The importance of phylogenetic scale in tests of Bergmann's and Rapoport's rules: lessons from a clade of South American lizards

F. B. CRUZ*,†, L. A. FITZGERALD,† R. E. ESPINOZA‡ & J. A. SCHULTE II§

*CONICET, CRUB-Universidad Nacional del Comahue, Quintral, S. C. Bariloche, Rio Negro, Argentina
†Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX, USA
‡Department of Biology, California State University, Northridge, CA, USA
§Division of Amphibians and Reptiles, National Museum of Natural History, Washington, DC, USA

Abstract

We tested for the occurrence of Bergmann's rule, the pattern of increasing body size with latitude, and Rapoport's rule, the positive relationship between geographical range size and latitude, in 34 lineages of *Liolaemus* lizards that occupy arid regions of the Andean foothills. We tested the climatic-variability hypothesis (CVH) by examining the relationship between thermal tolerance breadth and distribution. Each of these analyses was performed varying the level of phylogenetic inclusiveness. Bergmann's rule and the CVH were supported, but Rapoport's rule was not. More variance in the data for Bergmann's rule and the CVH was explained using species belonging to the *L. boulengeri* series rather than all species, and inclusion of multiple outgroups tended to obscure these macroecological patterns. Evidence for Bergmann's rule and the predicted patterns from the CVH remained after application of phylogenetic comparative methods, indicating a greater role of ecological processes rather than phylogeny in shaping the current species distributions of these lizards.

Introduction

The recent groundswell of species and higher level phylogenies coupled with the advent of modern comparative methods has provided evolutionary biologists with the opportunity to re-examine many long-held adaptive hypotheses. One area that has experienced such revitalization is the evaluation of various biological 'rules'. In particular, Bergmann's and Rapoport's rules have attracted considerable recent attention. Bergmann's rule was proposed to explain a general pattern of increasing body size with increasing latitude or elevation (Bergmann, 1847; Ashton *et al.*, 2000; Blackburn & Ruggiero, 2001; Ashton & Feldman, 2003; Reed, 2003), whereas Rapoport's rule describes the positive relationship between the geographical range size of species with increasing latitude or elevation (Stevens, 1989, 1992; Price *et al.*, 1997; Stephens & Wiens, 2003). Documenting the underlying pattern and a possible basis for these rules is crucial for understanding patterns of species richness and distributions (Reed, 2003).

In his seminal work, Bergmann (1847, translated in James, 1970) described a relationship between increasing body size with decreasing environmental temperature among closely related species. Nearly a century later Mayr (1956) revised the definition to describe latitudinal variation in size within a species. Recently, Blackburn *et al.* (1999) defined Bergmann's rule as a tendency for a positive relationship between body mass of species belonging to a monophyletic higher taxon and the latitude inhabited by these species. By requiring monophyly of examined taxa, Blackburn and coworkers identified the importance of phylogenetic scale for identification of Bergmann's rule. Blackburn & Ruggiero (2001) extended their definition to include elevation as well as latitude.

Four hypotheses have been offered to explain Bergmann patterns (Gaston & Blackburn, 2000;

Correspondence: CONICET, CRUB-Universidad Nacional del Comahue, Quintral 1250, (8400) S. C. Bariloche, Rio Negro, Argentina.
Tel.: +54 2944 461 021; fax: +54 2944 422 111;
e-mail: fcruz@crub.uncoma.edu.ar

Blackburn & Ruggiero, 2001): (1) phylogenetic history, (2) interspecific variation in migration, (3) variation in resistance to starvation and (4) variation in the ability of species to conserve or dissipate heat. However, there is no evidence that a single variable is responsible for Bergmann patterns (Partridge & Coyne, 1997) and these variables may be manifested differently among or within species. Gay & Best (1996) showed that among potential climatic variables affecting latitudinal gradients in body size within a species temperature was a better predictor than rainfall, although seasonality can be a better predictor than either rainfall or temperature in some cases (Lindstet & Boyce, 1985). Recent intraspecific studies found a decrease in body size of vertebrates presumed to be associated with global warming (O'Brien *et al.*, 2000; Portner, 2001).

Selection acting on variation in thermal tolerance may limit the extent of geographical species distribution, thereby acting as a mechanism underlying Rapoport's rule (Gaston & Blackburn, 2000). The climatic-variability hypothesis (CVH) predicts that species with broad thermal tolerances should be resistant to variable climatic conditions (Stevens, 1989; Addo-Bediako *et al.*, 2000). Hence, thermal tolerance should correlate positively with geographical range size. Yet, studies of the thermal tolerance of species over latitudinal or elevational gradients are rare (Addo-Bediako *et al.*, 2000). Other mechanisms proposed to explain Rapoport's rule are: (1) differential extinction rates as a consequence of glaciations, (2) less competition at higher latitudes due to lower species richness, (3) the land–area relationship, especially in the Northern Hemisphere and (4) hard biogeographical boundaries (Gaston & Blackburn, 2000). The first two hypotheses are difficult to test, whereas land area and boundary effects can be controlled through careful selection of the study system.

The relationship between body size, geographical range size and latitude is not straightforward. Diverse groups of organisms demonstrate a strong correlation between body size and geographical range with large species having a large geographical distribution and small species occupying both large and small land areas (Gaston & Blackburn, 1996a,b; Reed, 2003). If large-bodied species are found at higher latitudes in accordance with Bergmann's rule, these species also may occupy a larger geographical area, biasing the effect of Rapoport's rule (Reed, 2003). Therefore, the link between body size, latitude, and geographical range must be assessed when studying these rules. Ideally, a rigorous test of these patterns would include a monophyletic group whose range was extensive in latitude and elevation and for which related biological data are available.

Lizards of the *Liolaemus boulengeri* series and closely related clades (subgenera *Eulaemus* and *Liolaemus*) provide a unique opportunity to perform tests for Bergmann's and Rapoport's rules within a phylogenetic framework, as well as address the importance of body

size and the CVH for interpreting these ecological rules. The species in the *L. boulengeri* series range from 16 to 50°S latitude (spanning 3700 km of latitude) and from sea level to >5000 m. This group includes 26 described and several undescribed species (Etheridge, 1995; Etheridge & Espinoza, 2000; Etheridge & Christie, 2003). The taxonomy used in this paper follows Schulte *et al.* (2000). We present data collected for 21 species of the *L. boulengeri* series, including three undescribed, genetically distinct forms. Species belonging to this clade inhabit similar types of desert habitat (Monte, Puna and Patagonian steppe) and use similar microhabitats (Halloy *et al.*, 1997; Schulte *et al.*, 2004). Thus, we assume that by using similar microhabitats along similar types of deserts, the thermal characteristics of these microhabitats are comparable. Furthermore, the desert habitat occupied by members of the *L. boulengeri* series does not suffer the effect of narrowing towards the south (as with southern forests; Ruggiero & Lawton, 1998), so land area or profound biogeographical boundary effects are not expected.

Here, we test whether patterns of body size follow Bergmann's rule in the *L. boulengeri* series, as well as *Liolaemus* species sampled from other clades within the subgenera *Eulaemus* and *Liolaemus*. We also test whether the geographical distributions of these species follow Rapoport's rule. To evaluate thermal tolerance breadth as a mechanism to explain Rapoport's rule, we test for a relationship between this variable and latitudinal extent of geographical distribution. There has been increased interest recently in testing both rules (e.g. Gaston & Chown, 1999a; Addo-Bediako *et al.*, 2000; Ashton, 2001b; Blackburn & Ruggiero, 2001), and the validity of Bergmann's and Rapoport's rules has been called into question (Gaston *et al.*, 1998; Ashton, 2001b). For this reason, some authors refer to the patterns as effects instead of rules (Gaston *et al.*, 1998; Ruggiero & Lawton, 1998). Even though these patterns do describe effects, we retain the use of their traditional names to be consistent with previous use in the literature.

Although including taxa generally increases statistical power, addition of taxa also expands the phylogenetic scale over which ecological patterns can be evaluated. If species in different clades exhibit dissimilar macroevolutionary patterns, the variance attributed to the inclusion of more distantly related taxa may obscure the detection of such patterns even if they are present within some clades in the analysis (Fig. 1). Consequently, it is important to evaluate patterns within, as well as among clades. As noted above, previous authors have disagreed over whether these rules are more appropriately applied intra- vs. interspecifically. We tested the influence of phylogenetic scale in detecting Bergmann's rule, Rapoport's rule, and the CVH in *Liolaemus* lizards by testing for these patterns using phylogenetically independent contrasts for 34 taxa representing members of several related clades, and just within the monophyletic *L. boulengeri* series. The
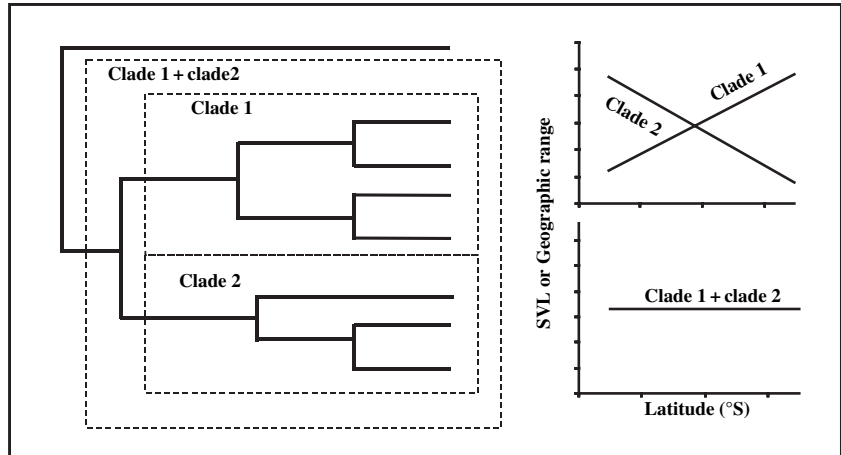
Fig. 1 Phylogenetic scale may obscure macroecological patterns such as Bergmann's or Rapoport's rules. When ecological patterns differ for clades 1 and 2, there may be no correlation when the two clades are plotted together.
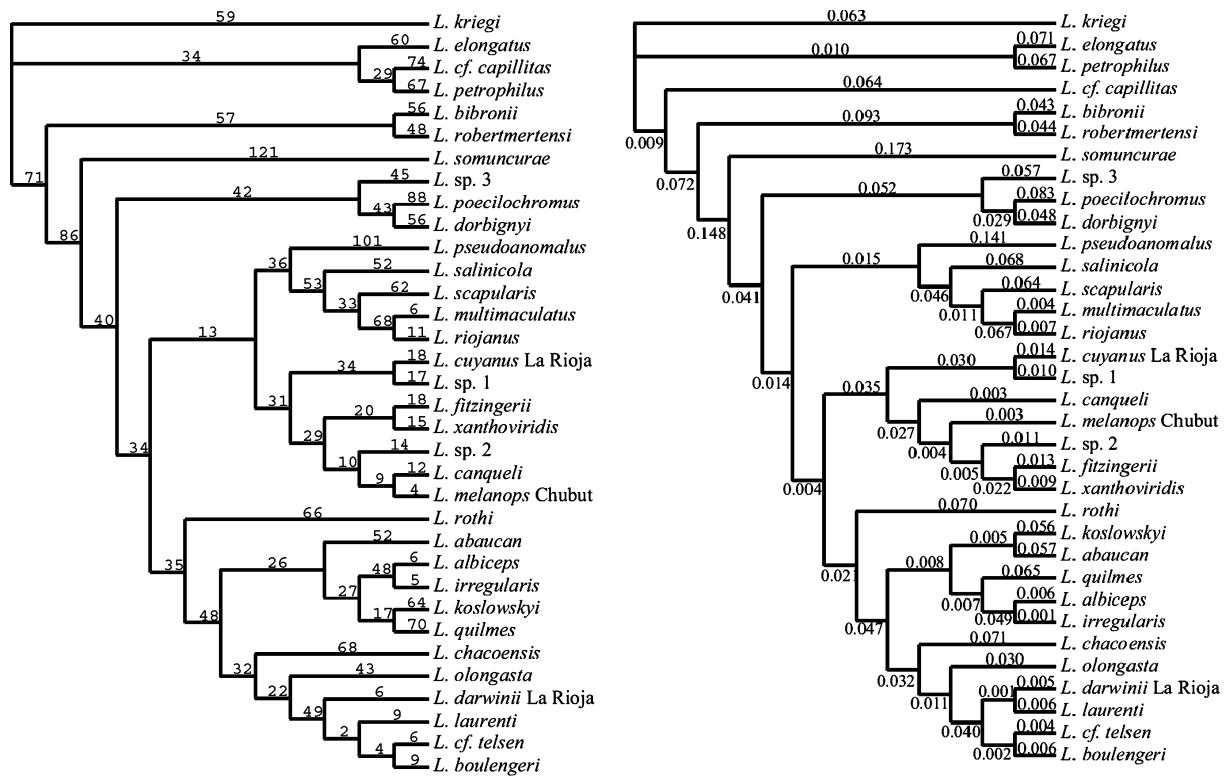

Fig. 2 Phylogeny of *Liolaemus* lizards sampled in the *L. boulengeri* series and several species from the subgenera *Liolaemus* (*L. kriegi, L. elongatus, L. petrophilus, L.* cf. *capillitas, L. bibronii, L. robertmertensi*) and *Eulaemus* (all other species). Numbers below branches represent branch lengths obtained from parsimony analysis (left) and likelihood analysis (right) of mtDNA sequence data.

availability of a phylogeny for lizards of the *L. boulengeri* series and related clades (Fig. 2) allowed us to evaluate the importance of phylogenetic scale in detecting broad ecological patterns such as Bergmann's rule and Rapoport's rule. The CVH has not been tested in ectothermic vertebrates with phylogenetically based comparative methods, despite arguments suggesting that

traits related to thermal tolerance may be inherited and are taxonomically constrained (Bogert, 1949).

Methods

We collected data from 333 specimens representing 34 lineages of *Liolaemus* and ranging from north-western
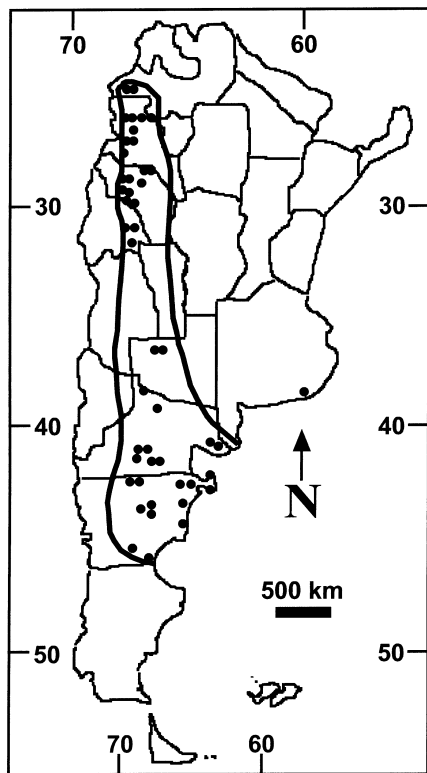
Fig. 3 Map of Argentina indicating collecting localities of *Liolaemus* species. The bold line indicates the extent of Patagonian shrub-steppe and Monte xeric habitats. The habitat of the single locality on the Atlantic coast is sand dunes.

to south-eastern Argentina and from sea level to over 3800 m (Fig. 3). Individuals of each species were collected from one locality except *L. multimaculatus* and *L. cuyanus* that were collected at two proximate localities, and *L. darwinii*, which was collected at three localities. No statistical differences in thermal tolerance were found among these populations (*L. darwini* $F_{2,17} = 2.56$, $P > 0.107$; *L. multimaculatus* $t_8 = 2.09$, $P > 0.83$, *L. cuyanus* $t_9 = 0.031$, $P > 0.73$); therefore, we pooled the data for each species, however we are aware of low sample size in these data sets. Twenty-four taxa are members of the *L. boulengeri* series, including four species in the *L. wiegmannii* subclade. The remaining 10 taxa are used as outgroups with six species in the subgenus *Liolaemus*, three members of the *L. montanus* series and one member of the *L. lineomaculatus* section (*L. somuncurae*). Temperature data were not available for *L. somuncurae* and sequences were not available for *L. kingii*. However, these taxa are more closely related to each other than any other taxa used in our analyses (see Etheridge, 1995), so they were subsequently used interchangeably. The 15 non-*boulengeri*-series species were used as outgroups and to improve statistical power of the bivariate analyses based on independent contrasts (Bonine & Garland, 1999).

Lizards were captured by noosing or by hand between November and early March (austral summer) 1999–2003. Lizards were housed in small groups of the same species in aquaria in the lab where room temperature was maintained near 29 °C and exposed to a (13L : 11D) photoperiod. Temperature experiments (described below) were conducted no more than 12 days after lizards were captured. Lizards were not fed during this period but water was available *ad libitum*. Only nonreproductive adults were used for thermal trials. Thus, our data are comparable to previous studies of critical temperatures (Lutterschmidt & Hutchison, 1997).

Measures of temperature tolerance

We measured the critical maximum and minimum temperature (CTMax and CTMin, respectively) for each specimen. The critical temperature was recorded as the temperature at which individuals lost the ability to right themselves after being placed in a supine position (Cowles & Bogert, 1944; Spellerberg, 1973; Carothers *et al.*, 1997). To determine CTMax, lizards where placed individually in an aluminium cylinder (260 mm diameter × 340 mm deep), containing a 30 mm layer of sand to avoid thermal conductance from the aluminium bottom. Individuals were previously cooled to 18 °C, then placed in the cylinder and heated by a 100 W light bulb 70 mm above the container. A thermocouple was taped to the lizard cloaca and body temperature (T_b) was monitored every 30 s, and every 10 s following the onset of gaping. To determine CTMin, lizards (T_b 20 °C) were placed individually in plastic containers (lids had holes for temperature and air exchange), which were placed in a −10 °C freezer, and their T_b was monitored every 20 s. The thermal tolerance range of each species was calculated by subtracting the mean CTMin from the mean CTMax.

Data on maximum body size (snout–vent length; SVL) and distribution (degrees latitude and elevation in m) were taken from the literature (Cei, 1986, 1993; Etheridge, 1995; Espinoza *et al.*, 2004, Table 1). SVL is a widely accepted measure of body size for squamate reptiles and is correlated with body mass and numerous ecological, morphological and life-history traits (Pough, 1973).

Recent work on the taxonomy and distribution of the *L. boulengeri* series has greatly improved our knowledge of this species-rich South American lizard clade (Etheridge & Espinoza, 2000; Etheridge & Christie, 2003). As noted above, there are several undescribed species included in our analyses, as well as other discovered, yet undescribed species. The taxa we sampled for this study are the most well studied members of the *L. boulengeri* series whose distribution is known with reasonably good accuracy. Undescribed species are expected to have a close phylogenetic relationship to all

Table 1 Species of *Liolaemus* lizards analysed.

Liolaemus species	n	SVL (mm)	Elevational range (m)	Latitudinal range (°S)	Thermal tolerance range CTMin–CTMax (°C)
L. abaucan	8	65	1200–1900	27°19′–27°47′	15.41–47.30
L. albiceps	11	93	3060–4020	23°30′–24°26′	7.05–44.33
L. andinus poecilochromus	6	72	3500–4400	24°00′–27°00′	9.35–44.16
L. bibronii	8	61	0–3000	32°00′–49°00′	8.49–44.53
L. boulengeri	9	78	0–2000	34°00′–42°00′	9.40–43.99
L. canqueli	12	100	900–900	43°00′–44°03′	6.99–44.60
L. capillitas	6	93	2500–3900	27°20′–27°27′	7.47–43.70
L . cf. telsen	18	75	0–800	42°55′–46°29′	8.98–44.60
L. chacoensis	4	55	700–700	23°00′–34°00′	14.90–44.10
L. cuyanus	18	102	400–2000	27°19′–33°00′	12.00–45.70
L. darwinii	20	69	800–3000	28°28′–42°55′	10.11–44.68
L. dorbignyi	6	101	3200–4400	22°02′–28°00′	8.83–43.91
L. cf. elongatus	4	85	700–3000	29°00′–46°00′	7.68–45.10
L. fitzingerii	16	108	0–1100	44°00′–50°00′	8.24–44.45
L. irregularis	5	90	3060–5000	23°55′–24°11′	6.96–44.98
L. kingii	7	100	0–1000	43°00′–51°40′	7.01–44.50
L. koslowskyi	26	82	800–2450	27°11′–29°18′	13.22–46.10
L. kriegi	4	115	950–2000	34°00′–42°04′	7.60–43.67
L. laurenti	16	73	800–1100	28°10′–30°12′	12.20–46.18
L. melanops	10	99	900–2070	36°26′–43°00′	5.65–44.94
L. multimaculatus	12	72	0–1000	35°00′–41°01′	8.93–43.83
L. olongasta	10	67	900–1770	28°38′–31°14′	11.85–44.58
L. petrophilus	8	100	900–1400	41°20′–43°50′	7.31–45.23
L. pseudoanomalus	11	68	990–1700	27°00′–32°00′	12.19–45.93
L. quilmes	10	89	1600–3000	24°43′–27°03′	8.46–44.69
L. riojanus	2	62	500–1000	29°00′–32°00′	10.70–45.20
L. robertmertensi	5	63	690–2600	27°00′–29°15′	14.07–43.00
L. rothi	2	97	500–1600	40°00′–41°25′	5.50–43.80
L. salinicola	9	74	0–2050	27°00′–32°07′	14.20–48.21
L. scapularis	22	77	1000–2100	23°00′–32°00′	9.39–45.57
L . sp. 1	3	95	400–2000	33°00′–37°39′	7.30–45.00
L . sp. 2	9	90	0–400	44°00′–44°45′	8.06–44.70
L . sp. 3	8	68	3300–3400	23°00′–23°22′	9.67–43.85
L. xanthoviridis	8	94	0–100	37°00′–44°00′	7.86–44.48

n is the number of individuals in thermal biology trials. Snout–vent length data are maximums reported by Cei (1986, 1993) or from Espinoza *et al.* (2004). Elevational and latitudinal distribution data are from Espinoza *et al.* (2004) and Cei (1986, 1993. Thermal range (CTMax–CTMin) was measured in the laboratory (see Methods for details).
SVL, snout–vent length; CTMin, critical minimum temperature; CTMax, critical maximum temperature.

species sampled for this study (Etheridge & Christie, 2003), so expected to have similar body size, geographical distributions, and life history traits.

Phylogenetic information

Two independent data sets are available that include most of the species in our analyses (Etheridge, 2000; Schulte *et al.*, 2000). We chose data from Schulte *et al.* (2000) because all taxa in this study could be included allowing the estimation of branch lengths for comparative analyses. We present new sequence data for species not considered in Schulte *et al.* (2000) and include sequences presented in Harmon *et al.* (2003). New

sequence data include *L*. cf. *telsen*, *L*. sp. 1, *L*. sp. 2, and *L*. sp. 3. New sequences have been deposited in GenBank (accession numbers to be included upon acceptance of the manuscript) and the alignment used for phylogenetic analyses is available from TreeBase (Study accession number S1281; Matrix accession number M2237). Harmon *et al.* (2003) include phylogenetic data for *L. canqueli*, *L. kriegi*, *L. riojanus* and *L. xanthoviridis*.

The phylogeny and branch lengths were obtained using PAUP* beta version 4.0b10 (Swofford, 2002) from maximum parsimony (MP) and maximum likelihood (ML) analysis of mtDNA sequences spanning the protein-coding genes ND1 to COI (Schulte *et al.*, 2000) using only the species for which ecological data were

available. Phylogenetic trees were estimated with 200 heuristic searches featuring random taxon addition under the MP optimality criterion. For ML analyses, the best fitting model parameters using the General Time Reversible substitution model with proportion of invariant sites and among site variation estimated from the sequence data were fixed then used in 25 heuristic searches with random addition of taxa to find the overall best likelihood topology. ModelTest v3.06 (Posada & Crandall, 1998) was used to find the best fitting model of sequence evolution for the tree from the unweighted parsimony analysis of these molecular data. The resulting phylogenies under MP and ML are shown in Fig. 2.

Geographical distribution

Temperature declines with increasing elevation as well as increasing latitude (Bergmann, 1847; Ashton, 2002a). Therefore, it is necessary to account for the effect of elevation on ambient temperature when investigating the temperature dependence of the latitudinal range of a species. Assuming equal conditions, temperature declines 0.65 °C for every 100-m increase in elevation (Lutgens & Tarbuck, 1998). To correct our dataset for latitudinal and elevational covariation in temperature, we plotted the reduction in temperature every 2° latitude from 20 to 55°S against the elevational temperature gradient (0.65 °C for every 100-m rise in elevation), and computed a correction factor by adding 1.752° latitude for every 200-m increase in elevation after a baseline of 600 m above sea level. We applied this constant to adjust the latitudinal range midpoint for each *Liolaemus* species according to its elevational midpoint occurrence. This value is referred hereafter as the adjusted latitudinal midpoint.

Bivariate linear regressions were calculated between each of the following variables: extent of geographical range (degrees latitude), latitudinal range midpoint, elevational range midpoint, CTMin, and adjusted latitudinal range of each species. To test for Bergmann's rule, we used SVL as the dependent variable. Extent of geographical range is the most common variable used when testing Rapoport's rule and tends to be highly correlated with area measures of range size (Gaston *et al.*, 1998; Reed, 2003). Thermal tolerance range and CTMin were used as dependent variables in regressions against extent of geographical range and adjusted latitude in testing the CVH as a mechanism underlying Rapoport's rule. As mentioned above, SVL in squamate reptiles correlates strongly with numerous biological traits. This body size measure was regressed against thermal tolerance range and CTMin to explore its impact on our analyses of Bergmann's rule, as well as extent of geographical range (Gaston & Blackburn, 1996a,b; Reed, 2003) to examine for a potential bias in our test of Rapoport's rule.

Comparative analyses

A priori and *a posteriori* tests for serial independence (TFSI; Abouheif, 1999) were used to assess the adequacy of applying independent contrasts to our data. We applied the tests for all 34 taxa, and for species only in the *L. boulengeri* clade. The null hypotheses in TFSIs were that trait data are independent and not significantly phylogenetically autocorrelated. When we failed to reject the null hypothesis of no phylogenetic autocorrelation by *a priori* TFSIs, we used conventional methods of analysis. When the hypothesis was rejected in an *a priori* test, we proceeded with independent contrast analyses (Felsenstein, 1985) for that trait dataset. *A posteriori* TFSIs were then performed on the independent contrasts, and the procedure ended if we failed to reject the null hypothesis of serial independence. Abouheif (1999) recommended caution in interpreting results in cases when the null hypothesis was rejected in *a posteriori* tests, because phylogenetic signal could persist in the dataset even after independent contrasts were computed.

We used environmental traits, specifically elevational and latitudinal range, in comparative analyses. Individuals inherit adaptations from ancestors that may also have inhabited similar environments (Garland *et al.*, 1992). For example, the ancestor of species capable of living in a certain elevational range may also have been capable of inhabiting the same elevational gradient. Hence, the heritability of these traits is complex because of heritability of traits at the individual level can scale up to heritabilities at the level of species (Jablonski, 1987). We computed phylogenetically independent contrasts (Felsenstein, 1985) using COMPARE v. 4.4 (Martins, 2001). Regressions of independent contrasts, with positivized horizontal axes, were forced through the origin to allow for meaningful interpretations (Garland *et al.*, 1992).

Traits such as body size or thermal tolerance may have evolved in different ways among members of a clade, and may fit one evolutionary model better than another (Garland *et al.*, 1992; Mooers *et al.*, 1999). For this reason, we applied three evolutionary models to our data prior to computing independent contrasts: (a) a nonhistorical model using untransformed species data for the ecological and geographical traits (internal nodes were collapsed and tip branch lengths set equal to one), (b) gradual model using branch lengths derived from the phylogenetic analysis, (c) speciational model where branch lengths were set equal to 1.0.

Results

Body size, geographical distribution and thermal tolerance

Adult SVL ranged from 55 to 115 mm among species, with a mean of 83.3 mm (SD = 15.6) for all 34 species

(Table 1). Species ranged from 22°02′S latitude (*L. dorbignyi*) in north-western Argentina to 51°40′S (*L. kingii*) in southern Patagonia (Fig. 3). None of the distributions of the species reached the geometrical southern limit of the continent (approximately 55°S). *Liolaemus rothi* had the lowest CTMin at 5.5 °C, and the highest CTMax recorded was 48.2 °C (*L. salinicola*). *Liolaemus melanops* had the broadest thermal tolerance range (39.3 °C), and *L. robertmertensi* had the narrowest (28.9 °C) (Table 1).

When body size was regressed against geographical range size, the relationship was not significant regardless of the phylogenetic analysis, evolutionary model, or if we used all species or only species of the *L. boulengeri* clade. The best fit obtained was the one for species belonging to the *L. boulengeri* clade, using the parsimony analysis and speciational model ($r^2 = 0.086$, $P > 0.235$, $N = 18$). The relationships among body size and thermal tolerance range and body size and CTMin were highly significant in nonhistorical analyses using only *L. boulengeri* series species, but not when all species were included (all 34 species, thermal tolerance $r^2 = 0.10$; n.s., $n = 34$; CTMin $r^2 = -0.106$; n.s., $n = 34$; *L. boulengeri* series species, thermal tolerance $r^2 = 0.754$; $P < 0.001$, $n = 19$; CTMin $r^2 = 0.710$; $P < 0.001$, $n = 19$). Regressions using the tree from MP analysis were not significant; however, regressions using the ML tree were significant for all analyses except that using a gradual model and only *L. boulengeri* series species (all 34 species, speciational model, thermal tolerance $r^2 = 0.422$; $P < 0.05$, $n = 33$, CTMin $r^2 = -0.398$; $P < 0.05$, $n = 33$; all 34 species, gradual model, thermal tolerance $r^2 = -0.342$; $P < 0.05$, $n = 33$; CTMin $r^2 = -0.340$; $P = 0.049$, $n = 33$; *L. boulengeri* series species, speciational model, thermal tolerance $r^2 = 0.546$; $P < 0.05$, $n = 18$, CTMin $r^2 = -0.408$; $P < 0.05$, $n = 18$).

Bergmann's rule

Tests for serial independence detected significant phylogenetic autocorrelation in analyses using all 34 species for SVL, elevation, and the two latitudinal variables under both models of evolutionary change based on both parsimony and likelihood trees (Table 2). We therefore computed phylogenetic independent contrasts for those variables.

We found statistical support for Bergmann's rule among the *Liolaemus* lizards studied. Bivariate regressions on the raw data (considered as nonhistorical) revealed statistically significant after Bonferroni correction ($P < 0.017$), positive correlations between SVL and latitudinal midpoint and adjusted latitudinal midpoint when all species were combined (Fig. 4). There was no relationship between elevational range and SVL.

The relationship between independent contrasts for SVL and adjusted latitude was statistically significant and positive for the gradual model for all species using

Table 2 Probability values from tests for serial independence (TFSI; Abouheif, 1999) calculated for geographical range, body size (snout–vent length), and thermal data for all species combined and for the *L. boulengeri* clade separately. Statistically significant results ($P < 0.05$) are indicated with asterisks. In cases where the null hypothesis of phylogenetic independence was not rejected in *a priori* tests, independent contrasts were not computed, and *a posteriori* TFSIs were not applicable (n/a). See Methods for explanation.

	Gradual model		Speciation model	
	A priori	A posteriori	A priori	A posteriori
Parsimony all species combined				
Snout–vent length	0.006*	0.115	0.016*	0.327
Latitude	0.003*	0.184	0.005*	0.021*
Elevation	0.003*	0.073	0.001*	0.118
Adjusted latitude	0.001*	0.387	0.001*	0.203
Extent of geographical range	0.324	n/a	0.352	n/a
Thermal tolerance range	0.146	n/a	0.130	n/a
CTMin	0.194	n/a	0.204	n/a
***L. boulengeri* clade only**				
Snout–vent length	0.005*	0.122	0.006*	0.097
Latitude	0.004*	0.413	0.006*	0.339
Elevation	0.244	n/a	0.291	n/a
Adjusted latitude	0.029*	0.159	0.013*	0.072
Extent of geographical range	0.008*	0.239	0.006*	0.211
Thermal tolerance range	0.060	n/a	0.048*	0.007*
CTMin	0.050*	0.047*	0.302	n/a
Likelihood All species combined				
Snout–vent length	0.007*	0.234	0.005*	0.429
Latitude	0.003*	0.247	0.002*	0.079
Elevation	0.001*	0.024*	0.001*	0.051
Adjusted latitude	0.001*	0.104	0.001*	0.454
Extent of geographical range	0.381	n/a	0.425	n/a
Thermal tolerance range	0.039*	0.364	0.039*	0.056
CTMin	0.025*	0.120	0.029*	0.045*
***L. boulengeri* clade only**				
Snout–vent length	0.002*	0.054	0.003*	0.482
Latitude	0.001*	0.371	0.001*	0.488
Elevation	0.004*	0.020*	0.003*	0.031*
Adjusted latitude	0.023*	0.147	0.018*	0.245
Extent of geographical range	0.232	n/a	0.245	n/a
Thermal tolerance range	0.025*	0.279	0.008*	0.512
CTMin	0.004*	0.377	0.023*	0.357

CTMin, critical minimum temperature.

parsimony analysis (Table 3; Fig. 4). The body size-adjusted latitude midpoint relationship calculated using nonhistorical data explained more variance in the dataset ($r^2 = 0.525$; $P < 0.001$, $n = 34$) than did independent contrasts using the gradual model (parsimony tree, $r^2 = 0.444$; $P < 0.01$, $n = 33$). Nevertheless, there was no justification for choosing the nonhistorical model because of phylogenetic nonindependence of the data.

When only the *L. boulengeri* species were included in analyses with raw data, the relationship between SVL and adjusted midpoint latitude was stronger than for all
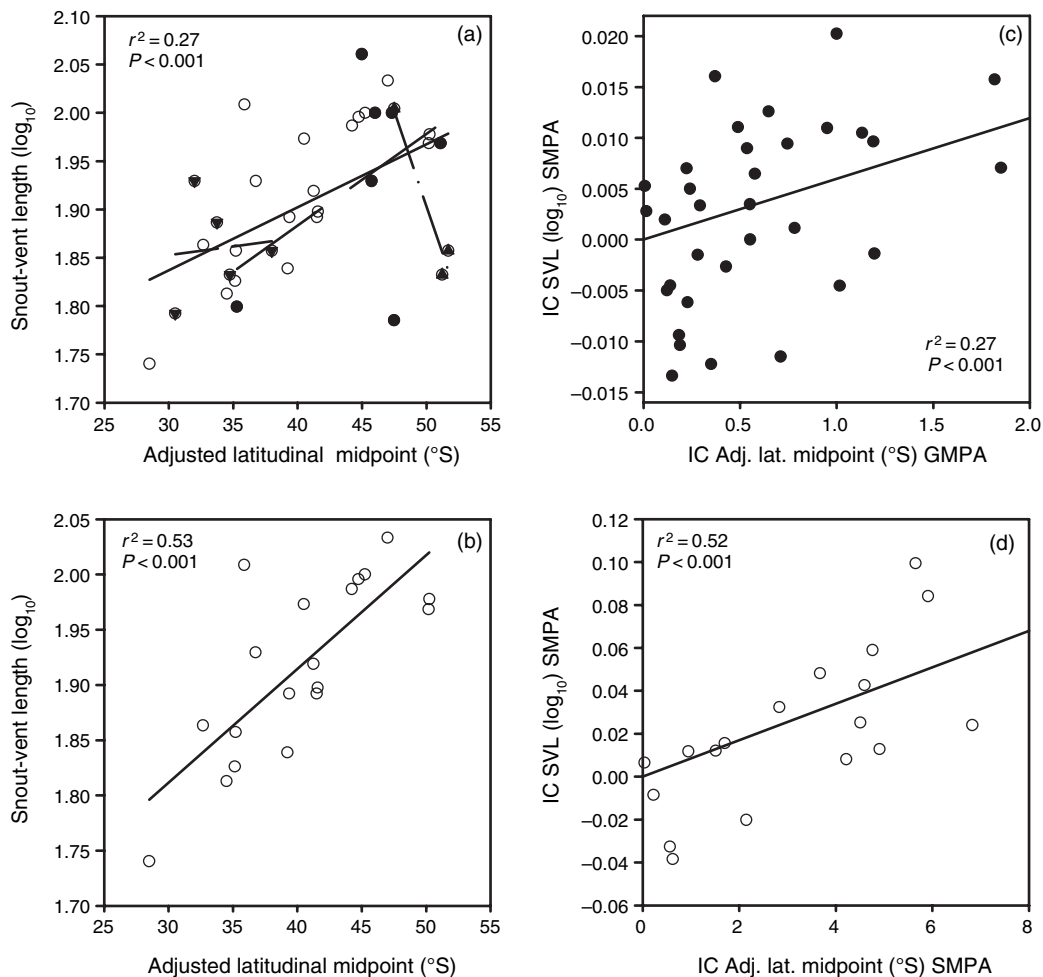
Fig. 4 Regression analyses of adjusted latitudinal midpoint and snout–vent length used to test for Bergmann's rule in *Liolaemus* lizards using raw data and phylogenetic independent contrasts (IC). (a) The relationship using raw data and all species. Unfilled circles denote species in the *L. boulengeri* clade; inverted triangles the *L. wiegmannii* clade, filled circles the *L. chiliensis* clade, and upright filled triangles the *L. andinus* clade. None of the three small clades showed a significant relationship. (b) The relationship using raw data for species only in the *L. boulengeri* clade. (c) The relationship based on IC of the traits for all species using parsimony analysis and gradual model (GMPA). (d) The relationship based on IC for species only in the *L. boulengeri* clade using parsimony analysis and speciational model (SMPA).

species, and accounted for 53% of the variance in the dataset compared with 28% using all taxa (Fig. 4). Within the *L. boulengeri* series, results of TFSI revealed that most trait datasets exhibited significant phylogenetic autocorrelations under both models and trees with few exceptions (Table 2). Support for Bergmann's rule was found within the *L. boulengeri* clade using independent contrasts for SVL and adjusted midpoint latitude (Table 4). Analyses using the likelihood tree were highly significant under both models (gradual, $r^2 = 0.600$; $P < 0.01$, $N = 18$; speciational, $r^2 = 0.604$; $P < 0.001$, $n = 18$). The fit using the parsimony tree was significant under the speciational model ($r^2 = 0.717$; $P < 0.001$, $n = 18$), and not the gradual model ($r^2 = 0.449$; $P = 0.059$, $N = 18$).

Rapoport's rule

The relationship between extent of geographical range and latitudinal midpoint was significant for all species in nonhistorical analyses ($r^2 = 0.455$; $P < 0.01$, $N = 34$; Fig. 5). However, adjusted latitudinal midpoint and elevation midpoint did not correlate with geographical range (Table 3). We did not find significant associations between extent of geographical range and elevation midpoint and adjusted latitudinal midpoint using raw data for species in the *L. boulengeri* clade or for all historical analyses (Tables 3 and 4).

The TFSIs for extent of geographical range and thermal variables for all species combined were not significant using the parsimony tree, and thermal tolerance range

Table 3 Results of hypothesis tests of Bergmann's rule, Rapoport's rule, and the climatic-variability hypothesis.

Variable and evolutionary model	Likelihood analysis			Parsimony analysis		
	Latitude midpoint	Adj. Lat. midpoint	Elevation midpoint	Latitude midpoint	Adj. Lat. midpoint	Elevation midpoint
Body size (SVL)						
Nonhistorical (raw data)	0.406* (0.017)	0.525* (0.000)	0.074 (0.678)			
Gradual model	0.395 (0.021)	0.393 (0.023)	0.135 (0.445)	0.380 (0.026)	0.444* (0.009)	0.114 (0.520)
Speciational model	0.335 (0.053)	0.363 (0.035)	0.044 (0.805)	0.320 (0.065)	0.379 (0.027)	0.051 (0.775)
Extent of geographical range (degrees latitude)						
Nonhistorical (raw data)	0.455* (0.007)	0.051 (0.774)	−0.257 (0.143)			
Thermal tolerance range (°C)						
Nonhistorical (raw data)	0.432* (0.011)	0.594* (0.000)	−0.046 (0.798)			
Gradual model	0.318 (0.066)	0.222 (0.207)				
Speciational model	0.465* (0.006)	0.564* (0.000)	0.026 (0.884)			
CTMin (°C)						
Nonhistorical (raw data)	−0.464* (0.006)	−0.714* (0.000)	0.025 (0.888)			
Gradual model	−0.523* (0.002)	−0.671* (0.000)	0.011 0.952			
Speciational model	−0.792* (0.003)	−0.713* (0.000)	−0.030 (0.856)			

Correlation coefficients are shown from bivariate regressions of environmental variables vs. body size, geographical range, thermal tolerance, and critical thermal minimum (CTMin) as the dependent variables. *P*-values are in parentheses, and statistically significant results after Bonferroni correction ($P < 0.017$) are indicated with asterisks. Correlation coefficients were calculated using raw data and phylogenetic independent contrasts under two models of evolutionary trait change for the entire dataset of 34 species. Coefficients were not calculated in cases where tests for serial independence indicated that phylogenetic independent contrasts were not appropriate.
SVL, snout–vent length.

Table 4 Results of hypothesis tests of Bergmann's rule, Rapoport's rule, and the climatic-variability hypothesis for the *L. boulengeri* series only (19 species). Format and abbreviations as in Table 3. Elevation Midpoint for Parsimony analysis was not calculated because of phylogenetic nonindependence.

Variable and evolutionary model	Likelihood analysis			Parsimony analysis	
	Latitude midpoint	Adj. Lat. midpoint	Elevation midpoint	Latitude midpoint	Adj. Lat. midpoint
Body size (SVL)					
Nonhistorical (raw data)	0.416 (0.077)	0.732* (0.000)	−0.078 (0.750)		
Gradual model	0.318 (0.185)	0.600* (0.009)	0.306 (0.202)	0.251 (0.287)	0.449 (0.059)
Speciational model	0.359 (0.131)	0.604* (0.008)	0.320 (0.181)	0.340 (0.156)	0.717* (0.001)
Extent of geographical range (degrees latitude)					
Nonhistorical (raw data)	0.301 (0.210)	0.360 (0.131)	−0.231 (0.340)		
Gradual model				0.349 (0.154)	0.140 (0.240)
Speciational model				−0.097 (0.591)	−0.120 (0.621)
Thermal tolerance range (°C)					
Nonhistorical (raw data)	0.337 (0.159)	0.807* (0.000)	−0.211 (0.385)		
Gradual model	0.243 (0.317)	0.267 (0.269)			
Speciational model	0.337 (0.170)	0.613* (0.006)		0.391 (0.107)	0.462 (0.043)
CTMin (°C)					
Nonhistorical (raw data)	−0.405 (0.086)	−0.824* (0.000)	0.225 (0.354)		
Gradual model	−0.433 (0.064)	−0.627* (0.004)	−0.070 (0.775)	−0.410 (0.081)	−0.402 (0.085)
Speciational model	−0.436 (0.062)	−0.721* (0.000)	−0.142 (0.563)		

SVL, snout–vent length.

and CTMin were significant using the likelihood tree. However, there was significant nonindependence of the data within the *L. boulengeri* clade using both trees for most variables (Table 2). Therefore, we tested for evidence of Rapoport's rule using phylogenetic independent contrasts, and did not find statistical support under either model of evolutionary change with either tree (Table 4).

We found support for the CVH based on analyses of raw data for all species. There were significant positive correlations between thermal tolerance range and mid-
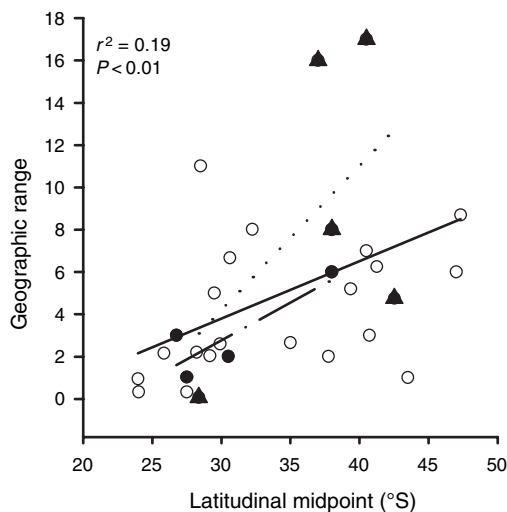
Fig. 5 Regression analysis of latitudinal extent of geographical range and latitudinal midpoint used to test Rapoport's rule for all species using raw data. None of the relationships for the three small clades was significant. Symbols follow those in Fig. 4.

point latitude, and adjusted latitudinal midpoint for all species combined. The most robust relationship was between thermal tolerance range and adjusted midpoint latitude, which accounted for 35% of the variance in the dataset for all species (Fig. 6). The CVH predicts a negative correlation between CTMin and latitude because high latitude species should have lower CTMin. Accordingly, we found significant negative correlations ($P < 0.017$, after Bonferroni correction; Rice, 1989) between CTMin and latitudinal midpoint, and adjusted latitudinal midpoint, with the latter providing the best fit (all species: $r^2 = 0.714$; $P < 0.001$, $n = 34$; Fig. 7).

The relationships between thermal tolerance range and adjusted midpoint latitude, and between CTMin and adjusted latitudinal midpoint were more robust when species in the *L. boulengeri* clade were analysed separately from the other *Liolaemus* species. Within the *L. boulengeri* clade, the relationship between thermal tolerance range and adjusted midpoint latitude explained 65% ($P < 0.001$, $n = 19$; Fig. 6) of the variance in the regression model. Similarly, the relationship between adjusted latitudinal midpoint and CTMin within the *boulengeri* clade explained 68% (Fig. 7).

The TFSIs revealed significant phylogenetic nonindependence for all species and within the *L. boulengeri* clade for both models using the likelihood tree. The results using independent contrasts for all species and the *L. boulengeri* clade also supported the CVH. Independent contrasts of adjusted latitudinal midpoint were positively correlated with contrasts of thermal tolerance range under the speciational model (all species, $r^2 = 0.564$; $P < 0.001$, $n = 33$; *L. boulengeri*, $r^2 = 0.613$; $P < 0.01$, $n = 18$; Fig. 6) and negatively correlated with contrasts

of CTMin under both models (all species, gradual model, $r^2 = -0.671$; $P < 0.001$, $n = 33$; all species, speciational model $r^2 = -0.713$; $P < 0.001$, $n = 33$; *L. boulengeri*, gradual model, $r^2 = -0.627$; $P < 0.01$, $n = 18$; *L. boulengeri*, speciational model, $r^2 = -0.721$; $P < 0.001$, $n = 18$; Tables 3 and 4; Fig. 7). The relationship between geographical range and thermal tolerance was significantly positive for the species of the *L. boulengeri* species, only when computing independent contrasts for both evolutionary models (speciational model $r^2 = 0.234$, $P < 0.05$, $n = 18$; gradual model $r^2 = 0.275$; $P < 0.05$, $n = 18$). No significant relationship was found between geographical range and CTMin.

Discussion

Phylogenetic scale and Bergmann's rule

Bergmann's rule, one of the oldest macroecological patterns (Gaston & Blackburn, 2000), is widely supported among species of endotherms (Blackburn *et al.*, 1999; Ashton *et al.*, 2000; Gaston & Blackburn, 2000; Ashton, 2002b); however, the pattern has seldom been tested for ectotherms at any taxonomic level (Hawkins & Lawton, 1995; Mousseau, 1997; Ashton, 2001a, 2002a; Ashton & Feldman, 2003). A recent analysis found a reverse intraspecific Bergmann trend for a large number of squamate reptiles, which was suggested to be the product of selection for rapid heating (therefore smaller body size) in cooler regions. The results of our interspecific analysis indicate that body size in the *Liolaemus* lizards we studied followed the traditional form of Bergmann's rule. Body size was larger for species at higher latitudes, particularly when latitude was adjusted for elevational effects.

Variation in the strength of Bergmann's rule in *Liolaemus* depended on the phylogenetic scale of the analysis. Although we found evidence for Bergmann's rule for the entire monophyletic clade of 34 species, inclusion of all species from the subgenera *Liolaemus* and *Eulaemus* weakened the relationship between body size and latitude (Table 3). There was no relationship between body size and latitude for the subset of taxa in the *L. chiliensis* clade and the correlation was weak in our sample of the *L. wiegmannii* group (results not shown). However, our sampling in these latter clades was decidedly sparse relative to that for members of the *L. boulengeri* series. Nevertheless, the strong, positive, size-latitude relationship in the *L. boulengeri* clade apparently accounted for the pattern observed for the entire dataset.

Sensitivity to phylogenetic (or taxonomic) scale has been demonstrated in studies of Bergmann's rule in other vertebrate lineages, although the effect was not explicitly discussed in those studies. Among Andean birds, Bergmann's rule was stronger when the dataset was analysed by genus than by family (Blackburn & Ruggiero, 2001). Different clades of *Crotalus viridis*
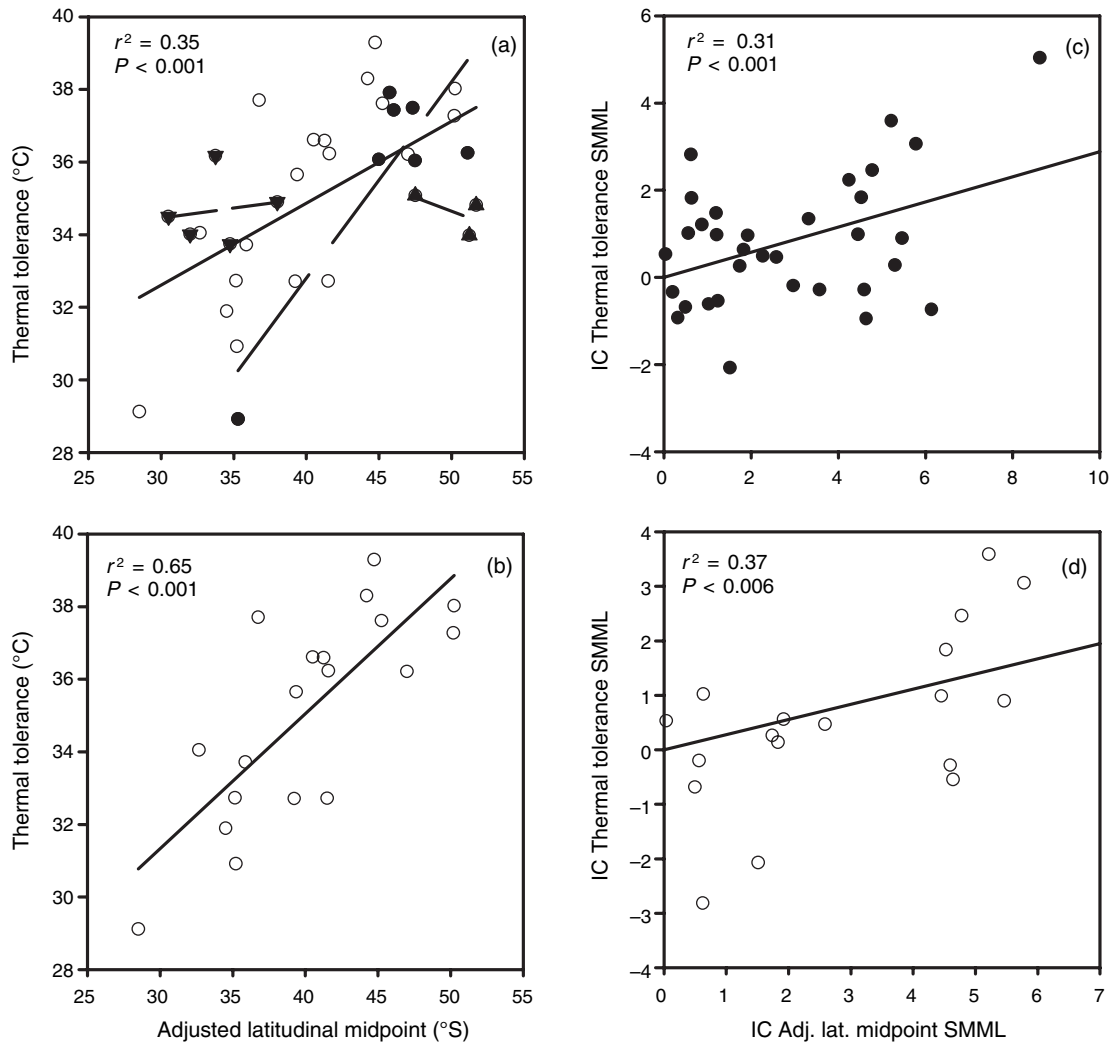
Fig. 6 Regression analyses of adjusted latitude midpoint and thermal tolerance range used to test the climatic-variability hypothesis. (a) The relationship using raw data and all species. *Liolaemus chiliensis* clade showed a significant positive correlation ($r^2 = 0.727$, $P < 0.016$, $N = 7$); the other clades were not significant. (b) The relationship using raw data for species only in the *L. boulengeri* clade. (c) The relationship based on IC using speciational model and maximum likelihood (SMML) for all species. (d) The relationship based on IC using SMML for the species within the *L. boulengeri* clade. Symbols follow those used in Fig. 4.

rattlesnakes also follow different size-latitude trends. Bergmann's rule held for the eastern clade of rattlesnakes that inhabit relatively homogeneous environments throughout their range, but the western sister clade is distributed along a heterogeneous environmental gradient, and exhibited a reverse Bergmann's pattern (i.e. smaller size with increasing latitude; Ashton, 2001a). The *L. boulengeri* clade species we studied also occur in similar habitats over most of their latitudinal range, and clearly followed Bergmann's rule. The remaining *Liolaemus* species sampled here occupy a variety of distinct habitats including several rock-dwelling species (*L. dorbignyi, L. petrophilus, L. elongatus*) that

may exhibit a different trend in body size because of constraints imposed by their lifestyle rather than by latitude. Latitudinal patterns in body size are presumably easiest to detect among closely related species with similar habitat requirements because of less extensive life-history variation among clades occupying distinct environments.

Our results suggest increased variance attributed to phylogeny may confound results of macroecological studies, and the degree of shared history at lower taxonomic levels should improve the detection of these trends. Indeed, Bergmann (1847, translated in James, 1970) himself restricted his analyses to closely related
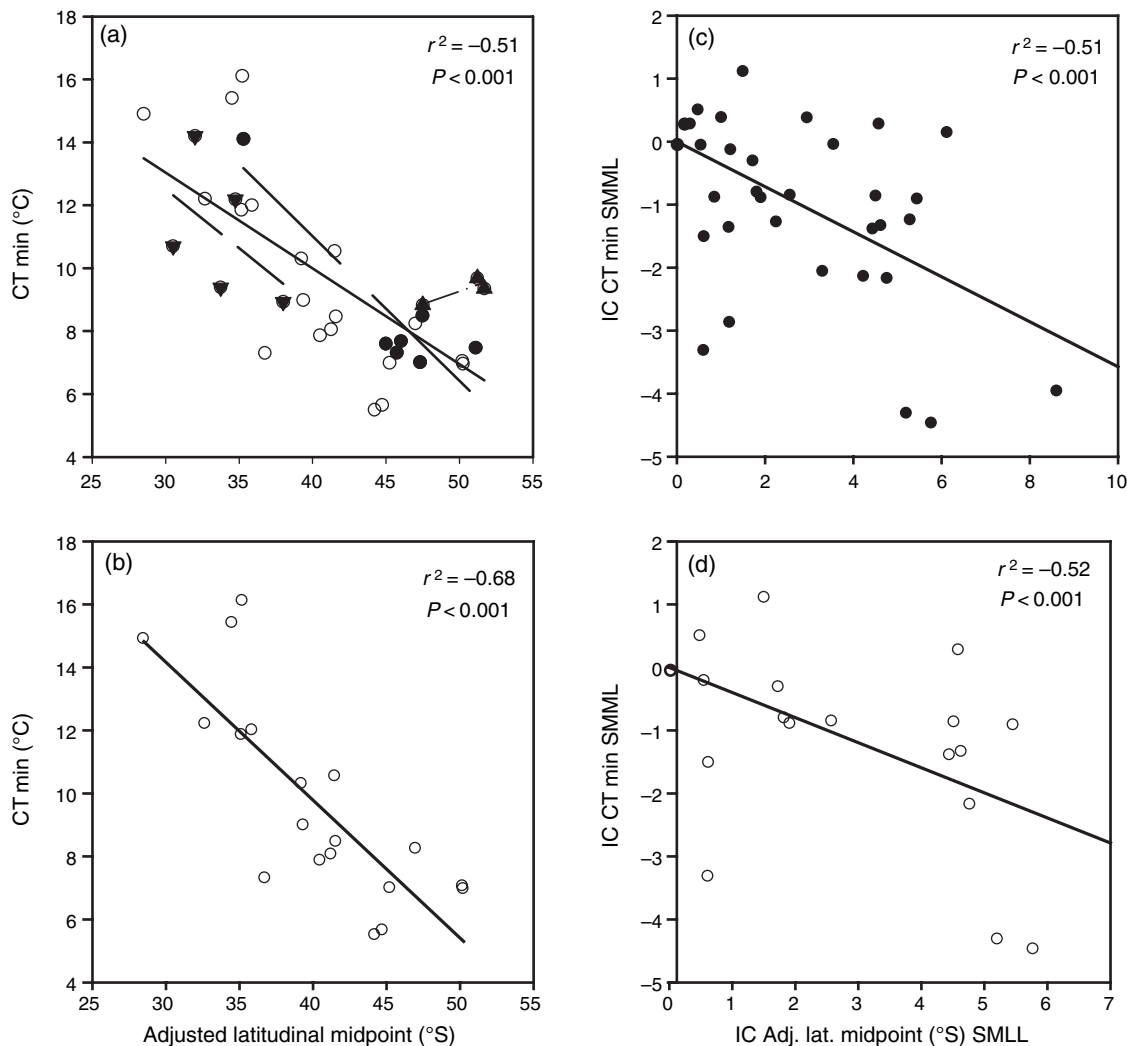
Fig. 7 Regression analyses of adjusted latitude and CTMin used to test the climatic-variability hypothesis. (a) The relationship using raw data and all species. Among the small clades, only the *L. chiliensis* clade showed a significant positive correlation ($r^2 = 0.807$, $P < 0.006$, $N = 7$). (b) The relationship using raw data for species only in the *L. boulengeri* clade. (c) The relationship based on IC for all the 34 species using maximum likelihood and speciational evolutionary model (SMML). (d) The relationship based on IC using SMML for the species belonging to the *L. boulengeri* clade. Symbols follow those used in Fig. 4.

species in a genus. Restricting analyses to species with a recently shared history (Ashton & Feldman, 2003) not only clarifies the ecological pattern, but also offers greater opportunities for identifying the mechanisms underlying these patterns.

Although no single mechanism may explain Bergmann's rule (Partridge & Coyne, 1997), our data can be used to address several of those that have been proposed (Gaston & Blackburn, 2000). First, we reject the hypothesis that the pattern is an artefact of phylogeny because the trends were apparent after conducting analyses that incorporated phylogenetic information. There are no data available to test the hypotheses that Bergmann's rule is a consequence of dispersal or

resistance to starvation (i.e. the premise that larger organisms take longer to starve) in presumably resource-poor environments such as high latitudes. However, it does not seem plausible that the body size range of *Liolaemus* lizards (55–115 mm SVL) is of sufficient magnitude to substantially influence dispersal capabilities or to impose dramatic differences in resistance to starvation. Our results demonstrating strong latitudinal and body-size relationships with thermal variables, coupled with the fact that thermal inertia is profoundly affected by body size in lizards (Huey, 1982), leads us to favour the heat-conservation hypothesis (Gaston & Blackburn, 2000) as the underlying mechanism for Bergmann's rule in *Liolaemus* lizards. The slower rate of

cooling associated with larger body size helps organisms conserve heat (Bell, 1980; Bartholomew, 1982), and is one mechanistic aspect of the heat-conservation hypothesis (Gaston & Blackburn, 2000; Blackburn & Ruggiero, 2001). Like other animals, larger *Liolaemus* lose heat more slowly than do smaller species (Carothers *et al.*, 1997).

The heat-conservation hypothesis for Bergmann's rule requires a physiological or anatomical mechanism. Dark coloration seems a reasonable adaptation for increasing the rate of heat gain in ectotherms at high latitudes (Pearson, 1977; Nussear *et al.*, 2001). *Liolaemus* lizards from cold climates tend to have black heads or black ventral surfaces (Cei, 1998), and these traits are known to facilitate heat absorption in lizards (Norris, 1967; Pearson, 1977; Porter & Tracy, 1983). Within the *L. boulengeri* clade in particular, the larger species tend to have either black heads or ventral surfaces, or both, and tend to occur at high latitudes. The exception is *L. cuyanus*, one of the largest species within the group, which inhabits moderate latitudes, and is typically not melanic. We suggest species in the *L. boulengeri* clade apparently possess two adaptations for inhabiting high latitudes, namely large body size and black coloration on one or more portions of the body, but this adaptive hypothesis requires further testing.

Climatic-variability hypothesis and Rapoport's rule

We found strong support for increasing thermal tolerance with increasing latitude for *Liolaemus* lizards in our study. Several important predictions of the CVH are consistent with our results. The CVH predicts that species should have lower CTMin at high latitudes and CTMax should be less variable among species than CTMin because CTMax more closely approaches the lethal temperature than does CTMin (Huey, 1982; Espinoza & Tracy, 1997). Thus, CTMin should be the primary constraint to latitudinal range limits because species with low CTMin should be able to occupy high, relatively cooler latitudes as well as warmer latitudes. Our results supported this prediction for all species in the analysis, and for those within just the *L. boulengeri* clade. Thermal tolerance range increased and CTMin decreased with increasing latitude. Within the *L. boulengeri* clade, CTMin averaged 10 °C lower for high-latitude species than for taxa from low latitudes. Following these predictions, CTMax was less variable than CTMin (Table 1).

An interspecific test of the CVH using conventional analysis for squamate reptiles found tropical lizards had narrower thermal tolerances than temperate species (van Berkum, 1988). The results presented here are the first test of the CVH in vertebrate ectotherms using phylogenetically comparative methods. As in the body size-latitude analyses, different clades of *Liolaemus* lizards exhibited different trends with significant phylogenetic autocorrelation within the *L. boulengeri* clade, but not when all 34 species were analysed together.

Spellerberg (1972) suggested that CTMin was less easy to avoid for lizards than CTMax, with the implication that CTMin should contribute more to setting distributional limits in relation to elevation or latitude. Evolutionary changes in lower thermal tolerances were greater than higher thermal tolerances in our study. Most iguanian lizards, including *Liolaemus*, exhibit bimodal daily activity patterns in temperate zones, escaping high temperatures by using retreats during the hottest hours of the day. However, for species in the *L. boulengeri* clade, it may be more difficult to avoid lower thermal limits. For example burrows used by these lizards are not very extensive (Halloy *et al.*, 1997). Thus, our findings support Spellerberg's (1972) premise that lower thermal tolerances play a role in defining latitudinal limits of species.

We found support for Rapoport's rule when all species were included in the nonhistorical analyses: latitudinal extent of geographical ranges of this sample of *Liolaemus* lizards was smaller at lower latitudes. However, we did not find support for Rapoport's rule within the *L. boulengeri* clade. A relationship between body size and range size (Reed, 2003), as well as incomplete data on species' distributions could create bias in analyses of Rapoport's rule (Brown *et al.*, 1996). Regardless, our phylogenetically corrected analyses did not reveal a pattern consistent with Rapoport's for our sample of *Liolaemus* species. Improved knowledge of the geographical ranges of *Liolaemus* species may help clarify this pattern but other possibilities should also be explored.

Thermal tolerance may be a better variable for use in tests of Rapoport-type effects than the geographical range for many groups, including the *Liolaemus* lizard species studied here. The alternative patterns exhibited by Northern and Southern hemisphere taxa in the New World (Gaston & Chown, 1999a) may reflect climatic conditions resulting from land-mass shape differences between North and South America rather than latitude alone. We found no evidence for phylogenetic non-independence in geographical range, which should not be surprising. Species' ranges result from complex interactions among many factors ranging from physiological traits, to the complex history of speciation and dispersal, and constraints resulting from continent shape (Webb & Gaston, 2003). Consequently, current geographical range size may not be reflected in patterns of inheritance across a phylogeny. Although geographical range may not follow a pattern of inheritance (but see Jablonski, 1987), there are underlying genetic components to thermal traits such as CTMin and CTMax. These traits could then play a role in determining species' ranges. For these reasons, the CVH has been a presumed proximate mechanism underlying Rapoport's rule (Gaston *et al.*, 1998; Gaston & Chown, 1999a,b; Addo-Bediako *et al.*, 2000; Gaston & Blackburn, 2000). The relationship between extent of geographical range and thermal tolerance range and CTMin produced mixed

results, suggesting that the CVH does not unequivocally explain the distribution patterns among these *Liolaemus* species.

Macroecological patterns could emerge as epiphenomena of land area effects and biogeographical boundaries (Ruggiero & Lawton, 1998; Gaston & Blackburn, 2000). Species' ranges should expand and contract easier within biomes than between them. In our datasets, body size and thermal tolerance ranges increased with latitude along arid environments of similar physiognomy, represented by the Monte, Patagonian shrub-steppe and Prepuna biotic provinces (Cabrera & Willink, 1980), where air temperature in lowlands is relatively constant from 25°N to 25°S (Terborgh, 1973). Continent size is different in the Northern and Southern Hemispheres and climatic changes are evident south of 25°S latitude (Gaston & Blackburn, 2000). Because of the general consistency of habitat along the latitudinal gradient we studied, land area and biogeographical boundaries were not likely to influence the positive correlations we found between body size, thermal variables and latitude.

Strong evidence for Bergmann's rule and predicted patterns from the CVH allowed us to infer macroecological patterns were more likely the result of ecological factors related to heat conservation rather than phylogenetic history. These patterns were sensitive to the scale of phylogenetic inclusiveness of the analysis, and including more species did not necessarily improve the strength of the relationships. The addition of species generally increases statistical power in comparative analyses; however, as demonstrated by our study of large-scale macroecological patterns, interactions among clades can weaken trends. Therefore, it is important to identify the phylogenetic scale relevant to the hypothesis investigated when applying phylogenetic comparative methods to studies of macroecology.

Acknowledgments

References

Abouheif, E. 1999. A method for testing the assumption of phylogenetic independence in comparative data. *Evol. Ecol. Res.* **1**: 895–909.

Addo-Bediako, A., Chown, S.L. & Gaston, K.J. 2000. Thermal tolerance, climatic-variability and latitude. *Proc. Roy. Soc. London B* **267**: 739–745.

Ashton, K.G. 2001a. Body size variation among mainland populations of the western rattlesnake (*Crotalus viridis*). *Evolution* **55**: 2523–2533.

Ashton, K.G. 2001b. Are ecological and evolutionary rules being dismissed prematurely? *Divers. Distrib.* **7**: 289–295.

Ashton, K.G. 2002a. Do amphibians follow Bergmann's rule. *Can. J. Zool.* **80**: 708–716.

Ashton, K.G. 2002b. Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. *Glob. Ecol. Biogeogr.* **11**: 503–523.

Ashton, K.G. & Feldman, C.R. 2003. Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution* **57**: 1151–1163.

Ashton, K.G., Tracy, M.C. & de Queiroz, A. 2000. Is Bergmann's rule valid for mammals? *Am. Nat.* **156**: 390–415.

Bartholomew, G.A. 1982. Physiological control of body temperature. In: *Biology of the Reptilia 12* (C. Gans & F. H. Pough, eds), pp. 167–211. Academic Press, New York.

Bell, C.J. 1980. The scaling of the thermal inertia of lizards. *J. Exp. Biol.* **86**: 79–85.

Bergmann, C. 1847. Ueber die Verhaltnisse der warmeokonomie der thiere zu ihrer grosse. *Gottinger Studien* **3**: 595–708.

van Berkum, F.H. 1988. Latitudinal patterns of the thermal sensitivity of sprint speed in lizards. *Am. Nat.* **132**: 327–343.

Blackburn, T.M. & Ruggiero, A. 2001. Latitude, elevation and body mass variation in Andean passerine birds. *Global Ecol. Biogeogr.* **10**: 245–259.

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

Bogert, C.M. 1949. Thermoregulation in reptiles, a factor in evolution. *Evolution* **3**: 195–211.

Bonine, K.E. & Garland, T. Jr 1999. Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. *J. Zool.* **248**: 255–265.

Brown, J.H., Stevens, G.C. & Kaufman, D.W. 1996. The geographic range: size, shape, boundaries and internal structure. *Ann. Rev. Ecol. Syst.* **27**: 597–623.

Cabrera, A. & Willink, A. 1980. Biogeografía de América Latina. Organización de los Estados Americanos (OEA), Washington D.C. *Ser. Biol., Monogr.* **13**: 1–122.

Carothers, J.H., Fox, S.F., Marquet, P.A. & Jaksic, F.M. 1997. Thermal characteristics of ten Andean lizards of the genus *Liolaemus* in central Chile. *Rev. Chil. Hist. Nat.* **70**: 297–309.

Cei, J.M. 1986. Reptiles del centro, centro-oeste y sur de la Argentina. *Mus. Reg.Sci. Nat., Torino, Monogr.* **4**: 1–527.

Cei, J.M. 1993. Reptiles del noroeste, nordeste y este de la Argentina. *Mus. Reg. Sci. Nat., Torino, Monogr.* **14**: 1–949.

Cei, J.M. 1998. La melanocephalie chez les lezards liolaemines et redecouverte de l'holotype de *Liolaemus melanops* Burmeister,

1888 longtemps considere momme perdu (Reptilia: Squamata: Iguania: Tropiduridae). *Rev. franc. d'Aquariol. Herpetol.* **25**: 59–62.

Cowles, R.B. & Bogert, C.M. 1944. A preliminary study of the thermal requirements of desert reptiles. *Bull. Am. Mus. Nat. Hist.* **83**: 264–296.

Espinoza, R.E. & Tracy, C.R. 1997. Thermal biology, metabolism, and hibernation. In: *The Biology, Husbandry and Health Care of Reptiles. Volume 1, Biology of Reptiles* (L. J. Ackerman, ed.), pp. 149–184. T.F.H. Publ., Neptune City, NJ, USA.

Espinoza, R.E., Wiens, J.J. & Tracy, C.R. 2004. Recurrent evolution of herbivory in small, cold-climate lizards: breaking the ecophysiological rules of reptilian herbivory. *Proc. Natl. Acad. Sci., USA* **101**: 16819–16824.

Etheridge, R. 1995. Redescription of *Ctenoblepharys adspersa* Tschudi 1845, and the taxonomy of Liolaeminae (Reptilia: Squamata: Tropiduridae). *Am. Mus. Nov.* **3142**: 1–34.

Etheridge, R. 2000. A review of the lizards of the *Liolaemus wiegmannii* group (Squamata, Iguania, Tropiduridae), and a history of morphological change in the sand-dwelling species. *Herpetol. Monogr.* **14**: 293–352.

Etheridge, R. & Christie, M.I. 2003. Two new species of the lizard genus *Liolaemus* (Squamta: Liolaemidae) from northern Patagonia, with comments on *Liolaemus rothi*. *J. Herpetol.* **37**: 325–341.

Etheridge, R. & Espinoza, R.E. 2000. Taxonomy of the Liolaeminae (Squamata: Iguania: Tropiduridae) and a semi-annotated bibliography. *Smithsonian Herpetol. Info. Serv.* **126**: 1–64.

Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.* **125**: 1–15.

Garland, T. Jr, Harvey, P.H. & Ives, A.R. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* **41**: 18–32.

Gaston, K.J. & Blackburn, T.M. 1996a. Range size–body size relationships: evidence of scale dependence. *Oikos* **75**: 479–485.

Gaston, K.J. & Blackburn, T.M. 1996b. Global scale macroecology: interactions between population size, geographic range size and body size in the Anseriformes. *J. Anim. Ecol.* **65**: 701–714.

Gaston, K.J. & Blackburn, T.M. 2000. *Pattern and Process in Macroecology*. Blackwell Science, Malden, MA, USA.

Gaston, K.J. & Chown, S.L. 1999a. Why Rapoport's rule does not generalize. *Oikos* **84**: 309–312.

Gaston, K.J. & Chown, S.L. 1999b. Elevation and climatic tolerance: a test using dung beetles. *Oikos* **86**: 584–590.

Gaston, K.J., Blackburn, T.M. & Spicer, J.I. 1998. Rapoport's rule: time for an epitaph? *Trends Ecol. Evol.* **13**: 70–74.

Gay, S.W. & Best, T.L. 1996. Relationship between abiotic variables and geographic variation in skulls of pumas (*Puma concolor*: Mammalia: Felidae) in North and South America. *Zool. J. Linn. Soc.* **117**: 259–282.

Halloy, M., Etheridge, R. & Burghardt, G.M. 1997. To bury in the sand: phylogenetic relationships among lizard species of the *boulengeri* group, *Liolaemus* (Reptilia, Squamata, Tropiduridae), based on behavioral characters. *Herpetol. Monogr.* **12**: 1–37.

Harmon, L.J., Schulte, J.A. II, Losos, J.B. & Larson, A. 2003. Tempo and mode of evolutionary radiation in iguanian lizards. *Science* **301**: 961–964.

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

Huey, R.B. 1982. Temperature, physiology, and the ecology of reptiles. In: *Biology of the Reptilia 12* (C. Gans & F. H. Pough, eds), pp. 25–91. Academic Press, New York.

Jablonski, D. 1987. Heritability at the species level; analysis of geographic ranges of Cretaceous mollusks. *Science* **238**: 360–363.

James, F.C. 1970. Geographic size variations in birds and its relationship with climate. *Ecology* **51**: 365–390.

Lindstet, S.L. & Boyce, M.S. 1985. Seasonality fasting endurance, and body size in mammals. *Am. Nat.* **125**: 456–465.

Lutgens, F.K. & Tarbuck, E.J. 1998. *The Atmosphere, an Introduction to Meteorology*, 7th edn. Prentice Hall, Upper Saddle River, NJ, USA.

Lutterschmidt, W.I. & Hutchison, V.H. 1997. The critical thermal maximum: history and critique. *Can. J. Zool.* **75**: 1561–1574.

Martins, E.P. 2001. *COMPARE, version 4.4. Computer Programs for the Statistical Analysis of Comparative Data*. Distributed by the author via the WWW at http://compare.bio.indiana.edu/. Depart. Biol., Indiana Univ., Bloomington, IN, USA.

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

Mooers, A.O., Vamosi, S.M. & Schluter, D. 1999. Using phylogenies to test macroevolutionary hypotheses of trait evolution in cranes (Gruinae). *Am. Nat.* **154**: 249–259.

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

Norris, K.S. 1967. Color adaptation in desert reptiles and its thermal relationships. In: *Lizard Ecology: A Symposium* (W. W. Milstead, ed.), pp. 162–229. Univ. Press Missouri, Columbia, MO, USA.

Nussear, K.E., Simandle, E.T. & Tracy, C.R. 2001. Misconceptions about colour, infrared radiation, and energy exchange between animals and their environments. *Herpetol. J.* **10**: 119–122.

O'Brien, C.M., Fox, C.J., Planque, B. & Casey, J. 2000. Fisheries: climate variability and North Sea cod. *Nature* **404**: 142.

Partridge, L. & Coyne, J.A. 1997. Bergmann's rule in ectotherms: is it adaptive? *Evolution* **51**: 632–635.

Pearson, O.P. 1977. The effect of substrate and of skin color on thermoregulation of a lizard. *Comp. Biochem. Physiol.* **58A**: 353–358.

Porter, W.P. & Tracy, C.R. 1983. Biophysical analyses of energetics, time-space utilization, and distributional limits. In: *Lizard Ecology: Studies of a Model Organism* (R. B. Huey, E. R. Pianka & T. W. Schoener, eds), pp. 55–83. Harvard Univ. Press, Cambridge, MA, USA.

Portner, H.O. 2001. Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. *Naturwissenschaften* **88**: 137–146.

Posada, D. & Crandall, K.A. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* **14**: 817–818.

Pough, F.H. 1973. Lizard energetics and diet. *Ecology* **54**: 837–844.

Price, T.D., Helbig, A.J. & Richman, A.D. 1997. Evolution of breeding distributions in the Old World leaf warblers (genus *Phylloscopus*). *Evolution* **51**: 552–561.

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

Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution* **43**: 223–225.

Ruggiero, A. & Lawton, J.H. 1998. Are there latitudinal and altitudinal Rapoport effects in the geographic ranges of Andean passerine birds? *Biol. J. Linn. Soc.* **63**: 283–304.

Schulte, J.A. II, Macey, J.R., Espinoza, R.E. & Larson, A. 2000. Phylogenetic relationships in the iguanid lizard genus *Liolaemus*: multiple origins of viviparous reproduction and evidence for recurring Andean vicariance and dispersal. *Biol. J. Linn. Soc.* **69**: 75–102.

Schulte J.A., II, Losos, J.B., Cruz, F.B. & Núñez, H. 2004. The relationship between morphology, escape behaviour and microhabitat occupation in the lizard clade *Liolaemus* (Iguanidae: Tropidurinae*: Liolaemini). *J. Evol. Biol.* **17**: 408–420.

Spellerberg, I.F. 1972. Temperature tolerances of south-west Australian reptiles examined in relation to reptile thermoregulatory behavior and distribution. *Oecologia* **9**: 23–46.

Spellerberg, I.F. 1973. Critical minimum temperature of reptiles. In: *Effects of Temperature on Ectothermic Organisms* (W. Wieser, ed.), pp. 239–247. Springer, Berlin.

Stephens, P.R. & Wiens, J.J. 2003. Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. *Am. Nat.* **161**: 112–128.

Stevens, G.C. 1989. The latitudinal gradient in geographical range: how so many species co-exist in the tropics. *Am. Nat.* **133**: 240–256.

Stevens, G.C. 1992. The elevational gradient in geographical range: an extension of Rapoport's latitudinal rule to altitude. *Am. Nat.* **140**: 893–911.

Swofford, D.L. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods), Version 4.0b10. Sinauer, Sunderland, MA, USA.

Terborgh, J. 1973. On the notion of favorableness in plant ecology. *Am. Nat.* **107**: 481–501.

Webb, T.J. & Gaston, K.J. 2003. On the heritability of geographic range sizes. *Am. Nat.* **164**: 553–566.