

BERGMANN'S RULE IN NONAVIAN REPTILES: TURTLES FOLLOW IT, LIZARDS AND SNAKES REVERSE IT

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Abstract.—Bergmann's rule is currently defined as a within-species tendency for increasing body size with increasing latitude or decreasing environmental temperature. This well-known ecogeographic pattern has been considered a general trend for all animals, yet support for Bergmann's rule has only been demonstrated for mammals and birds. Here we evaluate Bergmann's rule in two groups of reptiles: chelonians (turtles) and squamates (lizards and snakes). We perform both nonphylogenetic and phylogenetic analyses and show that chelonians follow Bergmann's rule (19 of 23 species increase in size with latitude; 14 of 15 species decrease in size with temperature), whereas squamates follow the converse to Bergmann's rule (61 of 83 species decrease in size with latitude; 40 of 56 species increase in size with temperature). Size patterns of chelonians are significant using both nonphylogenetic and phylogenetic methods, whereas only the nonphylogenetic analyses are significant for squamates. These trends are consistent among major groups of chelonians and squamates for which data are available. This is the first study to document the converse to Bergmann's rule in any major animal group as well as the first to show Bergmann's rule in a major group of ectotherms. The traditional explanation for Bergmann's rule is that larger endothermic individuals conserve heat better in cooler areas. However, our finding that at least one ectothermic group also follows Bergmann's rule suggests that additional factors may be important. Several alternative processes, such as selection for rapid heat gain in cooler areas, may be responsible for the converse to Bergmann's rule in squamates.

Key words.—Bergmann's rule, body size, ectotherms, geographic variation, meta-analysis, reptiles.

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The formulation of general ecological and evolutionary rules, such as Allen's rule, Cope's rule, and Gloger's rule, has a long and contentious history (see Mayr 1963; Gould 1997). Recently such rules have been criticized as artifactual or unproven (e.g., Gaston et al. 1998) because the data necessary to evaluate them have rarely been presented (Ashton 2001a). One such rule, originally proposed by Bergmann in 1847 and later redefined by Rensch (1938) and Mayr (1956), hypothesizes a general negative association between body size and environmental temperature within species of endothermic vertebrates. Bergmann's rule is often cited as an example of adaptive geographic variation (e.g., Mayr 1963; Ridley 1996; Futuyma 1998), yet the validity of this pattern and its underlying mechanisms has long been debated (e.g., Scholander 1955, 1956; Mayr 1956, 1963; Irving 1957). Recently, however, Bergmann's rule has received broad support in both mammals (Ashton et al. 2000) and birds (James 1970; Zink and Remsen 1986; Ashton 2002).

Despite the fact that general patterns of body size variation relative to environmental factors have been well studied in endothermic vertebrates for at least 150 years (reviewed in Rensch 1936; Mayr 1963; Ashton et al. 2000), no comprehensive surveys of intraspecific variation in body size exist for any group of ectothermic vertebrates. Several authors have hypothesized that ectotherms follow Bergmann's rule (Lindsey 1966; Atkinson and Sibly 1997) whereas others have contested the converse is true (Cowles 1945; Allee et al. 1949; Mousseau 1997). This debate recently resurfaced (e.g., Van Voorhies 1996, 1997; Mousseau 1997), prompted by two studies that suggested ectotherms in general follow Bergmann's rule. Atkinson (1994) reviewed laboratory ex-

periments that investigated the influence of developmental temperature on body size and found that individuals reared under cooler conditions were typically larger than those reared under warmer conditions. Van Voorhies (1996) found that decreased temperatures during development caused increased cell size in a species of nematode, and suggested the relationship between cell size and temperature may explain Bergmann's rule in ectotherms. Although these two studies suggest an underlying mechanism, neither reviewed body size patterns throughout the natural ranges of individual species, the evidence necessary to demonstrate Bergmann's rule in ectotherms. Despite current interest in body size trends of ectotherms, particularly with respect to underlying processes (Van Voorhies 1996, 1997; Atkinson and Sibly 1997; Azevedo et al. 1997; Partridge and Coyne 1997; Karan et al. 1998; Arnett and Gotelli 1999), little data on general patterns of size variation have been produced (except for a handful of species; e.g., Mousseau 1997 and references therein). It remains unclear whether Bergmann's rule holds for ectothermic vertebrates, let alone all ectothermic organisms. It seems logical then, to first determine whether any major groups of ectotherms follow Bergmann's rule.

Nonavian reptiles are of particular interest because interspecific faunal analyses suggest they either follow the converse to Bergmann's rule (i.e., larger body sizes in tropical areas; Dunham et al. 1988), or weakly follow Bergmann's rule (Lindsey 1966). Although such studies are suggestive, faunal analyses are somewhat limited because they examine body size relationships between groups of species at different latitudes. In other words, faunal analyses concern variation between groups of species rather than within species and thus do not directly evaluate Bergmann's rule.

Here we review intraspecific body size variation as it relates to latitude/elevation (combined) and temperature for two

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major groups of nonavian reptiles: chelonians (turtles), and squamates (lizards and snakes). The other clades of extant nonavian reptiles (tuataras and crocodylians) are far less speciose and have restricted latitudinal and elevational ranges. Consequently, we did not consider tuataras and crocodylians for this broad-scale study. We test whether chelonians and squamates follow Bergmann's rule, and briefly discuss processes that may account for the observed trends.

MATERIALS AND METHODS

Data

We collected information concerning intraspecific relationships between body size and latitude, elevation and environmental temperature from two sources: published literature (118 species) and museum specimens (nine species). Our literature review included any intraspecific study of the relationship between size and latitude, elevation or temperature for a single species of chelonian or squamate (see Electronic Appendix, currently available from the *Evolution* Editorial Office at evolution@asu.edu). Most studies used mean adult size as the measure of body size, but some used either the minimum or maximum, as measured by snout-vent length (SVL) for squamates, and plastron length (PL) or carapace length (CL) for chelonians. Body mass data were available for some species but these showed the same trends as length measures and are not reported. Comparisons within species always used identical size measures. We excluded island samples due to island effects on body size (e.g., Case 1978; Lomolino 1985). We attempted to use studies with the most extensive sampling over a species range (i.e., greatest number of populations surveyed over the widest range of latitudes, elevations, or temperatures). However, most taxa lack a single rangewide study of body size variation. Thus, for most species we combined data from two or more population-level studies that used identical size measures. When body size data were available for three or more populations, and the mean adult body size for each population was based on 10 or more individuals, then we calculated a correlation coefficient. However, population-level data for most species did not meet these criteria, thus only qualitative trends (i.e., + or - relationships between size and latitude/elevation or temperature) are noted for the majority of species (Electronic Appendix). Museum specimen data were generally pooled into northern and southern groups because of small sample sizes, thus trends are reported qualitatively in all cases except for *Opheodrys vernalis* (Electronic Appendix).

Although Bergmann's rule refers explicitly to environmental temperature, latitude and elevation have typically been used as proxies (Ashton et al. 2000). We combined the data for latitude and elevation because both are generally similar with respect to temperature (i.e., increasing latitude and elevation typically results in decreasing temperature). We present relationships between size and latitude/elevation separately from those with respect to temperature (Electronic Appendix).

Publication Bias

Publication bias can influence the conclusions of a meta-analysis, particularly when calculating an overall effect size

(Rosenthal 1979, 1991; Begg 1994; Palmer 1999). Publication bias can occur when authors fail to publish nonsignificant results. Funnel graphs plotting effect size versus some factor that may produce selective reporting (e.g., sample size) are useful for detecting publication bias (Begg 1994; Palmer 1999). If publication bias is present, such plots should produce a relationship between effect size and sample size and/or show a lack of nonsignificant studies based on small sample sizes (Palmer 1999). We plotted sample size (number of populations sampled) versus effect size (correlation coefficient) for studies of size and latitude/elevation as a qualitative test of selective reporting. We also performed regression analyses to evaluate any relationship between effect size and sample size. Lack of a relationship between effect size and sample size suggests publication bias is absent (Palmer 1999).

Vote-Counting Analyses

We tested the general relationship between size and latitude/elevation or temperature using nonphylogenetic and phylogenetic versions of two meta-analytical procedures: (1) vote-counting, and (2) grand mean effect size. For the vote-counting approach, we used all available information regardless of whether data for each species were qualitative or quantitative. We scored each species as either increasing in size with increasing latitude/elevation or decreasing temperature (Bergmann's rule), or as decreasing in size with increasing latitude/elevation or decreasing temperature (converse to Bergmann's rule), regardless of whether a trend was statistically significant. We then tested whether chelonians or squamates showed a significant overall relationship between size and latitude/elevation or temperature using the *G* statistic goodness-of-fit test with Yates' correction for continuity. Our observed values were the number of species that showed a positive or negative relationship between size and latitude/elevation or temperature, and the expected values were equal proportions of species with positive and negative associations. We excluded species with trends in different directions for males and females (chelonians: no exclusions; squamates: latitude, three species; temperature, six species; Electronic Appendix).

For phylogenetic versions of vote-counting analyses, we generated phylogenetically correct null distributions for chelonians and squamates for both latitude/elevation and temperature datasets. Assuming an evolutionary model of gradual Brownian motion, we used the composite phylogenies with equal branch lengths (Figs. 1 and 2) and PDSIMUL (Garland et al. 1993) to create 1000 simulated datasets, with parameters as follows: an initial trait value (correlation coefficient at the root of the tree) of 0; variances of 1.0; upper and lower bounds of +1.0 and -1.0 (limits for correlation coefficients). Note that we only used PDSIMUL to generate simulated datasets for one trait (correlation coefficients of size and latitude/elevation or temperature). Each simulated dataset had the same number of taxa as the actual data. For instance, we included 56 species in the vote-counting analysis of size and temperature for squamates; each simulated dataset had simulated correlation coefficients for 56 species. For each of the 1000 simulated datasets we counted the proportion of species with positive correlation coefficients and generated a histo-

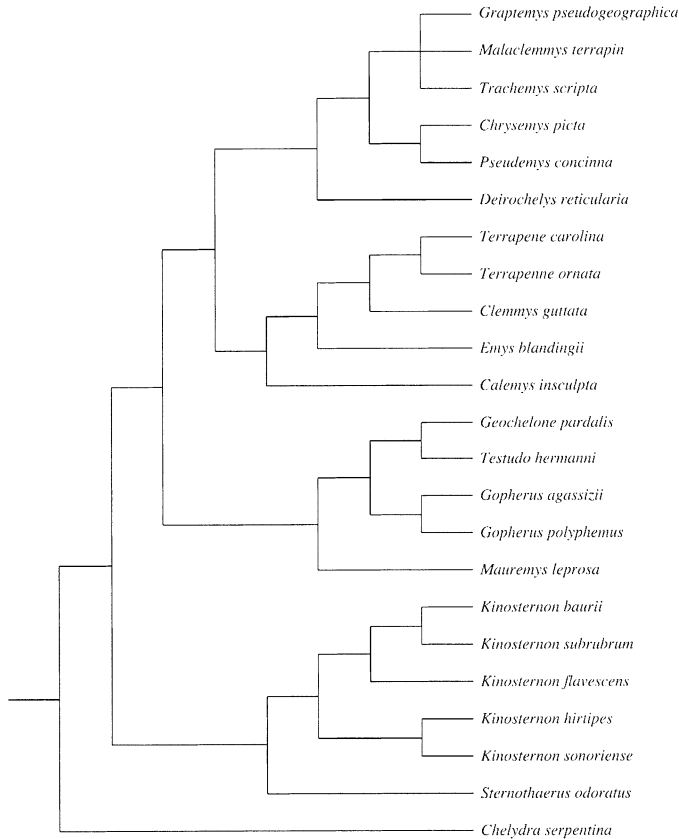


FIG. 1. Phylogenetic relationships among chelonian species for which intraspecific body size variation relative to latitude/elevation and/or temperature data are available (Electronic Appendix). The phylogeny is based on relationships presented by Gaffney and Meylan (1988), Bickham et al. (1996), Shaffer et al. (1997), Iverson (1998), Walker and Avise (1998), Serb et al. (2001) and Feldman and Parham (2002).

gram of the proportions positive for the 1000 simulated datasets, creating a phylogenetically correct null distribution of vote-count data. We then compared our observed vote counts (proportions positive) to the phylogenetically correct null distributions of vote scores (proportions positive) and assessed significance (i.e., a trend is significant if the proportions positive are below the 2.5 percentile or above the 97.5 percentile).

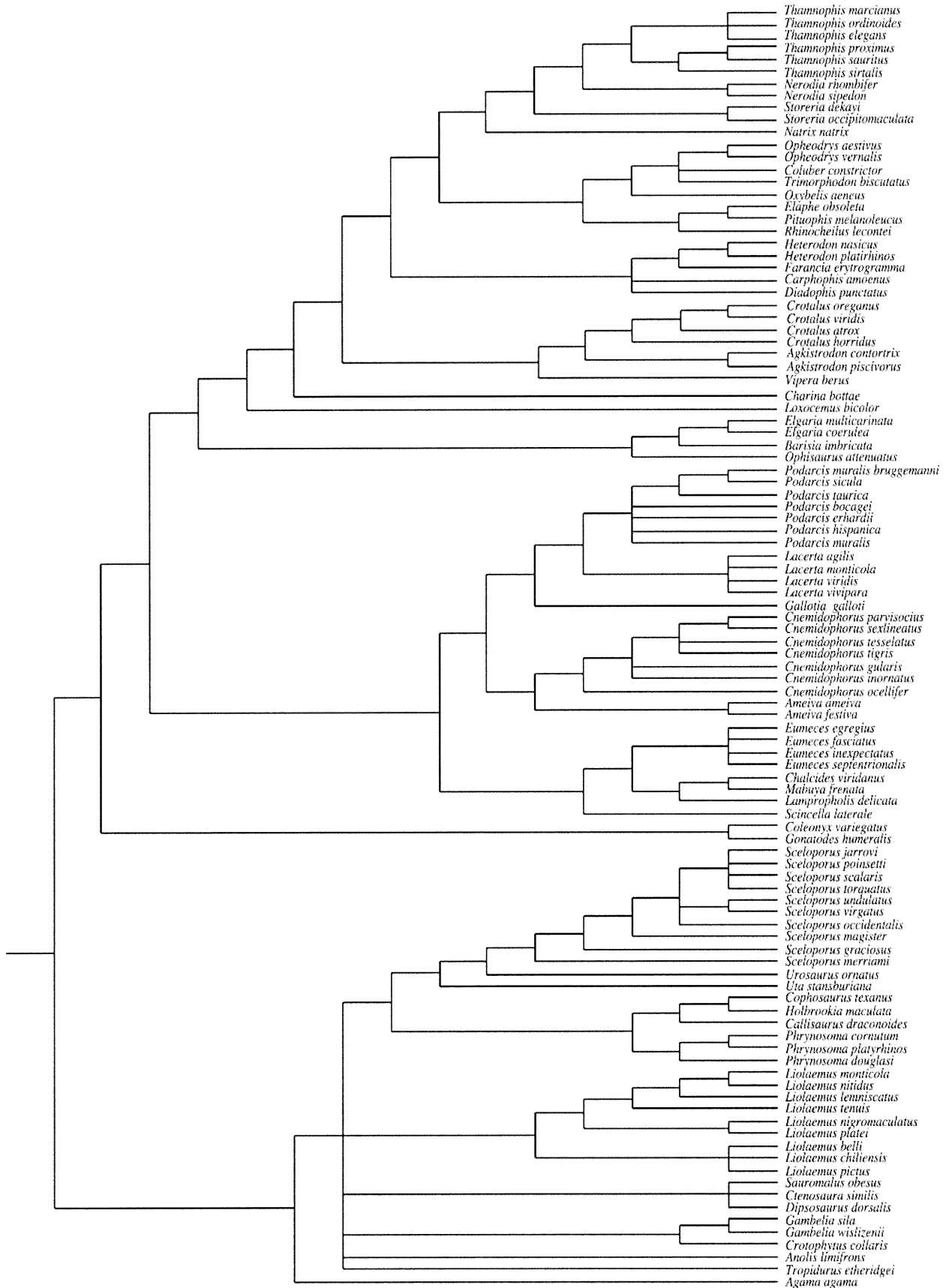
The vote-counting approach maximized included data because only qualitative statements about body size trends were available for many species (Electronic Appendix). Including such nonsignificant or qualitative data is disputable, yet we have no reason to expect a bias in direction of effect for nonsignificant or qualitative species values. If most species follow a particular pattern (e.g., + or - size association with latitude/elevation), this result should be due to a real effect. That many species lack statistically significant trends, due to low statistical power for most individual species datasets, does not preclude them from contributing to overall patterns (Hunter and Schmidt 1990; Bushman 1994). A more realistic vote-counting scheme would have included a third category: no significant association of size with latitude/elevation or temperature. We expect that some species lack significant size trends, but demonstrating that a species fails to show a

size trend requires statistical analyses with high power. Otherwise, correlation or regression analyses can fail to reject the null hypothesis (i.e., no body size trend) even when a pattern exists. Unfortunately, tests of body size trends for only a few chelonians and squamates have high power (i.e., ≥ 10 populations over $\geq 10^\circ$ latitude): chelonians *Chelydra serpentina*, *Chrysemys picta*, *Trachemys scripta*; lizards *Phrynosoma douglasi*, *Sauromalus obesus*, *Sceloporus undulatus*; snakes *Crotalus oreganus*, *Trimorphodon biscutatus* (Electronic Appendix). Thus, we consider a vote-counting analysis using three categories (+, -, and nonsignificant) inappropriate for these data. In fact, if we were to perform a three-category vote-counting analysis for these data, the probability of detecting any real patterns would essentially be zero because as the number of included studies with low power increases in such vote-counting analyses the method converges on a zero probability of rejecting the null hypothesis of no overall trend (Hedges and Olkin 1980).

Grand Mean Correlation Coefficient Analyses

In the second meta-analytical procedure we calculated overall effect sizes (i.e., grand mean correlation coefficient values). This approach is potentially a more rigorous test for patterns (Hunter and Schmidt 1990). For these analyses we separately pooled correlation values between body size and latitude/elevation for chelonians and squamates. When different correlation coefficients were reported for males and females we averaged the two values for that species. We then calculated overall effect sizes following Hedges and Olkin (1985). Specifically, we z -transformed all correlation coefficients, linearly weighted the z -transformed effect sizes based on sample size, calculated grand mean z -transformed effect sizes, then converted each grand mean value to a grand mean correlation coefficient. The Hedges and Olkin (1985) method can only use correlation coefficients based on data from greater than three populations for each species; correlation coefficients for six species of turtles and 13 species of squamates met this criterion.

For phylogenetic versions of the grand mean correlation coefficient analyses we generated phylogenetically correct null distributions of grand mean correlation coefficients for chelonian and squamate datasets. In PDSIMUL (Garland et al. 1993) we created 1000 simulated datasets (i.e., simulated correlation coefficients) assuming a model of gradual Brownian motion and using the known phylogenies with equal branch lengths (Figs. 1 and 2). Simulation parameters were: starting value (correlation coefficient at the root of the tree) of 0; empirical (default) values for variances (0.14 for chelonians, 0.40 for squamates); upper and lower bounds of +1.0 and -1.0 (limits for correlation coefficients). Note that PDSIMUL requires information for two traits, however we were only interested in a single trait (correlation coefficients of size and latitude/elevation or temperature). Thus, in PDSIMUL we set parameters for trait 1 as above and parameters for trait 2 were completely random and not used in any way. We calculated grand mean correlation coefficients for each of the simulated datasets in PDTIPS (Garland et al. 1993). We compared our actual grand mean correlation coefficients to the phylogenetically correct null distributions and deter-



mined significance (i.e., actual grand mean correlation coefficients are significant if below the 2.5 percentile or above the 97.5 percentile of simulated grand mean correlation coefficients).

Note that we did not perform the grand mean correlation coefficient analyses on body size-temperature data. These data are only available for two species of turtles. Furthermore, most of the size-temperature correlation data for squamates are from Schuster (1950), a problematic study due to small sample sizes and the use of maximum body size as the only precise size measure. Because statistical measures of range (e.g., minimum, maximum) are highly sensitive to sample size (Zar 1996), we did not perform grand mean correlation coefficient analyses for squamates.

Relationship between Bergmann's Rule and Latitude

The magnitude and direction of body size trends may vary with latitude, thus we tested whether the strength of Bergmann's rule is significantly related to latitude using taxa with correlation coefficient data (size and latitude; chelonians: $N = 10$; squamates: $N = 20$; Electronic Appendix). We calculated the mean latitude for each species based on reported sampling locations. When sampling locations were not reported, we used the midpoint of the range of latitudes sampled as the mean latitude. If separate correlation coefficients were presented for males and females, we used the correlation value for the sex that was more extensively sampled. When both sexes were equally well sampled, we averaged correlation coefficients.

We tested whether the strength of Bergmann's rule varied with latitude using nonphylogenetic (simple regression) and phylogenetic methods. Phylogenetic analyses were performed by independent contrasts (Felsenstein 1985) in PDPTREE (Garland et al. 1999; Garland and Ives 2000). For independent contrasts analyses, we assumed constant branch lengths and verified that contrasts were appropriately standardized (following Garland et al. 1992).

Phylogenetic Signal

Although we present both nonphylogenetic and phylogenetic versions of all statistical analyses, which are more appropriate for each dataset? To answer this question, we tested for phylogenetic signal in each dataset. If closely related species tend to have similar body size trends, then the data will show phylogenetic signal. If phylogenetic signal is present, then phylogenetic methods must be used, whereas a lack of phylogenetic signal suggests that nonphylogenetic

methods are more appropriate. However, failing to reject the null hypothesis of no phylogenetic signal is not equivalent to accepting that the data show no phylogenetic signal. Therefore, we used tests of phylogenetic signal to indicate which analyses (nonphylogenetic or phylogenetic) are more appropriate based on available evidence.

We assessed phylogenetic signal in both chelonian and squamate vote-counting datasets following Maddison and Slatkin (1991). We mapped the discrete vote-counting data (i.e., positive or negative association with latitude/elevation or temperature) onto the chelonian (Fig. 1) and squamate (Fig. 2) phylogenies, noting the number of steps required to generate the distribution of character states. We then randomly shuffled the character states on the phylogenies 1000 times to generate null distributions of the number of evolutionary steps using MacClade 4.0 (Maddison and Maddison 2001). We compared the tree scores (number of steps) of the actual data to the null distributions; scores significantly shorter than the null indicate phylogenetic signal. Note that the power of this test is unknown.

We tested for phylogenetic signal in the chelonian and squamate grand mean correlation coefficient data following Blomberg et al. (2003). This method is analogous to the Maddison and Slatkin (1991) test but operates on continuous characters (Blomberg and Garland 2002). We plotted the correlation coefficient data onto the known phylogenies for chelonians (Fig. 1) and squamates (Fig. 2), and calculated the variance of the contrasts of the actual correlation coefficients, assuming equal branch lengths, in PDPTREE (Garland et al. 1999; Garland and Ives 2000). We then generated 1000 random datasets by shuffling the actual correlation coefficients across the phylogenies using PDRANDOM (Lapointe and Garland 2001). We used PDERROR (Diaz-Uriarte and Garland 1996) to calculate variances of the contrasts for the 1000 random datasets. The variances of the contrasts of the randomized datasets should generally be larger than for the one real dataset if phylogenetic signal is present. We compared the actual variances of the contrasts of correlation coefficients to the phylogenetically random distributions; variances significantly lower than the null (i.e., less than 95% of the random datasets) indicate phylogenetic signal. Simulation studies indicate that the foregoing procedure has adequate statistical power (approximately 0.8) for phylogenies with 20 or more species (T. Garland, pers. comm.).

To test for phylogenetic signal of the strength of Bergmann's rule versus latitude datasets we used the method of Blomberg et al. (2003). In this case, significant phylogenetic

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FIG. 2. Phylogenetic relationships among squamate species for which intraspecific body size variation relative to latitude/elevation and/or temperature data are available (Electronic Appendix). The phylogeny is based on relationships presented by Taylor (1935), Malnate (1960), Klauber (1972), Cadle (1984), Good (1987), Lawson (1987), Montanucci (1987), Cadle (1988), Estes et al. (1988), Etheridge and de Queiroz (1988), Good (1988), Rieppel (1988a,b), Schwenk (1988), Densmore et al. (1989), Frost and Etheridge (1989), Moritz et al. (1989), Kluge (1991), de Queiroz (1992), Moritz et al. (1992), Cundall et al. (1993), Wiens (1993), Wright (1993), de Queiroz and Lawson (1994), Crother and Hillis (1995), Heise et al. (1995), Reeder (1995), Keogh (1996), Kraus et al. (1996), Reeder and Wiens (1996), Sites et al. (1996), Macey et al. (1997), Wiens and Reeder (1997), Harris et al. (1998), Kraus and Brown (1998), Murphy and Lovejoy (1998), Schulte et al. (1998), Harris and Arnold (1999), Macey et al. (1999), Rodriguez-Robles and de Jesus-Escobar (1999), Zaher (1999), Wiens et al. (1999), Flores et al. (2000), Griffith et al. (2000), Honda et al. (2000), Schulte et al. (2000), Vidal et al. (2000), Wiens and Hollingsworth (2000), Wilgenbusch and de Queiroz (2000), Ashton and de Queiroz (2001), Creer (2001) and Reeder and Montanucci (2001).

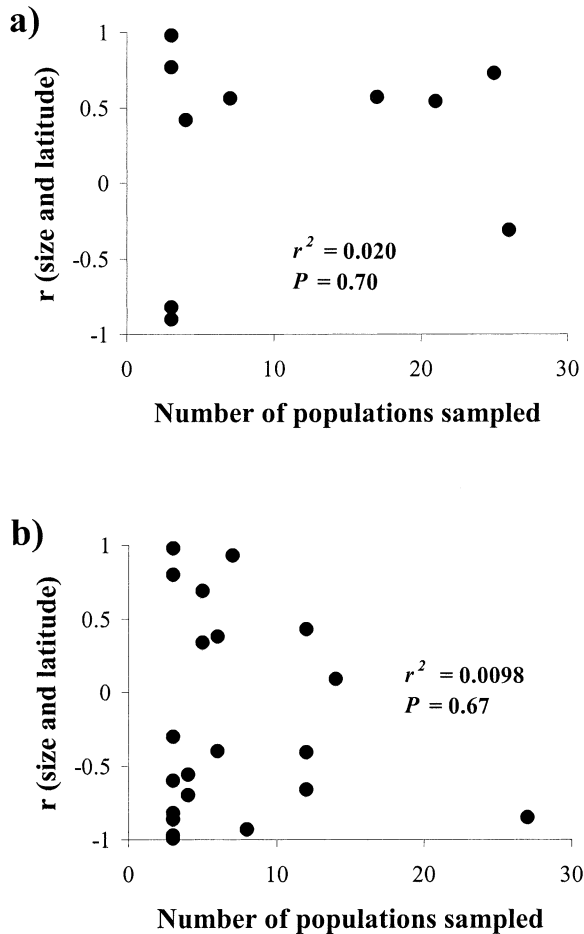


FIG. 3. Effect size (r , correlation coefficient of size and latitude/elevation) versus the number of populations sampled for species of (a) chelonians and (b) squamates.

signal would indicate that analyses require phylogenetically independent contrasts.

RESULTS

Publication Bias

Our plots of sample size (number of populations) versus effect size (correlation coefficient-latitude) show no evidence of publication bias for chelonians or squamates (Fig. 3). In fact, most investigations were based on small sample sizes. Further, regression analyses show no relationship between effect size and sample size for either chelonians ($r^2 = 0.020$; $F = 0.16$; $df = 1, 8$; $P = 0.70$; Fig. 3a) or squamates ($r^2 = 0.0098$; $F = 0.19$, $df = 1, 19$; $P = 0.67$; Fig. 3b). Thus, we find no evidence of publication bias in these data.

Vote-Counting Analyses

The chelonian vote-counting data show that most species (19 of 23) display a positive relationship between body size and latitude/elevation (Table 1). This overall trend is significant using nonphylogenetic ($G = 9.16$, $P < 0.01$) and phylogenetic ($P < 0.05$) methods. In addition, the majority of species in each of the five represented chelonian families have

TABLE 1. Number of chelonian and squamate species (organized by major clade) with positive or negative within-species relationships between size and latitude/elevation or temperature.

Taxon	Latitude/elevation		Temperature	
	+	-	+	-
Chelonia	19	4	1	14
Chelydridae	1	0	0	1
Emydidae	8	3	1	8
Kinosternidae	5	1	0	2
Testudinidae	4	0	0	3
Bataguridae	1	0	0	0
Terrestrial	6	0	0	5
Semi-aquatic	13	4	1	9
Squamata	22	61	40	16
Iguania	8	20	16	6
Scleroglossa	14	41	24	10
Gekkota	0	2	1	0
Scincomorpha	6	10	8	3
Anguimorpha	8	29	15	7
Lizards	15	35	26	10
Snakes	7	26	14	6

positive relationships between body size and latitude/elevation (Table 1). Bergmann's rule also holds for both fully terrestrial and semi-aquatic species (Table 1).

Additionally, most chelonians (14 of 15) show a negative relationship between body size and environmental temperature (Table 1), a significant overall trend (nonphylogenetic: $G = 11.06$, $P < 0.01$; phylogenetic: $P < 0.01$). This relationship is consistent for all four chelonian families surveyed (Table 1). Likewise, the trend is consistent for fully terrestrial and semi-aquatic species (Table 1).

The squamate vote-counting data show that most species of squamates (61 of 83) have a negative relationship between body size and latitude/elevation (Table 1). This overall trend is significant in the nonphylogenetic analysis ($G = 18.06$, $P < 0.001$), but only approaches significance in the phylogenetic analysis ($P = 0.056$). The overall pattern of smaller body size at higher latitudes is consistent for the two major squamate clades, Iguania and Scleroglossa, and for the three major scleroglossan lineages, Gekkota, Scincomorpha, and Anguimorpha (Table 1). Dividing squamates into lizards and snakes (this division does not reflect phylogeny because snakes render "lizards" paraphyletic; however, such a division may represent functional groups) demonstrates that lizards and snakes both display a general negative association between size and latitude/elevation (Table 1).

A significant majority of species of squamates (40 of 56) shows a positive relationship between size and environmental temperature in the nonphylogenetic ($G = 9.74$, $P < 0.01$) but not the phylogenetic ($P = 0.12$) analysis. The overall pattern of smaller body size in cooler areas holds for iguanians and scleroglossans, as well as for each scleroglossan lineage (Table 1). Both lizards and snakes exhibit a general positive relationship between body size and temperature (Table 1).

Grand Mean Correlation Coefficient Analyses

For chelonians we calculated a grand mean correlation coefficient of +0.41 between size and latitude/elevation. This

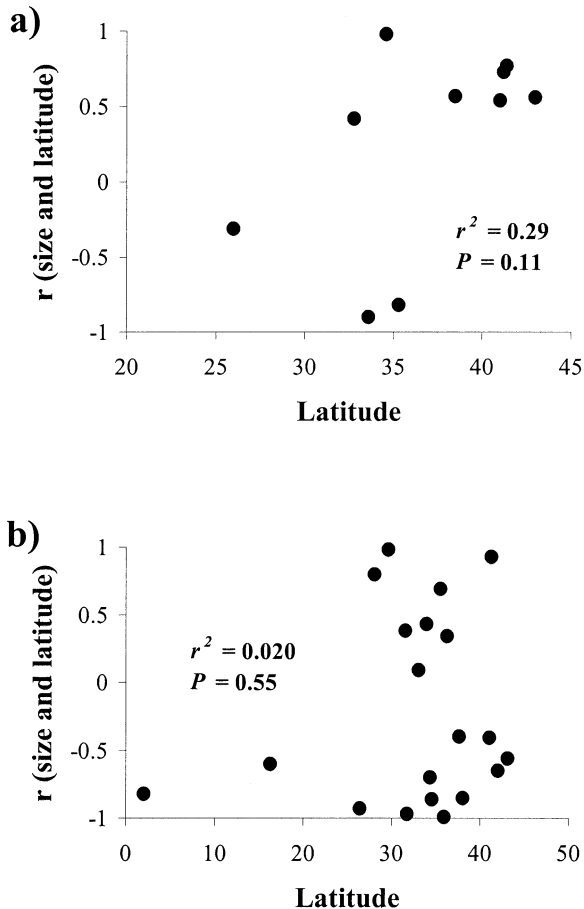


FIG. 4. Relationship between the strength of intraspecific body size trends (correlation coefficient between size and latitude) and mean latitude for species of (a) chelonians and (b) squamates. We present nonphylogenetic regression analyses because the data do not show phylogenetic signal. We include only species for which a correlation coefficient was reported (Electronic Appendix), and mean latitude could be calculated.

trend is significant in the nonphylogenetic ($z = 3.98$, $P < 0.001$; six species), but not phylogenetic (randomly generated r -values ranged from -0.55 to $+0.79$, $P = 0.46$), analysis. We calculated a grand mean correlation coefficient of -0.59 between size and latitude/elevation for squamates. The correlation value for squamates is significant using both nonphylogenetic ($z = 6.18$, $P \ll 0.001$; 13 species) and phylogenetic (randomly generated r -values ranged from -0.60 to $+0.49$, $P < 0.01$) methods.

Relationship between Bergmann's Rule and Latitude

We found no relationship between the strength (and direction) of body size trends and latitude for chelonians (nonphylogenetic: $r^2 = 0.29$; $F = 3.25$; $df = 1, 8$; $P > 0.05$; phylogenetic: $r^2 = 0.30$; $F = 3.50$; $df = 8$; $P > 0.05$; Fig. 4a). Likewise, body size trends of squamates show no evidence of variation with latitude (nonphylogenetic: $r^2 = 0.020$; $F = 0.38$; $df = 1, 18$; $P > 0.05$; phylogenetic: $r^2 = 0.00097$; $F = 0.017$; $df = 18$; $P > 0.05$; Fig. 4b).

Phylogenetic Signal

Vote-counting analyses

The chelonian latitude/elevation vote-counting data possess no phylogenetic signal. We needed four steps to optimize our latitude/elevation data on the chelonian phylogeny (23 species), whereas the randomly shuffled data ranged from one to four steps on the phylogeny. Therefore, the phylogenetic distribution of our latitude/elevation vote-counts does not differ ($P = 1.0$) from the phylogenetically correct null distribution. The chelonian temperature vote-counting data also display no phylogenetic signal; a single character state change occurs on a tip of the phylogeny (15 species).

The squamate latitude/elevation vote-counting data also lack phylogenetic signal. We needed 20 steps to reconstruct the distribution of latitude/elevation character states on the squamate tree (83 species), whereas the randomly shuffled data ranged from 14 to 22 steps. The actual number of steps was not significantly different from the randomly generated null distribution ($P = 0.85$). We needed 16 steps to plot temperature data on the phylogeny (56 species), whereas the number of steps for the randomly generated datasets ranged from 10 to 17. The number of steps for the actual data was not significantly different than the null ($P = 0.93$).

Grand mean correlation coefficients

The chelonian latitude/elevation correlation coefficient data exhibit no phylogenetic signal. Using the chelonian phylogeny (six species) we calculated an overall variance of the contrasts of actual correlation coefficients of 0.15. This value was not significantly smaller ($P = 0.86$) than the distribution of variances of the contrasts in the randomly generated data sets ($\bar{X} = 0.12$; range: 0.067–0.15). Likewise, the squamate latitude/elevation correlation coefficient data (13 species) show no phylogenetic signal. We calculated an actual variance of the contrasts of correlation coefficients of 0.32, a value not significantly lower than in the randomly generated data sets ($\bar{X} = 0.28$; range: 0.075–0.41; $P = 0.67$).

Relationship between Bergmann's rule and latitude

In the analysis of the strength of Bergmann's rule versus latitude we used correlation coefficient data for 10 chelonian species and 20 squamate species. We calculated overall variances of the contrasts of correlation coefficients of 0.37 and 0.39 for chelonians and squamates, respectively. The randomly generated datasets had variances of the contrasts ranging from 0.097 to 0.46 ($\bar{X} = 0.32$) for chelonians and from 0.16 to 0.49 ($\bar{X} = 0.34$) for squamates. Comparing these variance distributions to the variances of the contrasts of the actual data, we found no evidence of phylogenetic signal in either chelonian ($P = 0.75$) or squamate ($P = 0.78$) datasets.

DISCUSSION

It is widely accepted that comparative biological studies must account for phylogeny because related species often possess similar traits or trait values due to common ancestry and thus may not be considered independent in a statistical sense (Felsenstein 1985; Harvey and Pagel 1991). Whether

a dataset requires phylogenetic analysis, however, depends on the nature of the trait. In our case, the question is whether species inherit body size trends. Species might inherit body size trends in two ways. First, a widely distributed species might split into two species that, from inception, have large ranges and the same latitudinal size trend as the ancestral taxon. If bifurcating speciation (*sensu de Queiroz 1998*) is common, then phylogenetic analyses are appropriate. On the other hand, if most speciation events result from the isolation and subsequent independent evolution of small, peripheral populations (i.e., newly formed species do not show any size trends), then each new species evolves an independent body size trend. If speciation in chelonians and squamates usually proceeds in this manner, then nonphylogenetic analyses of body size trends are appropriate.

The second way that species may inherit body size trends is through some shared tendency to evolve a particular size trend. For instance, species of squamates might share some development pathway or potential for phenotypic plasticity that predisposes them to evolve a converse to Bergmann's rule size trend. If this is the case, and the question is how often the tendency for Bergmann's rule or its converse have evolved, then phylogenetic analyses are appropriate.

Here we focus on size trends themselves, not the tendency for the size trends. It is an important distinction. We argue that body size trends should be analyzed with nonphylogenetic methods because speciation likely occurs through the splitting of small peripheral isolates (Mayr 1963), and even if the peripheral isolates have some shared tendency for a size trend the actual size trend that evolves is independent because it depends on the abiotic and biotic conditions experienced by that species. Yes, species may share a tendency to evolve a particular size trend, but that is not the question here. Despite our position, we realize that the issue is not completely clear and therefore, to be conservative, analyze all data with nonphylogenetic and phylogenetic methods.

Assuming that phylogenetic analyses may be appropriate, the next step is to test for phylogenetic signal in our data. If phylogenetic signal is present, then phylogenetic methods are preferred. Neither chelonian nor squamate vote-count and correlation coefficient data display significant phylogenetic signal. In other words, the phylogenetic distribution of body size trends in chelonian and squamate lineages does not appear evolutionarily constrained such that phylogeny will bias the results of our analyses. Nevertheless, we present both nonphylogenetic and phylogenetically corrected analyses in the results section because a few of our tests for phylogenetic signal likely suffer from low power. However, given the lack of any evidence of phylogenetic signal, and the arguments presented above, we consider the nonphylogenetic analyses more appropriate.

Body Size Trends

We found that 83% of the sampled chelonian species (19 of 23) are larger at higher latitudes/elevations, whereas 73% of sampled squamate species (61 of 83) are larger at lower latitudes/elevations (Table 1; Electronic Appendix). The grand mean correlation coefficient between body size and latitude/elevation is +0.41 for chelonians and -0.59 for

TABLE 2. Number of species of squamates from the Northern and Southern Hemisphere with positive or negative associations between body size and latitude/elevation or temperature.

	Latitude or elevation		Temperature	
	+	-	+	-
Northern Hemisphere	21	56	34	15
Southern Hemisphere	1	5	6	1

squamates. Likewise, chelonians in general are larger in cooler environments (14 of 15 species), whereas squamates are larger in warmer areas (40 of 56 species). These patterns are consistent for all major chelonian and squamate clades for which data are available (Table 1). In addition, overall patterns of body size variation do not differ based on functional groups, for instance terrestrial versus semi-aquatic chelonians, or lizards versus snakes (Table 1). All nonphylogenetic analyses are significant whereas some phylogenetic analyses are not. We contend that the nonphylogenetic analyses are more appropriate for these data (see above). Thus, chelonians in general follow Bergmann's rule and squamates follow the converse to Bergmann's rule.

The strength and sign of body size trends do not vary with latitude for either chelonians or squamates (Fig. 4). However, available data are geographically biased. Most squamate data are from the Northern Hemisphere (Table 2), particularly temperate regions (approximately 30–50° N latitude; Fig. 4), and all chelonian data come from the Northern Hemisphere (except *Geochelone pardalis*). So, although data from Northern and Southern Hemispheres, and from temperate and tropical areas, are consistent with overall trends (Table 2; Electronic Appendix), more samples are needed before we can establish Bergmann's rule in chelonians and its converse in squamates at all latitudes. It is possible that Bergmann's rule and its converse predominantly occur in temperate regions, as has been demonstrated for Rapoport's rule (a positive relationship between geographic range size and latitude; Rohde 1996; Gaston et al. 1998; Ashton 2001a).

Studies of body size variation typically use simple correlation or regression analysis to detect any trends. However, data may follow a nonlinear model. For example, body size variation in some cricket species follows a "sawtooth" pattern, determined by the length of the active season (Masaki 1972, 1978; Mousseau and Roff 1989; Mousseau 1997). Some chelonians may follow an analogous but opposite pattern, in which the largest individuals inhabit areas with the shortest and longest activity seasons (J. Litzgus and T. A. Mousseau, pers. comm.). Pond sliders, *Trachemys scripta*, appear to follow this pattern, with the largest individuals in tropical and extreme temperate environments (Tucker et al. 1998). Data on size variation throughout the distribution of other wide-ranging species are needed to evaluate whether body size trends show a general nonlinear relationship with environmental variables. However, such wide-ranging taxa often consist of several independent lineages. Including samples from separate evolutionary species, albeit sister species, can completely obscure body size patterns, especially when those trends are in opposite directions (e.g., *Crotalus oreganus* and *C. viridis*; Ashton 2001b).

Several general environmental variables, besides latitude or temperature, have been suggested as better predictors of body size variation. In particular, combined effects of temperature and humidity (James 1970), annual evapotranspiration as a measure of productivity (Rosenzweig 1968a,b), and seasonality (Boyce 1978, 1979; Lindsted and Boyce 1985) are hypothesized to better explain size variation in vertebrates. Few studies have compared all of these variables as predictors of size variation in single species, yet in each case seasonality better explained size variation than other variables (Boyce 1978; Murphy 1985; Wigginton and Dobson 1999; Ashton 2001b).

Mechanism

The observed patterns of body size variation allow some inferences about the underlying mechanisms influencing body sizes of chelonian and squamate populations. First, different processes may explain the different body size patterns. For instance, fasting endurance, explicitly tied to seasonality, has been suggested to explain Bergmann's rule in both endotherms (Boyce 1979; Lindsted and Boyce 1985; Murphy 1985) and ectotherms (Cushman et al. 1993). This hypothesis states that larger individuals are better able to survive periods of food shortage because of their greater relative and absolute capacity for fat storage (Boyce 1979; Lindsted and Boyce 1985; Cushman et al. 1993). Periods of food shortage occur with greater frequency at higher latitudes, where environments are more seasonal, and thus more seasonal regions should have larger individuals. Fasting endurance, and its underlying selective advantages, should show the same relationship between body size and latitude for all animals. Body size patterns of chelonians, mammals (Ashton et al. 2000), and birds (James 1970; Zink and Remsen 1986; Ashton 2002) are consistent with this hypothesis, yet squamates display the opposite pattern of size variation. Based on available evidence, seasonality predicts body size variation in vertebrates better than other broad, environmental variables (Boyce 1978; Murphy 1985; Wigginton and Dobson 1999; Ashton 2001b). Thus, by association, fasting endurance likely contributes to Bergmann's rule in vertebrates. In this case, different processes must explain size trends in squamates.

Alternatively, the general processes responsible for body size trends may be the same, but have different effects on different groups. Two such processes may be competition and selection for maintenance of preferred body temperature. The competition hypothesis suggests that the severity of competition is negatively associated with latitude leading to larger body sizes at higher latitudes because of relaxed competition (Ashton et al. 2000). Competition has contrary effects on differently sized organisms (Damuth 1993), and it is possible that release from competition influences body size evolution differently for diverse taxonomic groups. For instance, squamates might tend to evolve toward smaller body sizes when released from competition.

Maintenance of preferred body temperature may also influence body size variation differently in various vertebrates. This hypothesis includes the traditional heat conservation explanation proposed for Bergmann's rule in endotherms, which suggests endothermic vertebrates tend to be larger in

cooler environments because a reduced surface area to volume ratio decreases heat loss (Bergmann 1847; Mayr 1963). Correspondingly, increased relative surface area is advantageous in warmer environments because it results in greater heat dissipation. These arguments assume internal heat production (i.e., endothermy), and do not apply to ectotherms. However, the same process, selection for maintenance of preferred body temperature, may act on ectotherms. For example, the pattern of smaller body sizes in cooler climates for squamates may be the result of selection for *increased* surface area to volume ratio to allow more rapid heating and cooling (Cowles 1945; Bogert 1949; Stevenson 1985). Because optimal body temperature may be constant throughout the geographic range of a species (Bogert 1949), smaller-sized individuals in cooler environments may be able to more delicately control their body temperature behaviorally, and be active for a greater proportion of the day. Such thermoregulatory abilities may be critically important for digestion and development in squamates that inhabit cooler areas because most squamates swallow food items whole and retain eggs or young for long periods. In warmer climates, on the other hand, thermoregulation may not be such an important factor (Shine and Madsen 1996), thereby relaxing selective pressure on an organism's surface area to mass ratio, and permitting squamates to attain larger sizes and accrue other size-related benefits (e.g., competition, predation; Peters 1983). Thermoregulation may be important in chelonians as well, but the thermal properties of the shell, and the dense, low surface area to volume body plan of chelonians may select for larger individuals that can maintain thermal inertia. In other words, the shell, density and size of chelonians are less suitable for rapid heating and cooling, but may convey advantages in heat conservation. Hence, this hypothesis suggests that selection for maintenance of preferred body temperature is accomplished by size variation to conserve heat (mammals, birds, turtles) or increase heat gain (lizards and snakes).

Although most explanations for geographic body size trends invoke selection (see Ashton et al. 2000), size variation in reptiles (Ferguson and Talent 1993; Sinervo and Adolph 1994) and other animals (Berven 1982; Riha and Berven 1991; Arnett and Gotelli 1999) appears to be influenced by both inherent (i.e., genetic and maternal) and external (i.e., direct environmental induction) factors. Thus, phenotypic plasticity and selection, including selection for plasticity (Gotthard and Nylin 1995; Via et al. 1995), are necessary to fully explain general body size patterns. Two environmental factors that have been shown to influence body size, and may partially explain the divergent patterns observed for chelonians and squamates, are temperature and food availability. For instance, developmental temperature appears to have opposite effects on chelonians and squamates, with lower developmental temperature resulting in larger offspring for some chelonians (e.g., Gutzke et al. 1987) but smaller size in some squamates (e.g., Tousignant and Crews 1995; Shine et al. 1997). Likewise, squamates are larger when given access to more radiant heat during development (Arnold and Peterson 1989). This developmental effect may be mediated by changes in cell size with temperature (Partridge and French 1996; Van Voorhies 1996). Prey availability is an

other factor that may directly influence body size. For example, snakes fed a high-energy diet are heavier at maturity than those fed a low-energy diet (Ford and Seigel 1989, 1994); how this result compares to geographic variation in squamates, and whether chelonians show similar effects, remain to be addressed. These studies suggest that patterns of size variation for chelonians and squamates may be partially explained by phenotypic responses to temperature and resource availability.

Geographic patterns of body size variation (i.e., Bergmann's rule and its converse) may relate to other biological rules, particularly Cope's rule (increased body size within a lineage over time; Stanley 1973; Alroy 1998) and Rapoport's rule (increased geographic range size with increased latitude; Stevens, 1989, 1992; Gaston et al. 1998). Smith et al. (1995) showed that body size in a woodrat species was negatively related to environmental temperature across the contemporary range, as well as over the last 20,000 years. This suggests that Cope's rule in mammals (Alroy 1998) may be a byproduct of Bergmann's rule, at least during certain periods. Because squamates show the converse to Bergmann's rule, we predict that on a temporal scale, size and environmental temperature should be positively related in this group. Body size tends to be positively related to range size, thus Rapoport's rule may also be a byproduct of the generally positive correlation between size and latitude for most vertebrates. We predict a negative relationship between range size and latitude for squamates if Rapoport's rule is truly a side effect of general patterns of body size variation. The relationship between latitude and range size is not clear for squamates because the only relevant study lumped reptiles and amphibians (Stevens 1989).

Conclusion

We present the first overview of the relationship between intraspecific body size variation and latitude/elevation and environmental temperature in nonavian reptiles. We found strong support for Bergmann's rule in chelonians and the converse to Bergmann's rule in squamates. To our knowledge, these findings represent the first case of a major group of animals showing the converse to Bergmann's rule, and the first report of a major clade of ectothermic vertebrates following Bergmann's rule. The strength and sign of these body size trends do not vary with latitude, however available data are biased to the Northern Hemisphere in general, and temperate regions in particular. Data from other geographic regions are greatly needed. Further research is also needed to test the nature of body size trends and to evaluate whether other environmental factors (e.g., seasonality) can better predict overall patterns of body size variation. Possible explanations for these size trends include differential responses to abiotic (e.g., seasonality, temperature) and biotic (e.g., interspecific competition) factors. Unfortunately, little information permits us to adequately test these hypotheses. The possible relationship between Bergmann's rule and other ecological and evolutionary trends is intriguing and also awaits further data. Despite the vast amount of literature on body size variation in vertebrates, much remains to be discovered.

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