ORIGINAL ARTICLE

LATITUDINAL AND CLIMATIC VARIATION IN BODY SIZE AND DORSAL SCALE COUNTS IN *SCELOPORUS* LIZARDS: A PHYLOGENETIC PERSPECTIVE

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Squamates often follow an inverse Bergmann's rule, with larger-bodied animals occurring in warmer areas or at lower latitudes. The size of dorsal scales in lizards has also been proposed to vary along climatic gradients, with species in warmer areas exhibiting larger scales, putatively to reduce heat load. We tested for these patterns in the diverse and widespread lizard genus *Sceloporus*. Among 106 species or populations, body size was associated positively with maximum temperature (consistent with the inverse of Bergmann's rule) and aridity, but did not covary with latitude. Scale size (inferred from the inverse relation with numbers of scales) was positively related to body size. Controlling for body size via multiple regression, scale size was associated negatively with latitude (best predictor), positively with minimum temperature, and negatively with aridity (similar results were obtained using scores from a principal components analysis of latitude and climatic indicators). Thus, lizards with larger scales are not necessarily found in areas with higher temperatures. Univariate analyses indicated phylogenetic signal for body size, scale counts, latitude, and all climate indicators. In all cases, phylogenetic regression models fit the data significantly better than nonphylogenetic models; thus, residuals for $\log_{10}$ number of dorsal scale rows exhibited phylogenetic signal.

KEY WORDS: Adaptation, aridity, comparative methods, meristic traits, precipitation, temperature.

Ectothermic vertebrates are particularly sensitive to temperature (e.g., Huey et al. 2009, 2010; Sinervo et al. 2010). Therefore, variation in phenotypes across climatic gradients is often interpreted as an adaptive (evolutionary) response to variation in a temperature-based selective regime. For example, some ectotherms in colder climates have evolved higher rates of growth and development, which would tend to counteract the proximate effects of lower temperatures, such as shorter annual periods for activity and growth (Conover and Schultz 1995; Oufiero and Angilletta 2006). Although climate is particularly likely to affect physiological and life-history traits, other aspects of the

phenotype, including morphological and meristic traits, may also exhibit adaptive variation along geographical climatic gradients.

Patterns of body size variation along climatic and latitudinal gradients have been analyzed in a large number of studies, following the proposal of Bergmann's rule in 1847 (Bergmann 1847; Rensch 1938). Bergmann's rule suggests that, within species of birds and mammals (endotherms), body sizes are larger at higher latitudes for adaptive reasons: the smaller surface area-to-volume ratio of larger endotherms confers thermoregulatory advantages with respect to heat loss in cooler environments (e.g., see James 1970; Blackburn et al. 1999). Although Bergmann's rule was

originally proposed for birds and mammals, many researchers have examined geographical variation in body size in a variety of taxa, often with reference to this biogeographic rule (e.g., reptiles: Ashton and Feldman 2003; mammals: Ashton et al. 2000; Freckleton et al. 2003; fish: Belk and Houston 2002; amphibians: Ashton 2002a; Adams and Church 2008; birds: Ashton 2002b; arthropods: Blanckenhorn and Demont 2004). In ectotherms, neither the generality nor the possible adaptive significance of body size versus climate relationships is clear. For example, it has been proposed that squamate reptiles (lizards and snakes) follow the inverse to Bergmann's rule at the intraspecific level, with larger individuals inhabiting lower latitudes (warmer environments; Ashton and Feldman 2003). However, opposite trends can even be observed within a single genus. For example, the lizard genus *Sceloporus* includes some species that follow Bergmann's rule (e.g., *S. undulatus*) and others that exhibit an inverse to Bergmann's rule (e.g., *S. graciosus*) at the intraspecific level (Sears and Angilletta 2004). Similarly, interspecific analyses in lizards have yielded conflicting results (Lindsey 1966; Dunham et al. 1988; Cruz et al. 2005; Olalla-Tárraga et al. 2006; Pincheira-Donoso et al. 2008).

As with body size, the dorsal scales of squamates exhibit substantial interspecific variation. One general trend is the decrease in the variability of scale counts concomitant with elongation and loss of limbs (Kerfoot 1970). This trend most likely stems from the close functional relationship between the ventral scales and the costocutaneous muscles used during locomotion in many limbless squamates (references in Dohm and Garland 1993). In squamates with well-developed limbs, however, the adaptive significance of scale variation is less clear. The scales of reptiles are considered key "preadaptations" for adaptive radiation in the terrestrial realm because they offer protection against abrasion and water loss (Walker and Liem 1994; Alibardi 2003; but see Licht and Bennett 1972). Beyond this, squamates have come to inhabit and thrive in some of the earth's most arid regions. Therefore, it seems plausible that variation in aspects of climate would lead to differing selection on the size, shape, number, and perhaps other features of scales.

Squamate scales are composed of layers of cells (Alibardi 2003). The outer epidermal generation is derived from dead cells that come into contact with the external environment. In contrast, the inner epidermal generation consists of living cells that remain protected from the external environment. These two layers form the whole epidermis of squamates. Although the general function of squamate scales is well understood, the functional significance of variation in scale size and morphology is not. The underlying general structure of scales is similar throughout squamates; however, scale shape, size, number, and surface ornamentation can vary substantially (Burstein et al. 1974; Arnold 2002 and references therein).

Some studies have explored the potential adaptive significance of variation in scale number and size among lizard populations or among a small number of closely related species; these studies usually focus on climatic correlates of scale size variation (inferred from counts of scales, but see Methods), and have yielded mixed results (Bogert 1949; Hellmich 1951; Horton 1972; Soulé and Kerfoot 1972; Lister 1976; Thorpe and Baez 1987; Calsbeek et al. 2006). The motivation for many of these studies was Soulé (1966), who examined populations and species of *Uta* inhabiting the islands in the Sea of Cortés. He found that lizards on larger islands had fewer, but larger scales and interpreted this as an adaptive response to the higher average temperatures on larger islands. He stated: "In *Uta*, surface area is proportional to scale size (Fig. 5). That is, large scales tend to be heavily keeled and overlapping, whereas small scales do not. Therefore, in localities where overheating is a chronic problem, *Uta* will have large dorsal scales (fewer scales); in localities where maintenance of suitably high body temperatures is often a problem, *Uta* will have small, relatively smooth dorsal scales (more scales)" (Soulé 1966, pp. 57–58). Similar patterns of scale size variation have been found in investigations of other lizards such as *Liolaemus* of South America (Hellmich 1951). Soulé (1966) hypothesized that given two planar surfaces—one smooth and flat and the other rough and irregular—the former will radiate less heat due to differences in surface area. Thus, smaller scales are less-efficient radiators of heat than are larger scales (the larger the surface area, the greater the amount of heat dissipated). On average then, large scales will occupy more surface area than small scales for a given area of lizard skin because they are both more imbricate (i.e., having regularly arranged, overlapping edges) and more heavily keeled. Building on Soulé's work, Regal (1975) developed a detailed conceptual model for the initial stages of the evolution of bird feathers from reptilian scale precursors, and devoted considerable space to whether lizard scale size and shape might affect heat transfer. Experimental evidence presented by Regal (1975) tended to support the idea that enlarged scales in lizards inhabiting warm climates may function as heat shields.

In the present study, we examine the statistical relationships of (1) body size and (2) dorsal scale counts with latitude and five climatic measures among 106 species or populations of *Sceloporus* lizards. Specifically, we examine variation in snout-vent length (SVL) and dorsal scale counts on a broad geographic scale to (1) test the hypothesis that body size is related to latitude or environmental characteristics, with the specific prediction that larger-bodied species will be found at lower latitudes and/or in warmer environments, similar to results of Ashton and Feldman (2003); and (2) test the hypothesis that lizards should have fewer, larger scales in warmer environments (Soulé 1966; Regal 1975). We use both conventional and phylogenetic statistical methods, with the latest phylogenetic hypothesis for *Sceloporus*

(Wiens et al. 2010). Using a phylogenetic approach is likely to be essential because closely related *Sceloporus* species often have similar scalation (Smith 1946) in addition to similarities in ecology, physiology, and other aspects of morphology—that is, the traits we studied are likely to exhibit phylogenetic signal (sensu Blomberg and Garland 2002; Blomberg et al. 2003).

Sceloporus is an excellent group for examining climatic and geographic variation in these traits. These lizards occupy a diverse array of habitats from Panama to the extreme Northwestern United States (Northern Washington state [Sites et al. 1992]), thus experiencing a wide range of climates. *Sceloporus* species also exhibit threefold variation in SVL, and vary extensively in scale size and number. In addition, intraspecific variation in scale size and number has been documented for numerous species (Smith 1946). Although *Sceloporus* species vary in body size and scale size/number, they do not exhibit the degree of ecomorphological variation in limb proportions or overall body form that is observed in some other species-rich lizard genera (e.g., *Anolis*; Smith 1946; Losos 1990, 2009; Warheit et al. 1999). In addition, they are evolutionarily conservative in their thermal physiology; *Sceloporus* species typically have similar optimal, preferred, and field-active body temperatures, despite inhabiting diverse thermal environments (Bogert 1949; Crowley 1985; Andrews et al. 1998; Angilletta 2001). Furthermore, several studies have focused on Bergmann-like clines in relation to phenotypic and life-history variation in *Sceloporus* lizards. In particular, Angilletta et al. (2004) found that the proximate mechanism for increased body size in colder environments for one species, *Sceloporus undulatus*, involved increased juvenile survivability and delayed maturation to a larger adult body size, as compared with lizards in warmer environments. In contrast, high juvenile survivorship was not associated with larger body size at cooler temperatures in *Sceloporus graciosus* (Sears and Angilletta 2004). Based on this two-species comparison (for caveats, see Garland and Adolph 1994), these authors concluded that natural selection was not the mechanism behind geographic patterns in body size. Regal (1975) used examples from *Sceloporus* to illustrate his ideas about scale function, and earlier studies also examined the climatic correlates of intraspecific variation in scale size and number in *Sceloporus* (Soulé and Kerfoot 1972; Jackson 1973). Finally, recent studies have highlighted the impact of global climate change on this group of organisms (Huey et al. 2010; Sinervo et al. 2010; Clusella-Trullas et al. 2011). We believe that examining the relationships between climate and morphological characteristics, in combination with quantitative-genetic analyses (e.g., Arnold 1988; Dohm and Garland 1993; Arnold et al. 2008), may give additional insight, and lead to the development of new hypotheses regarding how such organisms might respond to climate change.

Methods

DATA COLLECTION

We assembled data for 106 species and populations of *Sceloporus* from the literature and museum specimens. Maximum snout-to-vent length (SVL), the most common measure of body size in the herpetological literature, and the number of dorsal scale rows were obtained primarily from accounts by Smith (in particular Smith 1936; 1939; 1949). As defined by Smith (1946, p. 27), "dorsals—The scales on the back or on the upper surface. The dorsals are counted from the posterior head scale (generally the interparietal), in a straight line at or near the middorsal line as far back as a line about even with the posterior margins of the thighs, when the hind legs are held at right angles to the body. In all species except those with very small or very irregular dorsals the dorsal count is of great importance, since it reflects especially the size of the scales." Additional data were obtained from other publications (Van Denburgh 1922; Hartweg and Oliver 1937; Davis and Smith 1953; Smith and Bumzahem 1953; Maslin 1956; Axtell 1960; Etheridge 1962; Cole 1963; Lynch and Smith 1965; Smith and Lynch 1967; Webb 1967; Axtell and Axtell 1971; Stuart 1971; Degenhardt and Jones 1972; Dixon et al. 1972; Liner and Olson 1973; Olson 1973; Dassmann and Smith 1974; Smith and Savitsky 1974; Thomas and Dixon 1976; Lee and Funderberg 1977; Fitch 1978; Hall and Smith 1979; Guillette et al. 1980; Weintraub 1980; Lara-Góngora 1983; Mather and Sites 1985; Censky 1986; Liner and Dixon 1992, 1994; Smith and Perez-Higareda 1992; Smith et al. 1995), and in a few cases by examining museum specimens (see Appendix S1, Microsoft Excel file of data). Mean values were used if given by the author. If no mean value was given, then it was calculated from frequency distributions. Henceforth, reference to "dorsals" or "dorsal scale counts" refers to the rows of dorsal scales unless otherwise specified. Maximum rather than mean SVL was used as a measure of body size because the former is more commonly reported. Both SVL and dorsal scale count were $\log_{10}$ transformed prior to analyses to improve bivariate normality in correlations and/or normality of residuals in regressions. Species or populations of species were included in the analysis only if SVL, dorsal scale counts, and latitude could be obtained (see Appendix S1). Maximum SVL of the taxa in our dataset ranged from 47 to 143 mm; number of dorsal scale rows varied from 27 to 88.

We obtained latitude and longitude data for each population and species using information in the source literature in conjunction with maps. In some cases, authors reported a precise location where specimens were collected. In other cases, authors presented morphological data combined from a variety of locations, so we estimated the midpoint latitude and longitude of these locations or of the entire geographic range of the species or population in question (Gaston 2003). In the few cases where the midpoint

latitude and longitude were located outside a species' or populations' geographic range (due to its concave shape), we visually estimated the center of the range.

We then used latitude and longitude data to obtain climate information for each study species and population from the International Water Management Institute's World Water and Climate Atlas (http://www.iwmi.cgiar.org/WAtlas/Default.aspx). This climate atlas compiled data from approximately 30,000 weather stations around the world from 1961 to 1990. From these data, we constructed five indices of climate for each study species/population including an index of aridity, Q (Emberger 1955 as cited in Tieleman et al. 2002):

(1) Mean annual temperature (average of the 12 monthly mean temperatures, Mean Temperature).
(2) Mean temperature of the warmest month (Maximum Temperature).
(3) Mean temperature of the coolest month (Minimum Temperature).
(4) Total annual precipitation (Total Precipitation).
(5) The aridity measure: $\log_{10}(Q)$, where:

$$Q = P/((T_{max} + T_{min})(T_{max} - T_{min})) \times 1000,$$

where P is the average annual precipitation (mm), T_{max} is the highest monthly mean temperature and T_{min} is the lowest monthly mean temperature. Arid environments are characterized by a lower Q, whereas mesic environments have a higher Q (Emberger 1955, Tieleman et al. 2002). Because several of our climatic indicators were highly correlated (see Results), we also performed principal component analyses on latitude and four of the five climate measures ($\log_{10} Q$ was excluded because it is a composite variable).

PHYLOGENETIC INFORMATION

The phylogenetic tree used for analyses is presented in Figure 1 and Appendix S2. We used the combined mtDNA/nucDNA phylogenetic hypothesis of Wiens et al. (2010, their fig. 5). The topology of this phylogeny is similar to those previously published (Wiens and Reeder 1997), but differs in several ways—particularly in its strong support for several species-level relationships (although see Wiens et al. 2010 for further discussion), and having branch length information as substitutions. We modified the Wiens et al. (2010) tree as follows. First, we pruned taxa for which we did not have morphological data ($N = 5$). Second, using the Wiens and Reeder (1997) phylogeny (Fig. 9 of Wiens and Reeder, 1997), we added branches for taxa in which we had morphological information but were not included in Wiens et al. (2010 [$N = 26$]). We used the following heuristic when adding branches. When adding taxa to terminal branches, we simply added our new taxa exactly half way up the existing branch (creating a sister pair of taxa each with equal branch lengths). When

adding several taxa to an existing branch in a nested fashion (e.g., adding new taxon "B" to existing taxon "A" and then adding new taxon "C" to group "A, B"), we first divide one terminal branch (taxon "A") into three branches: two new internal branches one-quarter the length of the original terminal branch and one terminal branch half the length of the original terminal branch. From this, two additional terminal branches are added, one of which is half the length of the original terminal branch, the second of which is three-quarters the length of the original branch (represented in Newick format as "(((A:1,B:1)0.5,C:1.5):0.5,OUT:2);") The lengths of the branches for new taxa were arbitrarily set to equal the height of the longest branch in the newly created clade. All tree manipulation was done using Mesquite (version 2.74 for Macintosh).

Note that the tree used from Figure 5 of Wiens et al. (2010) has branch lengths in units of inferred nucleotide substitutions for their combined nuclear and mitochondrial DNA sequence data, and it is not ultrametric (i.e., the tips are not contemporaneous). Some have suggested that it could be preferable to reanalyze the sequence data by a method that constrains the branch lengths to yield an ultrametric tree. We chose not to do this because some such procedures could alter the topology (depending on the method used), potentially yielding more incorrect placements than in an unconstrained tree. In addition, there is no particularly strong reason to think that evolution of the characters of interest in the present study has been more closely related to divergence times (as can be estimated by an ultrametric tree in which all species are extant) rather than in the branch lengths obtained directly as the DNA sequence data used to estimate the tree. In any case, our analyses implicitly assume that the expected variance of evolutionary change along each branch for the traits analyzed is approximately proportional to the amount of molecular evolution for the genes studied by Wiens et al. (2010). All phylogenetic material is presented in Appendix S2 and we encourage readers to reanalyze as they see fit.

STATISTICAL ANALYSES

Although latitude and climatic indicators are not organismal traits and do not undergo evolution, we treat them here as a continuous traits equivalent to body size or scale counts, for purposes of our analyses. We follow the rationale of Garland et al. (1992), who suggest that if closely related species have similar ecological attributes, such as geographic distribution, then it can be appropriate to use climatic indicators in a phylogenetically based statistical analysis (see also Swanson and Garland 2009). This assumption should be particularly reasonable for animals with relatively low mobility and dispersal, such as *Sceloporus*.

We used both conventional (i.e., assuming a star phylogeny) and phylogenetically informed statistical analyses (Clobert et al. 1998; Garland et al. 2005). We used the univariate
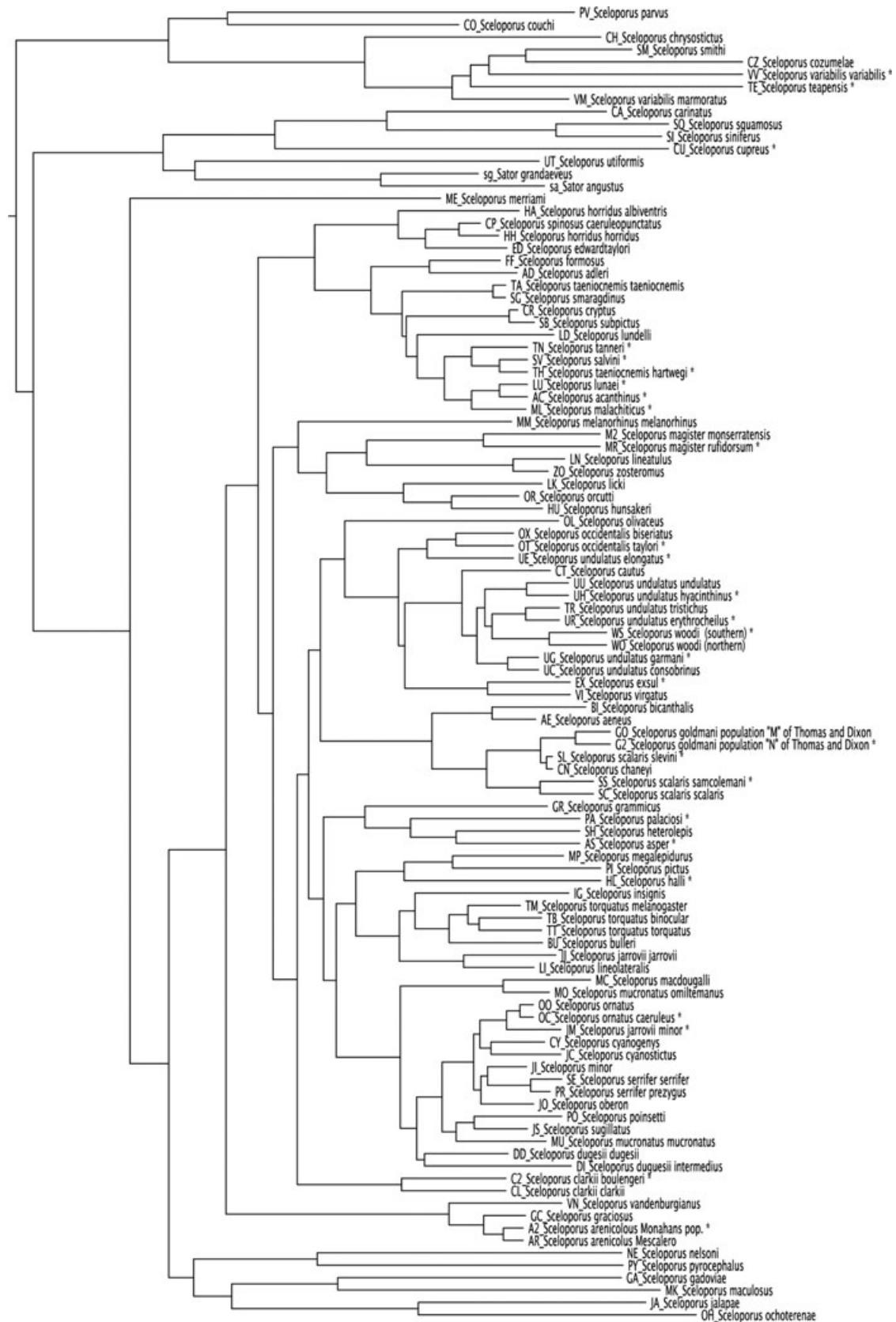
Figure 1. Hypothesized phylogenetic relationship of the 106 *Sceloporus* species or populations analyzed (topology and branch lengths from Fig. 5 of Wiens et al. 2010). Taxa not included in the original tree are marked with "∗" (see Methods). Two-character codes and species names (based on Wiens et al. [2010] nomenclature) at tips correspond to species as listed in Appendix S1.

randomization tests and descriptive statistics for phylogenetic signal from Blomberg et al. (2003; their Matlab program PHYSIG_LL.m). We performed simple linear regressions of $\log_{10}$ SVL on latitude and on each of the five climatic indicators to test the prediction that *Sceloporus* follow the inverse of Bergmann's rule. In preliminary analyses, we found that the number of dorsal scales was negatively related to $\log_{10}$ SVL; therefore, to address the Soulé-Regal hypotheses, we used multiple regressions of dorsal scales on $\log_{10}$ SVL in combination with either latitude or one of the five climatic indicators. We also performed multiple regressions of $\log_{10}$ dorsal scale counts on $\log_{10}$ SVL and the first three (of five) principal components, which explained >99% of the total variation in latitude and climate (see Results). For all regression analyses, we used the Regression version 2.m Matlab program of Lavin et al. (2008) and computed regressions in three ways: conventional, nonphylogenetic, ordinary least squares (OLS); phylogenetic generalized least squares (PGLS) with the branch lengths of Wiens et al. (2010; see above and Fig. 1); and regression in which the Wiens et al. (2010) branch lengths were used and the residuals modeled as having evolved via an Ornstein–Uhlenbeck process (RegOU), intended to model stabilizing selection (see Lavin et al. 2008).

In the RegOU model, the strength of phylogenetic signal in the residual variation is estimated simultaneously with the regression coefficients, by use of an additional parameter, d. In the RegOU model, d is used, in effect, to pull the internal nodes of the phylogenetic tree either toward the tips (terminal taxa) of the tree (indicated by d values > unity) or toward the root (basal node) of the tree (indicated by d values < unity). Hence, the estimate of d provides an indicator of the extent of phylogenetic signal in the residuals (Blomberg et al. 2003; Lavin et al. 2008). Small values of d indicate a model in which the residuals match a more star-like phylogeny, values near unity indicate that the original tree provides an appropriate variance–covariance matrix for the residuals, and values greater than 1 indicate that a tree even more hierarchical than the original is appropriate. The fit of the RegOU model can be compared with the OLS or PGLS models by a ln maximum likelihood ratio test, where twice the difference in the ln maximum likelihood is assumed to be distributed (asymptotically) as a χ^2 with 1 degree of freedom, for which the critical value at $\alpha = 0.05$ is 3.841. In the comparison with OLS, values greater than 3.841 indicate that the value of d is statistically greater than zero and hence that the residual variation in the dependent variable exhibits statistically significant phylogenetic signal. The OLS models were also checked against output from SPSS version 11.5 for Windows (SPSS Inc., 1999, Chicago IL). Note that maximum likelihoods are used for likelihood ratio tests, whereas restricted maximum likelihood (REML) is used for estimating coefficients in the models, including the value of d (see Lavin et al. 2008)

We also checked for outliers that might be influencing statistical results. We examined scatterplots of tip data as well as standardized independent contrasts, and also values for standardized residuals from the conventional and phylogenetic regression models. None were detected.

Results

UNIVARIATE ANALYSES OF PHYLOGENETIC SIGNAL

Both $\log_{10}$ snout-vent length ($K = 0.891$) and $\log_{10}$ dorsal scale counts ($K = 1.136$) showed strong and highly statistically significant (both $P < 0.001$) phylogenetic signal (Table 1). These results suggest that phylogenetic regression models would fit the data better than nonphylogenetic ones, and that expectation is upheld (see below). Latitude and the various climatic descriptors also showed significant phylogenetic signal, although K values were substantially lower.

LATITUDE AND CLIMATE

Four of five climate descriptors showed a significant negative relationship with latitude (Table 2); the only exception was maximum temperature, which tended to increase at higher latitudes (two-tailed $P = 0.056$). The three temperature indicators were all significantly positively correlated. Annual total precipitation was negatively related to maximum temperature, but significantly positively related to minimum temperature. Finally, aridity ($\log_{10}$ Q) was significantly negatively related to maximum temperature and significantly positively related to minimum temperature and total precipitation. Collectively, these relationships indicate that, based on the *Sceloporus* populations in our sample, those at higher latitudes tend to experience climates with lower mean annual and minimum temperatures, less rainfall, and greater aridity (i.e., lower $\log_{10}$ Q index—indicative of desert-like environments), but with a weak tendency for higher mean temperatures during the warmest month.

Results from the principal component analysis (Table 2) indicated that the first three PCs explained more than 99% of the total variation in latitude and the four climatic descriptors. PC1 (58%) reflected mainly the negative relation of latitude with mean and minimum temperature and precipitation, whereas PC2 (30%) had a strong positive loading for maximum temperature, and a negative loading for total precipitation. Therefore, PC1 describes an axis of latitude with temperature. PC2 is similar to an aridity index, with hot, dry climates at one end and cool, wet climates at the other. Variation in precipitation was approximately equally distributed across the first three PCs.

BODY SIZE, LATITUDE, AND CLIMATE

In all cases, the conventional regressions (OLS models) had much lower likelihoods than the corresponding phylogenetic (PGLS)

Table 1. Univariate measures of phylogenetic signal. *K* varies from 0 to 1 to >1, indicating, respectively, no phylogenetic signal, that relatives resemble each other as much as expected under Brownian-motion like evolution, and that relatives are more similar to each other than expected under Brownian motion (Blomberg et al. 2003). *P*-values indicate significant phylogenetic signal based on randomization tests of the mean squared error (MSE; lower values indicate better fit of tree to data). Results are from the PHYSIG_LL.m Matlab program of Blomberg et al. (2003) using the tree shown in Figure 1 (modified from Wiens et al., 2010).

Trait	Expected MSE_0/MSE	Observed MSE_0/MSE	K	MSE	MSE_{star}	P	ln maximum likelihood	ln maximum likelihood$_{star}$
$\log_{10}$ snout-vent length	2.97	2.65	0.891	0.0074	0.0141	<0.001	110.30	76.00
$\log_{10}$ dorsal scale counts	2.97	3.38	1.136	0.0064	0.0117	<0.001	117.65	86.04
Latitude	2.97	1.80	0.604	22.70	40.66	<0.001	−315.38	−346.28
Mean temperature	2.97	1.02	0.345	19.11	17.78	<0.001	−306.27	−302.40
Maximum temperature	2.97	0.80	0.269	19.90	13.626	0.029	−308.43	−288.30
Minimum temperature	2.97	1.27	0.427	32.44	40.32	<0.001	−334.32	−345.84
Total precipitation	2.97	1.19	0.402	$2.04 \times 10^{+5}$	$2.28 \times 10^{+5}$	<0.001	−797.96	−803.69
$\log_{10}$ Q	2.97	1.61	0.543	0.200	0.300	<0.001	−64.67	−86.12

Table 2. Nonphylogenetic Pearson's correlation coefficients and two-tailed *P* values for our measure of body size, latitude, and five climatic measures (top panel; see Data Collection in Methods). Bottom panel presents a principal components analysis (shown are correlations of each trait with each PCs) of the correlation matrix for the climatic measures (excluding Q because it is derived from others). Scores for the first three PCs were used in the multiple regressions shown at the bottom of Table 4.

	Latitude	Mean temperature	Maximum temperature	Minimum temperature	Total precipitation	$\log_{10} Q$
$\log_{10}$ SVL	$r = 0.016$	$r = 0.164$	$r = 0.210$	$r = 0.119$	$r = -0.029$	$r = -0.145$
	$P = 0.873$	$P = 0.094$	$P = 0.030$	$P = 0.223$	$P = 0.767$	$P = 0.137$
Latitude		$r = -0.580$	$r = 0.186$	$r = -0.858$	$r = -0.566$	$r = -0.733$
		$P < 0.001$	$P = 0.056$	$P < 0.001$	$P < 0.001$	$P < 0.001$
Mean Temperature			$r = 0.672$	$r = 0.892$	$r = 0.261$	$r = 0.168$
			$P < 0.001$	$P < 0.001$	$P = 0.007$	$P = 0.186$
Maximum Temperature				$r = 0.280$	$r = -0.171$	$r = -0.445$
				$P = 0.004$	$P = 0.080$	$P < 0.001$
Minimum Temperature					$r = 0.445$	$r = 0.484$
					$P < 0.001$	$P < 0.001$
Total Precipitation						$r = 0.857$
						$P < 0.001$
	1	2	3	4	5	
Latitude	−0.847	0.442	0.272	0.118	0.008	
Mean temperature	0.902	0.426	−0.025	0.016	0.058	
Maximum temperature	0.326	0.908	0.253	−0.064	−0.030	
Minimum temperature	0.978	0.013	−0.177	0.106	−0.037	
Total precipitation	0.571	−0.560	0.601	0.005	0.001	
Eigenvalue	2.919	1.515	0.531	0.030	0.006	
% of Variance	58.38	30.31	10.61	0.59	0.11	
Cumulative	58.38	88.68	99.29	99.89	100.00	

regressions (Table 3), and these differences are great enough that they could be considered statistically significant (see Mooers et al. 1999). Likelihood ratio tests revealed that the RegOU model was significantly better than the conventional OLS model for all traits, and significantly better than the PGLS model for mean and maximum temperatures (Table 3). Considering only the phylogenetic models (PGLS and RegOU), maximum temperature was a

significant positive predictor of body size, and aridity ($\log_{10}$ Q) was a significant negative predictor of body size (Table 3, Fig. 2). Although these relationships are statistically significant, their strength is relatively weak ($r^2 < 0.10$). Nevertheless, larger lizards tend to be found in areas that are more arid and have higher maximum temperatures. Similar results were obtained when PC1, PC2, and PC3 were used as predictors of body size; larger lizards

Table 3. Univariate regressions of $\log_{10}$ snout-vent length (SVL) on latitude and five climatic indicators (see Data Collection in Methods) using conventional statistics (OLS regressions), phylogenetic generalized least-squares (PGLS) regressions, and phylogenetic regressions with the residuals modeled as an Ornstein−Uhlenbeck process (RegOU of Lavin et al., 2008; *d* is OU parameter estimated by REML). The phylogenetic regression analyses used the tree shown in Figure 1 (modified from Wiens et al., 2010). Regressions significant at *P* < 0.05 are in bold. Shown are slopes (β), two-tailed significance levels (*P*), ln maximum likelihoods, AIC corrected for small sample sizes (and based on ln maximum likelihoods), and coefficient of determination (r^2). Also shown are ln maximum likelihood ratio test statistics (twice the difference in the ln ML values) for comparing the RegOU model to the OLS and PGLS models (see Statistical Analysis in Methods), with an * indicating models significantly different at *P* < 0.05 (critical value for a χ^2 distribution with one df = 3.841).

| Regression of log SVL on	OLS (Star)	PGLS	RegOU	ln ML ratio test statistic	
				RegOU vs. OLS	RegOU vs. PGLS
Latitude	0.00026	0.0026	0.0026		
P	0.6577	0.1445	0.1513		
ln maximum likelihood	76.013	111.386	112.917	73.808*	3.062
AICc	−145.791	−216.537	−217.437		
r^2	0.0002	0.0204	0.0197		
d			0.8049		
Mean temperature	0.0046	0.0021	0.0028		
P	0.0949	0.2834	0.1726		
ln maximum likelihood	77.431	110.885	112.844	70.826*	3.918*
AICc	−148.627	−215.535	−217.292		
r^2	0.2659	0.0111	0.0178		
d			0.7768		
Maximum temperature	0.0067	0.0044	0.0051		
P	**0.0327**	**0.0191**	**0.0095**		
ln maximum likelihood	78.340	113.106	115.326	73.972*	4.440*
AICc	−150.444	−219.977	−222.256		
r^2	0.0431	0.0516	0.0628		
d			0.7647		
Minimum temperature	0.0026	0.0002	0.0006		
P	0.2168	0.8901	0.7106		
ln maximum likelihood	76.784	110.306	111.948	70.328*	3.284
AICc	−147.333	−214.376	−215.501		
r^2	0.0146	0.0002	0.0013		
d			0.7950		
Total precipitation	-7.065×10^{-6}	-1.384×10^{-5}	-1.491×10^{-5}		
P	0.7726	0.4580	0.4425		
ln maximum likelihood	76.046	110.578	112.173	72.254*	3.190
AICc	−145.856	−214.92	−215.951		
r^2	0.0008	0.0053	0.0057		
d			0.7989		
$\log_{10}$ Q (aridity index)	−0.0310	−0.0402	−0.0429		
P	0.1437	**0.0312**	**0.0229**		
ln maximum likelihood	77.098	112.672	114.546	74.896*	3.748
AICc	−147.96	−219.108	−220.697		
r^2	0.0204	0.0439	0.0488		
d			0.7823		

were found in areas with higher maximum temperatures and lower aridity as evidenced by a significant positive effect of PC2 (RegOU B = 0.215, $F_{1,102} = 6.59$, $P = 0.0117$, model $r^2 = 0.069$, model maximum likelihood = 115.65).

DORSAL SCALE COUNT, LATITUDE, AND CLIMATE

In simple linear regressions, $\log_{10}$ dorsal scale count was always significantly negatively related to $\log_{10}$ SVL under all three evolutionary models (OLS or "star," PGLS, and RegOU; all
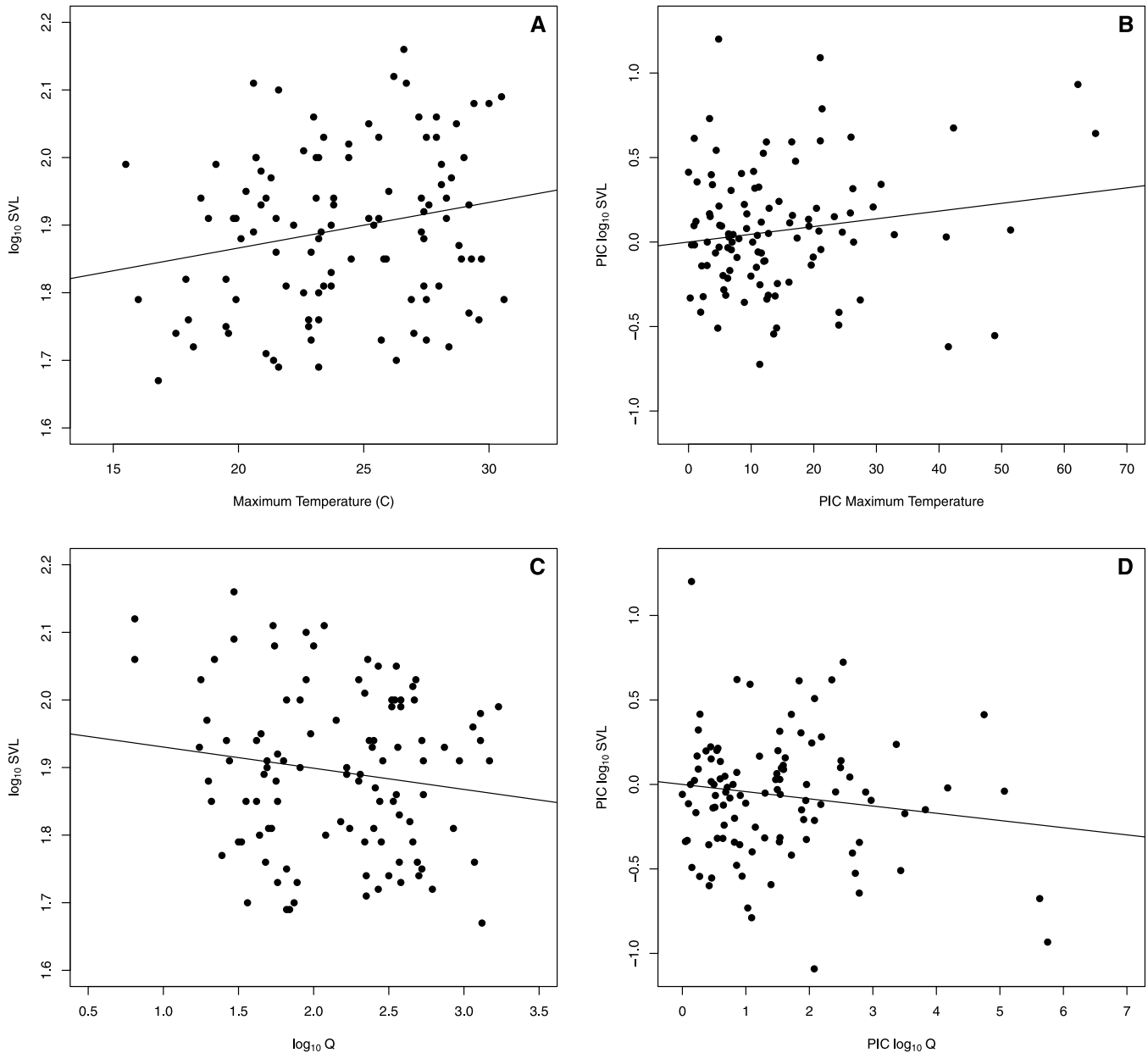
Figure 2. Bivariate scatterplots of the relationships between $\log_{10}$ snout-vent length (SVL) and maximum temperature (A and B) and $\log_{10}$ Q (C and D). Both tip data (A and C) and (positivized: Garland et al. 1992) phylogenetically independent contrasts (PIC) are presented (B and D). Maximum temperature was a statistically significant ($P < 0.05$) positive predictor of $\log_{10}$ SVL in both conventional (OLS) and phylogenetic (PGLS and RegOU) regression models (Table 2); $\log_{10}$ Q was a significant negative predictor only for the phylogenetic models (Table 3). Note that the PGLS models in Table 3 correspond to a regression through the origin (as shown) fitted to the scatterplots for independent contrasts (B and D).

$P < 0.0001$). Figure 3A depicts the relationship using phylogenetically independent contrasts, which is equivalent to the PGLS regression. Therefore, to test the hypothesis that lizards in warmer environments have (by inference) larger scales, we used multiple regressions that included $\log_{10}$ SVL under all three evolutionary models. In addition, for each multiple regression, we tested for interactions between $\log_{10}$ SVL and the climate indicator of in-

terest. These interaction terms were never statistically significant, and so they were not included in the final models (Table 4).

Results are shown in Table 4 (see also bivariate scatterplots in Fig. 3). The phylogenetic regression models always fit the data better than the nonphylogenetic alternative (based on AICc [Burnham and Anderson 2002] and ln maximum likelihood ratio tests comparing RegOU with OLS models [results not shown but

easily calculated from ln ML values shown in Table 4]). Thus, phylogenetic signal was present in the residuals of the regressions. ΔAICc values indicate that RegOU models fit the data marginally better than PGLS models for most traits, except Maximum Temperature and Mean Temperature. Regardless, ΔAICc scores between any of the two phylogenetic models (PGLS or RegOU) are always less than 1 (Table 4). This is expected, given that the OU transformation parameters for all models (all $d \sim 0.8$) was relatively close to unity, a value that would equate to the original PGLS "starter" tree.

Controlling for body size, dorsal scale count was significantly positively related to latitude, but significantly negatively related to minimum temperature and $\log_{10} Q$. The strength of these relationships is stronger than those predicting body size (Table 3). Based on model likelihoods and AICc, as well as partial F statistics, a RegOU model with latitude was the best predictor of $\log_{10}$ dorsal scales (Table 4).

We also tested whether addition of our aridity measure, $\log_{10} Q$, to the model that included SVL and latitude further improved predictive ability under the RegOU model. The addition of Q did not appreciably change the effect of latitude, and $\log_{10} Q$ was not a significant predictor ($P = 0.8095$). Similarly, the addition of other climatic indicators separately did not substantially change the effect of latitude, and none had a significant effect (maximum temperature $P = 0.8452$; minimum temperature $P = 0.6609$; mean temperature $P = 0.9968$; total precipitation $P = 0.4616$).

Finally, because our climate indicators and latitude are in several cases strongly correlated (Table 2) we examined a multiple regression model with the first three PC axes and $\log_{10}$ SVL as predictors of $\log_{10}$ dorsal scale count. Similar to other results shown in Table 4, PC1 and PC2 had significant effects on $\log_{10}$ dorsal scale count, and the phylogenetic models (PGLS and RegOU) had a better fit than the nonphylogenetic (OLS). Specifically, PC1 had a significant negative effect on $\log_{10}$ dorsal scale row count (see also Fig. 3E) and PC2 (see also Fig. 3F) had a significant positive effect. Inspection of the PC axes (see Table 2) suggests that species with fewer dorsal scale rows are found at higher latitudes, with lower mean and minimum temperatures, and less rainfall (negative effect of PC1). Conversely, the positive effect of PC2 suggests that species with more dorsal scale rows are found in areas with higher maximum temperatures and less precipitation. This second PC describes an "aridity axis," similar to $\log_{10} Q$.

Discussion

UNIVARIATE ANALYSES OF PHYLOGENETIC SIGNAL

Both biological traits, latitude, and all of the climatic descriptors showed statistically significant phylogenetic signal, although the amount of signal was much higher for the biological traits (Table 1). This general pattern of higher phylogenetic signal in biological traits is consistent with the survey presented in Blomberg et al. (2003) and with other subsequent papers (e.g., see Swanson and Garland 2009, references therein). In two of the eight cases shown in Table 1 (Mean and Maximum Temperature), the likelihood of the star phylogeny is higher than for the specified phylogenetic tree (Fig. 1), suggesting that mean and maximum temperature do not exhibit phylogenetic signal. As discussed elsewhere (Fusco et al. In press), this discrepancy can occur because comparing likelihoods is not the same as the randomization test of Blomberg et al. (2003) and because these measures of temperature have low levels of signal ($K \sim 0.3$).

LATITUDE AND CLIMATE

Latitude is often used as a proxy for climate, with the assumption that higher latitudes equate with colder environments (Pincheira-Donoso et al. 2008 and references therein). However, our data suggest that the use of latitude as a proxy for climate can sometimes be misleading, particularly at the finer spatial scales over which an individual species may exist (Blackburn et al. 1999). For instance, based on our dataset for localities of *Sceloporus* lizards, latitude is negatively related to mean annual temperature and temperature of the coolest month, both suggesting colder environments, but weakly positively related to temperature of the warmest month (Table 2). Furthermore, a principal components analysis yielded a first axis that suggests the same trends (Table 2). The PC analysis also produced a second axis that can be described as an aridity axis, where maximum temperature loads positively, but total precipitation loads negatively. Taken together, these results illustrate the complex interactions between latitude and climate indicators. Therefore, *Sceloporus* lizards at higher latitudes may be experiencing more desert-like environments, whereas those from lower latitudes are experiencing more subtropical and thermally stable environments (Brown and Lomolino 1998; Phillips and Comus 2000). For example, *S. malachiticus,* the southernmost species (11.86˚ lat, 85.54˚ long.; Appendix S1) occurs in tropical Central America; whereas *S. graciosus*, the species from the highest latitude (41.62˚ lat., 112.73˚ long., Appendix S1) occurs in a more arid environment in the Great Basin Desert of Nevada and western Utah, as well as in montane environments in California. Thus, the interpretation of morphological characteristics in relation to only one of these environmental factors or latitude may be misleading. In such instances, a multivariate approach—such as done here using PC scores as independent variables in a multiple regression—may prove more informative than analyzing single climatic indicators alone. These interrelationships need to be kept in mind when comparing our results with those of studies that examined latitude but not (particular) climatic measures, or vice versa.
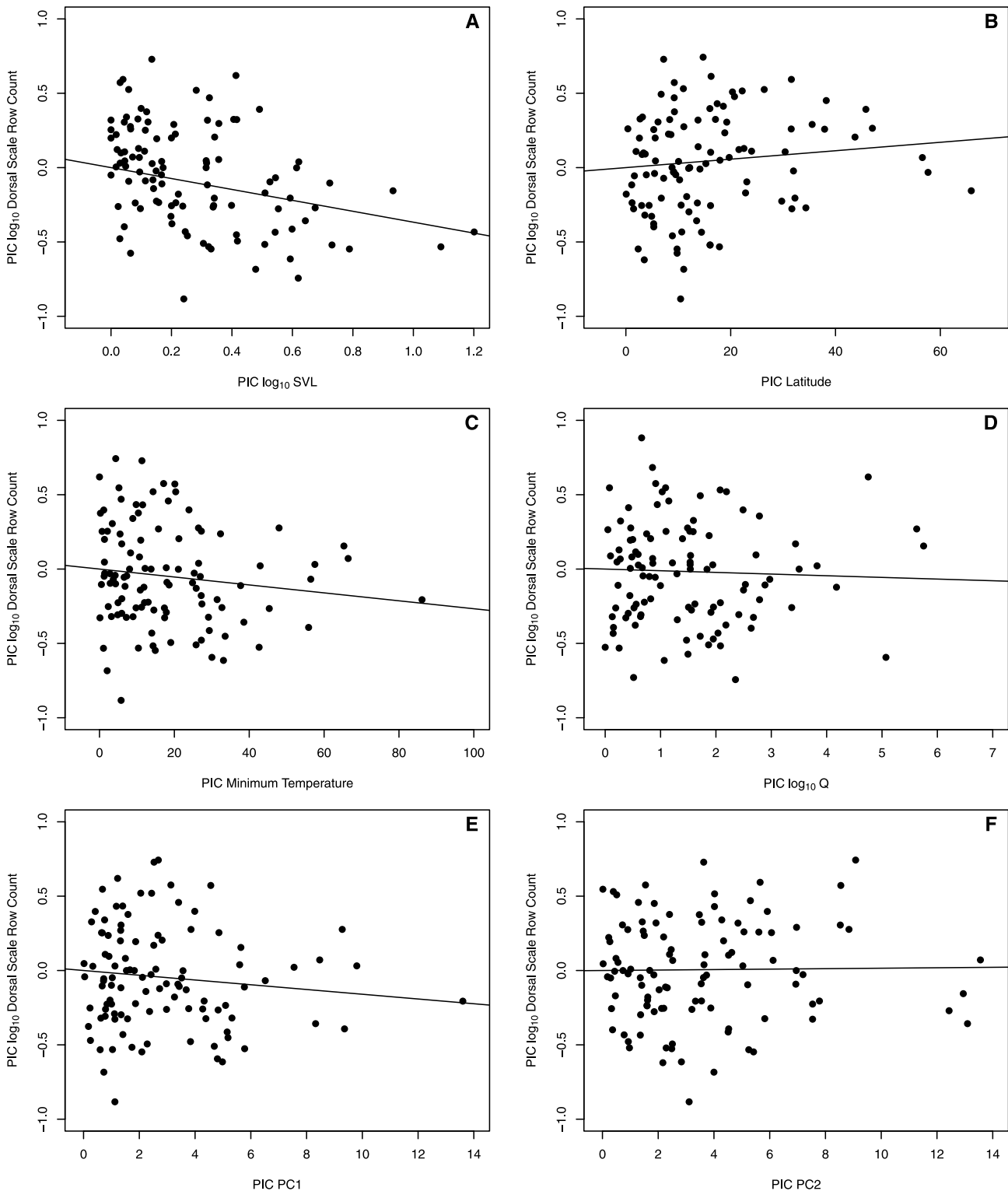
Figure 3. Bivariate scatterplots of (positivized: Garland et al. 1992) phylogenetically independent contrasts (PIC) depicting the relationships between $\log_{10}$ dorsal scale counts and (A) $\log_{10}$ snout-vent length (SVL), (B) latitude, (C) minimum temperature, (D) $\log_{10}$ Q (aridity index), (E) scores on PC1 (see Table 2), and (F) scores on PC2. Regression lines shown (through the origin) are from univariate regressions and do not correspond to analyses shown in Table 4. Only the regression shown in panel (A) is statistically significant ($P = 2.6 \times 10^{-5}$). Significance levels for regressions shown in panels (B–F) are, respectively, two-tailed $P = 0.084$, $P = 0.051$, $P = 0.522$, $P = 0.074$, and $P = 0.833$. However, based on multiple regressions that included $\log_{10}$ SVL (see best models in Table 4), $\log_{10}$ dorsal scale counts are significantly positively associated with latitude and PC2, but negatively associated with minimum temperature, $\log_{10}$ Q, and PC1.

Table 4. Multiple regressions examining the effects of log$_{10}$ SVL, latitude, five climatic indicators, and principal components (see Data Collection in Methods) on log$_{10}$ dorsal scale counts under three models of evolution. The best regression model for each predictor based on AICc is in bold.

Model	ln ML (multiple r^2)	AICc	Independent variables	Partial regression coefficients	$F_{1,103}$	P
Latitude						
OLS (Star)	112.114	−215.833	log$_{10}$ SVL	−0.547	60.95	<0.0001*
	($r^2 = 0.3886$)		Latitude	2.918×10^{-3}	5.00	0.0275*
PGLS	130.592	−252.787	log$_{10}$ SVL	−0.406	24.38	<0.0001*
	($r^2 = 0.2167$)		Latitude	4.0163×10^{-3}	7.33	0.0079*
RegOU[1]	**131.967**	**−253.334**	**log$_{10}$ SVL**	**−0.429**	**27.13**	**<0.0001***
($d = 0.803$)	**($r^2 = 0.2358$)**		**Latitude**	**4.351×10^{-3}**	**8.21**	**0.0051***
Mean temperature						
OLS (Star)	109.710	−211.025	log$_{10}$ SVL	−0.540	55.13	<0.0001*
	($r^2 = 0.3602$)		Mean temp.	$−9.373 \times 10^{-04}$	0.21	0.6477
PGLS	**127.463**	**−246.530**	**log$_{10}$ SVL**	**−0.365**	**18.80**	**<0.0001***
	($r^2 = 0.1690$)		**Mean temp.**	**$−1.661 \times 10^{-3}$**	**1.01**	**0.3173**
RegOU	128.512	−246.423	log$_{10}$ SVL	−0.381	20.12	<0.0001*
($d = 0.826$)	($r^2 = 0.1826$)		Mean temp.	$−1.931 \times 10^{-3}$	1.24	0.2681
Maximum temperature						
OLS (Star)	110.967	−213.538	log$_{10}$ SVL	−0.570	61.86	<0.0001*
	($r^2 = 0.3752$)		Max. temp.	3.818×10^{-3}	2.69	0.1040
PGLS	**127.292**	**−246.188**	**log$_{10}$ SVL**	**−0.390**	**20.50**	**<0.0001***
	($r^2 = 0.1663$)		**Max. temp.**	**1.359×10^{-3}**	**0.67**	**0.4149**
RegOU	128.208	−245.817	log$_{10}$ SVL	−0.409	22.10	<0.0001*
($d = 0.832$)	($r^2 = 0.1774$)		Max. temp.	1.414×10^{-3}	0.66	0.4184
Minimum temperature						
OLS (Star)	111.137	−213.879	log$_{10}$ SVL	−0.530	55.32	<0.0001*
	($r^2 = 0.3772$)		Min. temp.	$−2.317 \times 10^{-3}$	3.03	0.0847
PGLS	129.476	−250.555	log SVL	−0.372	20.44	<0.0001*
	($r^2 = 0.2000$)		Min. temp.	$−2.781 \times 10^{-3}$	5.03	0.0271
RegOU	**130.829**	**−251.058**	**log$_{10}$ SVL**	**−0.388**	**22.20**	**<0.0001***
($d = 0.805$)	**($r^2 = 0.2191$)**		**Min. temp.**	**$−3.133 \times 10^{-3}$**	**5.86**	**0.0172**
Total precipitation						
OLS (Star)	112.459	−216.522	log$_{10}$ SVL	−0.550	61.87	<0.0001*
	($r^2 = 0.3926$)		Total precip.	$−4.15 \times 10^{-5}$	5.70	0.0188*
PGLS	127.967	−247.539	log$_{10}$ SVL	−0.383	20.96	<0.0001*
	($r^2 = 0.1769$)		Total Precip.	$−2.25 \times 10^{-5}$	2.00	0.1603
RegOU	**129.281**	**−247.963**	**log$_{10}$ SVL**	**−0.407**	**23.54**	**<0.0001***
($d = 0.799$)	**($r^2 = 0.1965$)**		**Total precip.**	**$−2.73 \times 10^{-5}$**	**2.71**	**0.1028**
log$_{10}$ Q						
OLS (Star)	113.969	−219.542	log$_{10}$ SVL	−0.575	68.18	<0.0001*
	($r^2 = 0.4096$)		log$_{10}$ Q	−0.045	8.84	0.0037
PGLS	128.430	−248.465	log$_{10}$ SVL	−0.405	22.70	<0.0001
	($r^2 = 0.1841$)		log$_{10}$ Q	−0.028	2.92	0.0905
RegOU	**130.022**	**−249.444**	**log$_{10}$ SVL**	**−0.438**	**26.44**	**<0.0001**
($d = 0.779$)	**($r^2 = 0.2096$)**		**log$_{10}$ Q**	**−0.034**	**4.20**	**0.0430***

Continued

BODY SIZE, LATITUDE, AND CLIMATE

Our finding of significant phylogenetic signal in both body size and midpoint latitude (Table 1) is consistent across at least two separate phylogenetic hypotheses indicating that these results ap-pear generally robust to at least some changes in topology and branch lengths (see Appendix S3). Further, our findings of sig-nificant phylogenetic signal in these traits are consistent with several previous studies (Freckleton et al. 2002; Blomberg et al.

Table 4. Continued

Model	ln ML (multiple r^2)	AICc	Independent variables	Partial regression coefficients	$F_{1,103}$	P
PC1, PC2, PC3 (from Table 2)						
OLS (Star)	113.900 ($r^2 = 0.4089$)	−214.952	$\log_{10}$ SVL	−0.564	62.67	<0.0001*
			PC1	−0.014	2.67	0.1054
			PC2	0.020	5.67	0.0191*
			PC3	-1.422×10^{-3}	0.03	0.8628
PGLS	131.207 ($r^2 = 0.2257$)	−249.57	$\log_{10}$ SVL	−0.412	23.99	<0.0001*
			PC1	−0.022	6.61	0.0116*
			PC2	0.014	3.69	0.0576
			PC3	4.009×10^{-3}	0.43	0.5135
RegOU ($d = 0.780$)	**132.720** ($r^2 = 0.2491$)	**−250.297**	**$\log_{10}$ SVL**	**−0.438**	**26.71**	**<0.0001***
			PC1	**−0.024**	**7.61**	**0.0069***
			PC2	**0.015**	**4.12**	**0.0450***
			PC3	**3.797×10^{-3}**	**0.34**	**0.5611**

*P-value < 0.05

[1]Overall best model based on AICc.

2003; Ashton 2004; Rezende et al. 2004; Huey et al. 2006; Swanson and Garland 2009). We found that mean temperature of the warmest month (maximum temperature) was a significant positive predictor of body size, and $\log_{10}$ Q (aridity index) a significant negative predictor of body size, under phylogenetic models (which had the best fit; Table 3). Thus, *Sceloporus* lizards from warmer and more arid environments tend to be larger (Fig. 2), consistent with the inverse of Bergmann's rule when viewed from a climatic perspective (Ashton and Feldman 2003).

Several factors may underlie the observed pattern of body size variation in *Sceloporus*. Most generally, as noted by Ashton and Feldman (2003), different processes may affect body size evolution in different vertebrate lineages, and those processes might lead to different outcomes in different lineages. One possibility pertains to the expected relationship between fasting endurance and body size. Specifically, larger body size could be advantageous in warm, dry areas, if they are more likely to impose periods of food or water shortage—note that dehydration endurance should also increase with body size (cf. Mautz 1982; Nagy 1982).

A second possibility is interspecific competition (cf. Ashton et al. 2000 on mammals). Reduced competition in areas further from the equator may allow for larger body sizes. Conversely, smaller body sizes may be the rule in more equatorial latitudes, where competition for food and other resources is often presumed to be relatively fierce (e.g., Scheibe 1987). However, in the absence of more detailed knowledge of *Sceloporus* natural history and community ecology, such hypotheses are at this point highly speculative.

Third, it is likely that maintenance of preferred body temperature influences the evolution of body size in *Sceloporus*. Bergmann's Rule, as applied to endotherms, invokes the heat con-

servation explanation, suggesting that larger-bodied endotherms are favored at higher latitudes and/or lower temperatures because of a reduced surface/volume ratio. In lizards, the pattern of smaller body sizes in colder climates may be the result of selection for more rapid heating abilities (Pianka and Vitt 2003). Field-active body temperatures are often relatively static across the geographic range of a lizard species (Bogert 1949; Crowley 1984; Ashton and Feldman 2003). Thus, smaller individuals living in thermally dynamic areas (i.e., temperate areas with greater daily fluctuations in temperature) may be able to exert finer-scale control of body temperature by behavioral means and thus be active for a greater amount of time during each day. This may be particularly important in areas that are more seasonal, where resources may be scarce and extended periods of activity are beneficial.

The significant positive association between *Sceloporus* body size and maximum temperature (Table 3) is similar to the altitudinal trends in body size that have been discussed by several authors. For example, Bogert (1949) pointed out an altitudinal trend in body size (and scale size) involving four species of *Sceloporus* in several southern California mountain ranges: the small-bodied, small-scaled *S. graciosus* occurs at the highest elevations, the large-bodied, large-scaled desert species *S. magister* occurs lowest, and *S. occidentalis* and *S. orcutti* occur at intermediate elevations. In the Southern California mountains, temperature decreases as elevation increases, so the results of our genus-wide analyses are consistent with this trend observed on a small group of *Sceloporus* species within a geographically restricted region.

We did not find a statistically significant relationship between body size and latitude in either phylogenetic or nonphylogenetic analyses (Table 3). In an interspecific (but nonphylogenetic)

analysis of all lizards for which data were available ($N = 935$ species), Lindsey (1966) also found no relation between latitude and body size, and a slight tendency for snakes (which evolved from lizards) to be larger at higher latitudes. Similarly, Dunham et al. (1988) in a nonphylogenetic study of 185 lizard taxa (limited to those for which life-history data were available), reported no significant difference in mean female SVL at maturity or in mean adult female SVL between temperate and tropical taxa. More recently, Cruz et al. (2005) reported a significant positive relationship between SVL and latitude in *Liolaemus* ($N = 21$ species of the *L. boulengeri* complex) using phylogenetic statistics, whereas Pincheira-Donoso et al. (2008) found no significant relationship between adjusted midpoint latitude and SVL in *Liolaemus* lizards ($N = 63$ species) using phylogenetic statistics. Using a nonphylogenetic interspecific analysis, Olalla-Tárraga et al. (2006) found an increase in body size with latitude among European lizards ($N = 43$) versus a decrease in body size with latitude among European snakes ($N = 28$); they also did not find any simple latitude-body size relationships for North American lizards ($N = 100$) or snakes ($N = 124$). Thus, interspecific analyses have not revealed a consistent relationship between body size and latitude in squamates. The reasons for this inconsistency probably include complex patterns of selection, lineage-specific sensitivities to climatic indicators (e.g., temperature: Huey et al. 2009), alternate evolutionary responses to similar selection (multiple solutions sensu Garland et al. 2011), and variability in the relations between latitude and climatic indicators (as discussed above).

DORSAL SCALES, CLIMATE, AND LATITUDE

The Soulé (1966) and Regal (1975) hypotheses for variation in the size of lizard scales was based on the putative adaptive significance of scale variation in relation to the thermal environment. Specifically, lizards were predicted to have (1) larger scales in warmer environments to reduce overheating and (2) smaller scales in colder environments to facilitate heat retention. We found no support for prediction (1); maximum temperature was not a significant predictor of dorsal scale count (Table 4). Our finding that (inferred) scale size is positively related to minimum temperature and PC1 (a latitude and temperature axis: Table 2) does not seem germane to the first prediction because overheating is unlikely to be an issue during the coldest month. However, this finding can be viewed as consistent with prediction (2). Previous studies of the potential temperature correlates of dorsal scale size and number in other lineages of lizards have found inconsistent results; these studies have typically compared either populations within a single species or in some cases a small number of closely related species (*Egernia*: Horton 1972; *S. graciosus*: Soulé and Kerfoot 1972; *Sceloporus woodi*: Jackson 1973; Lesser Antillean *Anolis*: Malhotra and Thorpe 1994; *Anolis sagrei* and among species of *Anolis*: Calsbeek et al. 2006).

In addition to temperature, we found that *Sceloporus* tended to have larger scales (fewer scale rows) if they inhabited areas that are less arid, as indicated by higher Q, or having higher scores on PC2 (Table 4). These results are similar to those of Soulé and Kerfoot (1972). They analyzed dorsal scale count variation among 15 populations of *S. graciosus* in the western United States and found that August rainfall was the strongest overall (negative) predictor of scale count. Temperature, however, was not a consistent predictor of scale count (Soulé and Kerfoot 1972). Other studies examining the relationship between scale size and aspects of aridity (e.g., humidity) have found conflicting results (Horton 1972; Malhotra and Thorpe 1994). No previous studies, however, have used the aridity index Q or scores on principal component axes as potential predictors of scale size or number.

A comparison of likelihoods and AICc values for the models with climatic indicators or latitude (in addition to body size) suggests that the model with latitude is the best (Table 4). Such a result could occur because the "measurement error" in our values of latitude is lower than for the climatic indicators (e.g., see Ives et al. 2007). Alternatively, many other aspects of the environment probably vary with latitude, including such selectively important factors as food availability and competition. Nonetheless, our analyses do suggest that both temperature and precipitation (hence aridity) are important to the evolution of *Sceloporus* dorsal scale counts (Table 4).

Why might selection favor more dorsal scales (hence smaller scales) in arid regions? Although squamate scales have traditionally been viewed as features that reduce water loss, squamates can nevertheless lose a substantial proportion of water through their skin (cutaneous water loss). For example, Bentley and Schmidt-Nielsen (1966) found that cutaneous water loss accounted for 66–72% of total water loss in two lizard species (*Iguana iguana* and *Sauromalus obesus*), although they did not distinguish between the contribution of scale versus skin in their estimation. Soulé and Kerfoot (1972) suggested that "...large scaled sceloporines will have significantly higher rates of cutaneous evaporation than small scaled individuals, both intra- and inter-specifically," potentially because of a looser association between adjoining scales in "large-scaled" individuals. However, they did not provide any measurements of cutaneous evaporation. We are unaware of functional studies that have examined cutaneous water loss in relation to scale number and size (but see Licht and Bennett 1972), but our results lend support to this idea with species from more arid environments (lower Q) tending to have more scales. If scale number and size variation is important for differences in cutaneous water loss, then we would expect species in areas with less precipitation and/or those that are more arid to have more, and hence smaller, scales to decrease rates of cutaneous water loss, consistent with our results. Additionally, temperature per se may not be as important a selective agent on scale attributes because

Sceloporus lizards can behaviorally thermoregulate (e.g., Bogert 1949; Huey 1974; Regal 1975), whereas they cannot, to our knowledge, control rates of evaporation behaviorally through the skin, but potentially can alter rates of evaporation through adjustments of body temperature (Thorpe and Kontogiannis 1977). Clearly, direct measures of water loss in a variety of lizard species, combined with measures of scale size and number, are warranted.

Our results indicate that smaller scales are found at higher latitudes when examined in the context of latitude alone (Table 4); and inclusion of climatic indicators in multiple regressions does not change the significance of latitude. This suggests that aside from climatic differences, there may be other selective factors occurring at different latitudes, perhaps related to population density, competition or sexual selection. For instance, it has been demonstrated that high-elevation populations of the Sierra fence lizard, *S. occidentalis taylori*, are darker and have more ventral pigmentation than similar animals at lower elevations. These lizards may indirectly receive thermoregulatory benefits as a result of selection on scale color as opposed to scale size (Clusella-Trullas et al. 2008; Leaché et al. 2010; A. Leaché pers. comm.). Our results for the effect of latitude should be interpreted with caution primarily because the correlation between latitude and the other climatic indicators used in our study breaks down at finer spatial scales. Mid-point latitude may not be able to capture the fine-scale climatic variation seen within many ecosystems, such as deserts, where *Sceloporus* may live.

We are aware of only two field studies examining selection on scale number in lizards. Fox (1975) found no evidence of directional or stabilizing selection on dorsal scale counts in *Uta stansburiana*. Calsbeek et al. (2006) found evidence of weak selection favoring fewer labial scales in *Anolis sagrei* in areas with less precipitation and higher temperatures or more open arid habitats.

CAVEATS

We have implicitly assumed that scale size is inversely related to scale number, for lizards of a given size. This assumption is typical in the herpetological literature; for example, Smith (1946 and elsewhere) consistently refers to large-scaled and small-scaled *Sceloporus*, while presenting quantitative data only for the number of scales. Likewise, Soulé and Kerfoot (1972), referring to *Sceloporus*, state that the number of dorsal scales is an inverse measure of scale size. Direct measurements of scale size are surprisingly rare; we have not found any for *Sceloporus*. It is possible that the scale size versus scale number relationship could also be affected by variation in body shape (e.g., girth) or the degree to which scales overlap (e.g., dorsal scales exhibit relatively little overlap in *S. jarrovi*; Regal 1975). Although these phenomena may occur among *Sceloporus* species (or populations), our qualitative observations of several dozen species in the field and in

museum collections are consistent with other researchers' assumption that scale numbers are a reliable inverse measure of scale size. Ideally, future studies on the functional significance of scale size would measure it directly, in addition to scale number and the amount of scale overlap.

As with all such comparative studies, interpreting variation in scale counts in an adaptive context (i.e., as an evolved response to variable selective regimes) makes the implicit assumption that the observed variation among populations and species reflects underlying trait-specific genetic differences. Our data do not derive from animals raised under common-garden conditions, so we cannot be sure this assumption is valid (Garland and Adolph 1991). In some snakes, scale counts are affected by developmental temperatures ([Fox 1948; Fox et al. 1961] but see Osgood [1978], Arnold and Peterson [2002]), raising the possibility that at least part of the observed geographic or interspecific variation in scale counts is caused by proximate environmental effects rather than genetic differentiation. Whether lizard scale size and number are affected directly by environmental temperatures is apparently unknown, but it is implausible that the full range of variation exhibited among species of *Sceloporus* (see Appendix S1) could simply be a reflection of direct environmental effects acting during ontogeny (i.e., developmental plasticity). Dohm and Garland (1993) showed that various scale counts were heritable in a garter snake (*Thamnophis sirtalis*), although the heritability estimates varied substantially among different scale count traits; Calsbeek et al. (2006) provide evidence that scale counts in lizards can be heritable.

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Associate Editor: G. Hunt

Supporting Information

The following supporting information is available for this article:

Appendix S1. Microsoft Excel file of data.

Appendix S2. Phylogenetic tree used for analysis.

Appendix S3. General description.

Appendix S4. Earlier phylogenetic tree.

Table S1. Univariate phylogenetic statistics on a star phylogeny with no hierarchical structure and with four different types of arbitrary branch lengths with the best fit evolutionary model in bold.

Table S2. Slopes from univariate regressions of $\log_{10}$ snout-vent length (SVL) on latitude and five climatic indicators (see Data Collection in Methods) using conventional statistics and phylogenetic statistics with either constant branch lengths, Nee's arbitrary branch lengths, or Nee's branch lengths under an Ornstein–Uhlenbeck model of residual trait evolution (RegOU).

Table S3. Multiple regressions examining the effects of $\log_{10}$ SVL, latitude, and five climatic indicators (see Data Collection in Methods) on $\log_{10}$ dorsal scale counts under four models of evolution, with dummy variables for two possible "outlier" or "influential" species included in the models.

Supporting Information may be found in the online version of this article.

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