore, they are monophyletic, a condition enhancing the scope of studies on the evolution of body size (Blackburn *et al*., 1999).
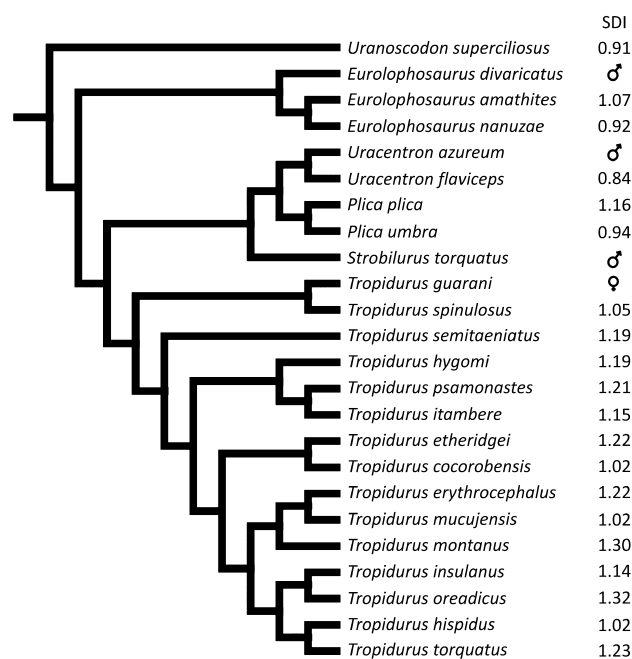

	SDI
Uranoscodon superciliosus	0.91
Eurolophosaurus divaricatus	♂
Eurolophosaurus amathites	1.07
Eurolophosaurus nanuzae	0.92
Uracentron azureum	♂
Uracentron flaviceps	0.84
Plica plica	1.16
Plica umbra	0.94
Strobilurus torquatus	♂
Tropidurus guarani	♀
Tropidurus spinulosus	1.05
Tropidurus semitaeniatus	1.19
Tropidurus hygomi	1.19
Tropidurus psamonastes	1.21
Tropidurus itambere	1.15
Tropidurus etheridgei	1.22
Tropidurus cocorobensis	1.02
Tropidurus erythrocephalus	1.22
Tropidurus mucujensis	1.02
Tropidurus montanus	1.30
Tropidurus insulanus	1.14
Tropidurus oreadicus	1.32
Tropidurus hispidus	1.02
Tropidurus torquatus	1.23

Figure 1 Topology of the Tropidurinae lizard species used in the comparative analyses, based on Frost *et al*. (2001). The column to the right indicates the calculated sexual dimorphism index (SDI) of body size (snout-vent length) between males and females, or the correspondent gender symbol if only males or females were sampled for that species. SDI values larger than 1 indicate species in which males are the larger sex.

Methods

Data set

The data on lizard body size (snout-vent length) used in this study comes from Brandt & Navas (2011) (females) and Grizante *et al*. (2010) (males, see Fig. 1). We obtained data on latitude and climate from available localities of individuals sampled in the collection, therefore this data do not necessarily represent the latitudinal midpoint of their distributional range. We extracted climatic data from Worldclim (Hijmans *et al*., 2005; http://www.worldclim.org) using DIVA-GIS (Hijmans *et al*., 2001) version 7.1 and pooled data for populations of the same species. The variables extracted were: annual precipitation (AP), annual mean temperature (AMT), isothermality, maximum temperature of the warmest month (MTWM), mean diurnal range (MDR), minimum temperature of the coldest month (MTCM), precipitation seasonality (PS), precipitation of the driest quarter (PDQ), precipitation of the wettest quarter (PWQ) and temperature seasonality. Although Worldclim data are obtained at a much greater scale than that composing the climatic envelope of individual lizards, within some constraints (Suggitt *et al*., 2011; Graae *et al*., 2012), we assume value for testing macrogeographical

patterns. Some consistency between data at these scales is expected (Holmes & Nelson Dingle, 1965).

Analyses

We conducted statistical analyses with R 2.14.1 (R Core Team, 2011) using RStudio (version 0.95.263). We reduced climatic variables to principal components and used in analyses those with eigenvalues larger than one. We used linear regression to analyze the relationship between climate and latitude. Because we had data for males in 23 species and for females in 21 species, we used slightly different topologies (Fig. 1) for each gender, both based on Frost *et al.* (2001). Unfortunately, we do not have enough information to estimate branch lengths, so we focused only on the topology. We applied the diagnosis plots proposed by Garland, Harvey & Ives (1992), which consists on relating standardized phylogenetic independent contrasts (PIC) to their standard deviations. Models with all branches equal one (All-One) and Pagel (1992) arbitrary branch lengths passed the diagnostics. We performed this tests using Mesquite v2.74 (Maddison & Maddison, 2010) with PDAP:PDTREE v1.15 (Midford, Garland & Maddison, 2010). Our approach to relate size and climate is based on Revell (2010). Briefly, we interpret the results of phylogenetic and standard models based on both phylogenetic association and regression, using phylogenetic regression with simultaneous optimization of the degree of phylogenetic correlation (Pagel's λ, PGLS$_\lambda$). The use of a PGLS$_\lambda$ modeling also allows for simultaneous detection of whether shared evolutionary history explains the observed patterns in the data. We compare models based on traditional and phylogenetic methods with Akaike Information Criterion (AIC) corrected for sample size (AICc) assuming best fit in the model with the smaller AICc value (Burnham & Anderson, 2002). Models with AICc values within two units of the best one were considered to exhibit similar fit.

We represented SSD by an index (SDI) over using the residuals of the regression of male to female body size data (reviewed by Smith, 1999). Specifically, we used the two-step ratio (Smith, 1999) with log transformed body size, which is a modification of the index originally proposed by Lovich & Gibbons (1992). Indexes > 1 indicate males are larger than females. We calculated PIC (Felsenstein, 1985) of male and female body size and used these contrasts to estimate the allometric slope of SSD by standard major axis (SMA, Warton *et al.*, 2006) regression through the origin. This analysis was implemented with the R package smatr 3 (Warton *et al.*, 2012). In this analysis, a slope greater than one suggests an allometric trend consistent with Rensch's rule. We also tested for the minimal amount of evolutionary divergence between genders using paired *t*-tests comparing male and female PIC of body size. In this context, PICs of body size larger in males than in females indicate that body size allometry is consistent with Rensch's rule. We did not evaluate if Rensch's rule follows a latitudinal pattern (e.g. Blanckenhorn *et al.*, 2006) because it turned out that tropidurines do not display a latitudinal pattern of variation in body size, and do not conform to Rensch's rule.

Table 1 Loadings of a principal component analysis performed on climatic variables for male tropidurines

Climatic variable	Component		
	1	2	3
Precipitation of wettest quarter	0.28	−0.07	0.95[a]
Precipitation of driest quarter	0.20	−0.89[a]	0.27
Annual precipitation	0.31	−0.37	0.87[a]
Precipitation seasonality	0.07	0.93[a]	−0.08
Minimum temperature of coldest month	0.86[a]	−0.41	0.19
Maximum temperature of warmest month	0.81[a]	0.47	0.11
Annual mean temperature	0.96[a]	−0.02	0.16
Temperature seasonality	0.88[a]	0.18	−0.30
Isothermality	0.78[a]	0.18	−0.30
Mean diurnal range	−0.15	0.87[a]	−0.12
Eigenvalue (% variation explained)	5.22 (39%)	2.67 (30%)	1.028 (20%)

Variables contributing most to each component are indicated by [a].

Table 2 Effect of latitude on climatic components retained for males and females

Gender	Component	r	P
Males	PC1	0.8547211	<0.001
	PC2	−0.1834239	0.4022
	PC3	0.1934378	0.3765
Females	CC1	−0.6641704	0.0014
	CC2	−0.1898345	0.4228

CC, climatic component (Brandt & Navas, 2011); PC, principal component of climatic variables.

Results

Body size, latitude and climate along Tropidurinae

The environmental data associated with male localities produced three main principal components (Table 1). PC1 (39% of total variance) displayed high loads for temperature variables and extreme events, and was the only component that correlated to latitude (Table 2). PC2 (30% of total variance) related to central tendency of temperature and precipitation variables and PC3 (20% of total variance) had high loads for precipitation only. Thus, tropidurines at higher latitudes experienced more seasonality in temperature, and lower MTCM, MTWM and AMT. Variables such as AP, MDR, PDQ, PS and PWQ, mainly related to PC2 and PC3, bore no relationship with latitude. In female tropidurines, a relationship between body size and latitude was supported only by a non-phylogenetic model (Table 3) and no model supported this relationship for males (Table 4). In contrast with published

Table 3 Latitude effect on body size across female tropidurines

Effect	Model	Slope	P	λ	AIC	AICc	dAICc
Null	GLS null	–	<0.00001	–	4.158	4.8	13.8
	PGLS$_{λAllOne}$	–	<0.00001	1	−10.354	−8.9	0
	PGLS$_{λPagel}$	–	<0.00001	0.929	−5.05	−3.6	5.3
Latitude	GLS	0.015	0.037	–	9.738	11.1	20.1
	PGLS$_{λAllOne}$	0.000	0.876	1	1.924	4.4	13.4
	PGLS$_{λPagel}$	0.003	0.557	0.891	5.425	7.9	16.8

AIC, Akaike Information Criterion; AICc, Akaike Information Criterion corrected for sample size; dAICc, difference between the best model (smallest AICc) and each model; GLS, general least squares (non-phylogenetic): PGLS, phylogenetic general least squares.

Table 4 Latitude and climate effect on body size across male tropidurinae

Effect	Model	Slope	P	λ	AIC	AICc	dAICc
Null	GLS	–	<0.00001	–	2.77	3.4	0.0
	PGLS$_{λAllOne}$	–	<0.00001	0.64	2.81	4.1	0.7
	PGLS$_{λPagel}$	–	<0.00001	0.39	3.55	4.8	1.4
Latitude	GLS	0.012	0.094	–	9.95	11.2	7.8
	PGLS$_{λAllOne}$	0.009	0.186	0.28	11.82	14.0	10.7
	PGLS$_{λPagel}$	0.011	0.133	0.11	11.88	14.1	10.7
PC1	GLS	0.076	0.103	–	6.33	7.6	4.2
	PGLS$_{λAllOne}$	0.064	0.162	0.48	7.32	9.5	6.2
	PGLS$_{λPagel}$	0.070	0.128	0.30	7.55	9.8	6.4
PC2	GLS	−0.002	0.972	–	9.04	10.3	6.9
	PGLS$_{λAllOne}$	0.108	0.060	0.93	5.49	7.7	4.3
	PGLS$_{λPagel}$	0.113	0.057	0.80	6.81	9	5.7
PC3	GLS	5.496	0.182	–	7.21	8.5	5.1
	PGLS$_{λAllOne}$	0.035	0.437	0.49	0.44	11	7.6
	PGLS$_{λPagel}$	0.050	0.282	0.147	9.12	11.3	8.0

AIC, Akaike Information Criterion; AICc, Akaike Information Criterion corrected for sample size; dAICc, difference between the best model (smallest AICc) and each model; GLS, general least squares (non-phylogenetic); PGLS, phylogenetic general least squares.

patterns for females (Brandt & Navas, 2011; see Discussion), climate did not influence body size of male tropidurines (Table 4).

Sexual size dimorphism and Rensch's rule

Across species, males were on average 7.55 mm larger than females (paired t-test, t = 3.2328, d.f. = 19, P-value = 0.004). The SSD (SDI two-step ratio) ranged from 0.842 (*Uracentron flaviceps*) to 1.318 (*Tropidurus oreadicus*), and is larger than one in 16 of the 20 studied species (Fig. 1). Body size was more evolutionarily flexible in males than in females (SMA, slope = 1.245, r^2 = 0.75, P-value < 0.001) although the relationship between male and female body size was isometric (95% confidence interval: 0.975–1.589, r = 0.4, d.f. = 17, P-value = 0.08), as corroborated also by the paired t-test between PIC of male and female body size (t = −1.7148, d.f. = 18, P-value = 0.1036).

Discussion

Latitude as a proxy for climate

We found that climatic variation cannot be predicted by latitude within the latitudinal gradient experimented by Tropidurinae species. Latitude has been used as a proxy for climate under the assumption that higher latitudes exhibit colder climates (Hawkins & Diniz, 2004), in a historical approach predating large-scale climatic databases. However, latitude may display spurious correlations with biological variables such as species richness (Hawkins & Diniz, 2004), so that variables directly linked to climate may be more informative to test biological relationships. Within the spectrum of our study, latitude seems a good proxy for thermal regime, particularly extreme events. This is still significant in ecogeography because larger temperature variability has been associated with an increase in the geographic range of species, possibly because larger thermal tolerance breadths are favored (Addo-Bediako, Chown & Gaston, 2000). In contrast, the precipitation components of climate bear no clear relationship with latitude, perhaps because they are more heavily influenced by other phenomena such as continentality (Ruggiero & Lawton, 1998), which in Brazil affects wind circulation and rain patterns (Cavalcanti *et al.*, 2009). Therefore, ecogeographical trends involving rain patterns may be independent of latitude within the range studied.

Body size, climate and gender in Tropidurinae

Not all squamata conform to Bergmann's rule. Lizard lineages may (Cruz *et al.*, 2005; Olalla-Tárraga *et al.*, 2006) or may not (Lindsey, 1966; Dunham, Miles & Reznick, 1988; Pincheira-Donoso *et al.*, 2008; Oufiero *et al.*, 2011) exhibit a relationship between body size and latitude; and snake lineages may slightly increase (Lindsey, 1966; Ashton, 2001) or decrease (Ashton, 2001; Olalla-Tárraga *et al.*, 2006) body size with latitude. It is possible that these various patterns reflect differential constrains of latitude on energy uptake, which would be modulated by both activity time and productivity. At a given latitude, the geographical heterogeneity of the thermal environment may constrain activity time in some lizard lineages (Adolph & Porter, 1993; Sears, 2005), but this seems not the case of tropidurines. Indeed, it seems viable that individual tropidurine lizards can remain active for around 10 hours a day within the latitudinal range of our study (Martori & Aun, 1994; Vitt & de Carvalho, 1995; Vitt & Zani, 1996; Faria & Araújo, 2004). Rain patterns, on the other hand, are expectedly related to productivity (Dunham, 1978). Therefore, they may affect tradeoffs between growth and reproduction, particularly in females, because of their strong energy allocation to eggs (Fitch, 1981). This scenario is compatible with observations on tropidurines because habitats with greater indexes of precipitation favor larger females (Brandt & Navas, 2011) but this relationship does not hold for males. Under this view, reproduction would constrain female growth rates whereas juvenile or

non-reproducing females would escape such constrain (Schwarzkopf, 1993). In addition, male tropidurines exhibit faster growth rates in comparison with females (e.g. *T. itambere*, Van Sluys, 1998; and *T. torquatus*, Pinto, Wiederhecker & Colli, 2005). Similar patterns have been reported in other lizard taxa (van Devender, 1978). Therefore, female of various lizard taxa, tropidurines among them, may be resource limited in relation to males.

Sexual dimorphism in body size and Rensch's rule

We corroborate a trend in which males are larger than females in tropidurine species (Vitt, 1991; Vitt & Zani, 1996; Van Sluys, 1998; Pinto *et al.*, 2005; Rocha & Siqueira, 2008). The underlying evolutionary mechanisms involved in this trend may be explored based on the independent analysis of pattern in males and females. When sexual selection is a factor, the prediction is positive allometry consistent with Rensch's rule (Abouheif & Fairbairn, 1997; Dale *et al.*, 2007). Therefore, enhanced body size and SSD are expected, because males would increase size at higher evolutionary rates than females (Abouheif & Fairbairn, 1997). However, tropidurines present an isometric pattern that is not easily explained by sexual selection alone. Therefore, although sexual selection cannot be discarded as an influential factor, conceivably, females experience a stronger tradeoff between growth and reproduction.

Acknowledgments

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