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Bergmann's Clines in Ectotherms: Illustrating a Life-History Perspective with Sceloporine Lizards

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ABSTRACT: The generality and causes of Bergmann's rule have been debated vigorously in the last few years, but Bergmann's clines are rarely explained in the context of life-history theory. We used both traditional and phylogenetic comparative analyses to explore the causes of latitudinal and thermal clines in the body size of the eastern fence lizard (*Sceloporus undulatus*). The proximate mechanism for larger body sizes in colder environments is delayed maturation, which results in a greater fecundity but a lower survival to maturity. Life-history theory predicts that a higher survivorship of juveniles in colder environments can favor the evolution of a Bergmann's cline. Consistent with this theory, lizards in colder environments survive better as juveniles and delay maturation until reaching a larger body size than that of lizards in warmer environments. We expect similar relationships among temperature, survivorship, and age/size at maturity exist in other ectotherms that exhibit Bergmann's clines. However, life-history traits of *S. undulatus* were more strongly related to latitude than they were to temperature, indicating that both abiotic and biotic factors should be considered as causes of Bergmann's clines. Nonetheless, analyses of the costs and benefits of particular body sizes in different thermal environments will enhance our understanding of geographic variation.

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Bergmann's rule, after languishing for decades as an anecdotal statement about clinal variation in body size, has resurfaced at the center of a new debate on the utility and veracity of ecogeographic rules. Although Bergmann's rule originally was formulated to describe interspecific variation in endotherms (Bergmann 1847), today it is used more loosely to describe an increase in the body size of a species as latitude increases or environmental temperature decreases (a phenomenon that is also referred to as James's rule; Blackburn et al. 1999). Ironically, at a time when more sophisticated hypotheses are being offered to explain Bergmann's rule, its generality is still being debated vigorously (Mousseau 1997; Blackburn et al. 1999; Ashton 2001a; Belk and Houston 2002; Bernardo and Reagan-Wallin 2002). Current evidence suggests that Bergmann's rule applies not only to endotherms (Ashton et al. 2000; Ashton 2002b; Freckleton et al. 2003; Meiri and Dayan 2003) but also to certain groups of ectotherms (Arnett and Gotelli 1999; Huey et al. 2000; Ashton 2002a; Ashton and Feldman 2003; Heinze et al. 2003; Morrison and Hero 2003). Central to understanding the debate is the recognition that Bergmann's rule has garnered attention because biologists are interested not only in the generality of the pattern but also in the mechanisms that produce it.

In our opinion, the focus on Bergmann's rule as an ecogeographic phenomenon has distracted researchers from investigating the causes of clinal variation in body size in the framework of life-history theory. Documenting the generality of Bergmann's rule is a reasonable precursor to investigating its causal basis, but geographic variation in body size is interesting in a variety of contexts that are not necessarily related to Bergmann's rule (see Palkovacs 2003). In fact, the patterns, causes, and consequences of geographic variation in body size are fundamental themes

in the literature on life-history evolution (Roff 2002). A life-history framework can advance our understanding of Bergmann's clines because it provides a means of analyzing the costs and benefits of variations in growth rate and age-specific body size (Roff 1980, 1986). For ectotherms, this task is complicated by the fact that temperature influences so many aspects of behavior and physiology (Huey and Stevenson 1979; Angilletta et al. 2002), most of which have implications for survival and fecundity.

When viewed in the context of life-history theory, the challenge of understanding the origin and maintenance of a Bergmann's cline becomes one of understanding the evolution of thermal reaction norms for age and size at maturity. A relatively large body size results from faster growth, a longer duration of growth, or both. Since ectotherms typically grow more slowly at lower temperatures, a relatively large body size in cold environments is usually achieved by prolonged growth and delayed maturation (Atkinson 1994 and references therein). The benefits of delayed maturation must outweigh the costs of reduced survival to maturity, especially if individuals in colder environments are to delay maturation long enough to outgrow individuals in warmer environments (Partridge and Coyne 1997). Growth is favored over reproduction when an individual can expect a gain in future reproductive success that exceeds the loss of current reproductive success that results from forgoing reproduction; generally, this condition requires a relatively large increase in fecundity with age and a relatively high probability of surviving until the next opportunity for reproduction (Stearns 1992; Roff 2002). Nevertheless, few theories predict that slow-growing individuals should reach a larger size at maturity than that of fast-growing individuals because this outcome requires a relatively long delay of maturation in cold environments (Berrigan and Charnov 1994; Atkinson 1996).

Models that predict life histories consistent with Bergmann's rule include thermal constraints on growth and maturation or thermal effects on survivorship (reviewed by Angilletta et al. 2004). As an example of the former, Berrigan and Charnov (1994) presented a model that predicts a Bergmann's cline when an organism grows asymptotically and when higher temperatures reduce the asymptotic body size; however, no direct evidence supports the assumptions that growth must decelerate with age and that such a constraint depends on temperature (Angilletta and Dunham 2003). Similarly, other models that predict Bergmann's clines to be the result of thermal constraints on growth and maturation are poorly supported (Angilletta et al., in press). Additionally, optimal life histories can be consistent with Bergmann's rule if higher environmental temperatures are associated with lower survivorships of juveniles (Sibly and Atkinson 1994). If the effect

of temperature on survivorship were sufficiently great, individuals at low temperatures should outgrow those at high temperatures (Angilletta et al. 2004; Kozlowski et al. 2004). Therefore, empirical studies that establish relationships among environmental temperature, survivorship, and age/size at maturity will help us to construct evolutionary explanations for Bergmann's clines.

In this article, we illustrate the value of a life-history perspective by examining the proximate and ultimate causes of Bergmann's clines in sceloporine lizards. First, we use both traditional and phylogenetic comparative methods to confirm the existence of latitudinal and thermal clines in the body size of the eastern fence lizard (*Sceloporus undulatus*). Then, we evaluate the hypothesis that these clines are the by-product of adaptive covariation between juvenile survivorship and age/size at maturity. Unlike previous efforts to understand the maintenance of Bergmann's clines, our analyses address both proximate and ultimate causation while considering both the costs and benefits of body size in different thermal environments.

Bergmann's Clines in Sceloporine Lizards

Lizards of the genus *Sceloporus* are widely distributed in the United States and Mexico, and the life histories of numerous species have been studied along latitudinal or altitudinal gradients. Of 10 species studied to date, only four exhibit larger body sizes in colder environments (Ashton and Feldman 2003; A. D. Leaché, unpublished data), making most members of this genus exceptions to Bergmann's rule. The most parsimonious interpretation is that a set of life histories consistent with Bergmann's rule evolved at least twice within the genus (fig. 1). *Sceloporus undulatus*, the most thoroughly studied sceloporine (see reviews by Tinkle and Dunham [1986]; Niewiarowski [1994]), is one of the four species that follows Bergmann's rule. Based on a recently proposed phylogeny (Leaché and Reeder 2002), *S. undulatus* has expanded its range latitudinally on multiple occasions, making it an ideal subject of comparative tests of hypotheses about the causes of geographic variation in body size.

Because lizards grow slower in colder environments (Sinervo and Adolph 1994; Angilletta 2001*a*; Niewiarowski 2001), delayed maturation is the proximate mechanism for a relatively large body size at higher latitudes. Since sceloporines typically mature within 2 years of birth, Bergmann's clines result from maturation at approximately 1 and 2 years of age for individuals in warm and cold environments, respectively (table 1). In *S. undulatus* and *Sceloporus jarrovi*, two species that exhibit Bergmann's clines, individuals in warm environments mature at 10–12 months of age, and those in cold environments mature at
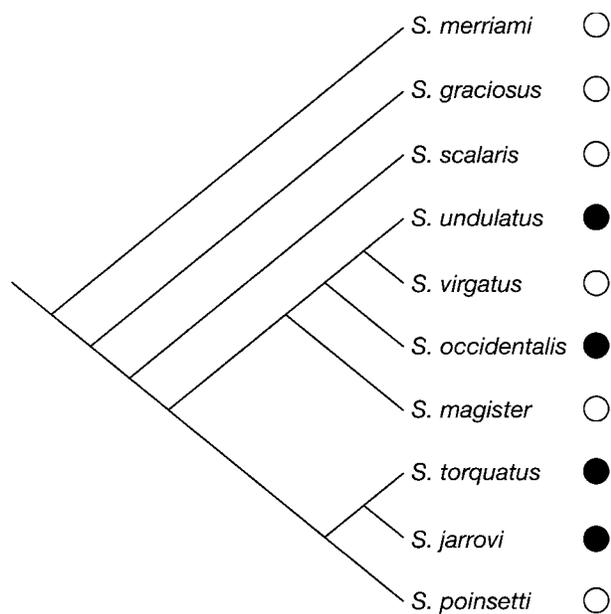
Figure 1: Cladogram showing the distribution of Bergmann's clines in the genus *Sceloporus*. Solid circles denote species in which a Bergmann's cline has been documented, and open circles denote species in which no Bergmann's cline or a reversed cline has been documented. The most parsimonious interpretation is that life histories consistent with Bergmann's rule have evolved twice within the genus if we assume a reversal in *Sceloporus virgatus* or three times if we assume independent origins in *Sceloporus occidentalis* and *Sceloporus undulatus*. The phylogenetic hypothesis for *Sceloporus* follows Wiens and Reeder (1997), Wiens et. al. (1999), and Leaché and Reeder (2002). Clines in body size are from Ashton and Feldman (2003) and sources listed in table 1.

20–24 months of age. In *Sceloporus merriami* and *Sceloporus graciosus*, two species that do not follow Bergmann's rule, individuals exhibit delayed maturation in colder environments, but few if any individuals delay maturation for more than a couple of months (i.e., all individuals overwinter the same number of times before maturation). The seasonality of reproduction results in the prolonged growth of individuals that delay maturation, which accounts for the difference in size at maturity (Adolph and Porter 1996). Therefore, strategies of maturation in a seasonal environment are an important element of a proximate explanation for Bergmann's clines in sceloporines and other perennial ectotherms (e.g., Rohr 1997; Camp and Marshall 2000). Importantly, a delay of maturation is not always sufficient to enable individuals in colder environments to reach a larger size than that reached by individuals in warmer environments. For example, *Sceloporus occidentalis* matures at 2 years of age at high elevations and at 1 year of age at low elevations, but adults of this species can be either smaller or larger at higher elevations (table 1).

Discovering the ultimate mechanisms that underlie Bergmann's clines in *Sceloporus* is important because these clines are partially caused by genetic differences among populations. Common garden and reciprocal transplant experiments have revealed that individuals in some populations of *S. undulatus* exhibit a fixed strategy of slow growth relative to individuals in other populations (Ferguson and Brockman 1980; Niewiarowski and Roosenburg 1993; Niewiarowski 1995). Additional experiments have confirmed that differences in the physiology of growth exist between northern and southern populations (Angilletta 2001*a*, 2001*b*). Similarly, *S. jarrovi* has evolved distinct life histories along an elevational gradient; hatchlings that were transplanted from high elevation to low elevation exhibited a fixed strategy of delayed maturation compared with hatchlings that were residents at low elevation (Ballinger 1979). These observations indicate that reaction norms for age and size at maturity have diverged among populations of sceloporines. For this reason, we used phylogenetic comparative methods to examine the Bergmann's cline within *S. undulatus* in the context of an adaptive life history.

Methods

Selection of Populations

For our analyses, we used published and unpublished data on the life history of *Sceloporus undulatus*. Juvenile survivorships and ages/sizes at maturity of females were available for 13 populations, and mean body sizes of adult females were available for 18 populations (app. A; fig. 2). The phylogeny of Leaché and Reeder (2002) was used as a framework for phylogenetic comparative analyses. Based on this phylogeny, the populations belong to four major clades: an eastern clade (nine populations), a central clade (three populations), a western clade (four populations), and a southwestern clade (two populations). We also included data for one population of *Sceloporus woodi* because phylogenetic analyses of morphological and molecular information indicate that this species is nested within *S. undulatus* (Wiens and Reeder 1997; Leaché and Reeder 2002; Miles et al. 2002).

We note that the populations considered here probably span intraspecific and interspecific levels, and Leaché and Reeder (2002) argued each of the major clades should be recognized as an evolutionary species. This point is important because researchers are still debating whether the mechanisms that cause intraspecific and interspecific clines in body size should be the same (Blackburn et al. 1999). However, our use of phylogenetic relationships hypothesized by Leaché and Reeder (2002) does not rely on their recommendation for delimiting species because phyloge-

Table 1: Variation in life histories of lizards in the genus *Sceloporus* along altitudinal and latitudinal gradients

Sceloporus species	Gradient	Growth rate	Size at maturity	Juvenile survivorship	Age at maturity (months)		Source
					Low	High	
S. jarrovi	Altitudinal	Negative	Positive	Positive	10	20	1, 2
S. undulatus	Latitudinal	Negative	Positive	Positive	9.5–12	20–23	3–14
S. merriami	Altitudinal	Unimodal	Unimodal	Positive	12	10	15, 16
S. graciosus	Altitudinal	Positive	Constant	Negative	22	22	17, 18
S. occidentalis	Altitudinal	Negative	Negative/positive	…	12	24	19–21

Note: Relationships between latitude/altitude and life-history traits are characterized as positive, negative, or unimodal. Also, age at maturity at extremes of the gradient are given. Sources of data are as follows: 1 = Ballinger 1973; 2 = Ballinger 1979; 3 = Ballinger et al. 1981; 4 = Marion 1970; 5 = Tinkle 1972; 6 = Tinkle and Ballinger 1972; 7 = Vinegar 1975; 8 = Ferguson et al. 1980; 9 = McKinney 1982; 10 = Tinkle and Dunham 1986; 11 = Gillis and Ballinger 1992; 12 = Niewiarowski 1992; 13 = Niewiarowski 1994; 14 = Parker 1994; 15 = Dunham 1981; 16 = Grant and Dunham 1990; 17 = Tinkle et al. 1993; 18 = Sears and Angilletta 2003; 19 = Sinervo et al. 1991; 20 = Sinervo and Adolph 1994; 21 = A. D. Leaché, unpublished data.

netic comparative methods do not explicitly recognize taxonomic rank. For simplicity, we refer to *S. undulatus* (sensu lato) simply as *S. undulatus.*

Environmental Data

We obtained mean monthly air temperatures from the National Climate Data Center (Asheville, N.C.) for localities that were closest to the populations included in our analyses. Generally, we used data collected from 1975 to 2002. However, we used data collected between 1954 and 1959 for the population in Hidalgo County, New Mexico, because data for other years were unavailable. We adjusted air temperatures for adiabatic cooling if the elevation of a weather station differed by more than 100 m from that of the corresponding population. The grand mean of mean monthly air temperature at each locality, which we refer to as environmental temperature, was used in the analyses described below.

Because *S. undulatus* thermoregulates effectively in different environments (Angilletta 2001a), we used a biophysical model to estimate the potential for thermoregulation by lizards in each population. The model combined the microclimate program of Porter and colleagues (2000, 2002), the solar radiation program of McCullough and Porter (1971), and the thermoregulation program of Grant and Porter (1992) to estimate the daily number of hours that an individual can maintain its body temperature within a preferred range. The model required monthly minimal and maximal air temperatures and monthly relative humidities for each locality; these parameters were obtained from the same source as mean air temperatures. Other parameters of the model were specified as by Adolph and Porter (1996). The programs calculated thermal properties of both the environment and a lizard in that environment. For example, the microclimate program estimated the hourly intensity of solar radiation and hourly profiles of air temperature and wind speed from a height of 0–2 m aboveground. The thermoregulation model used output from the microclimate model to determine which hours of the day an ectotherm could maintain its preferred body temperature. By summing daily activities over 12 months, we arrived at an estimate of the maximal duration of activity per year, which we refer to as potential activity. Our estimate of potential activity describes the seasonality of the environment because a lizard in a less seasonal environment can be more active than a lizard in a more seasonal environment.

Adolph and Porter (1996) previously reported estimates of potential activity for 10 of the populations considered here. Our values differ quantitatively from those of Adolph and Porter because of subsequent refinement of the biophysical model (see app. B). The two sets of data are similar, however, and our values are significantly correlated with theirs ($t = 4.40$, $P = .002$, $r^2 = 0.71$).

Independent Contrasts

All comparative analyses were performed using both raw data and phylogenetically independent contrasts (Felsenstein 1985). Although a previous analysis suggested the existence of a Bergmann's cline in the body size of *S. undulatus* (Ashton and Feldman 2003), this analysis did not account for the fact that data for populations of a species are not independent (Garland et al. 1999). Independent contrasts can be used to achieve statistical independence of data, but one must know the phylogenetic relationships and the timing of divergence among taxa to compute independent contrasts (Garland et al. 1992). Although gene flow among populations can reduce the accuracy of this knowledge, genetic and phenotypic sources of evidence indicate that gene flow among populations of *S. undulatus* is limited (Niewiarowski et al. 2004). By computing contrasts for environmental variables, we assumed
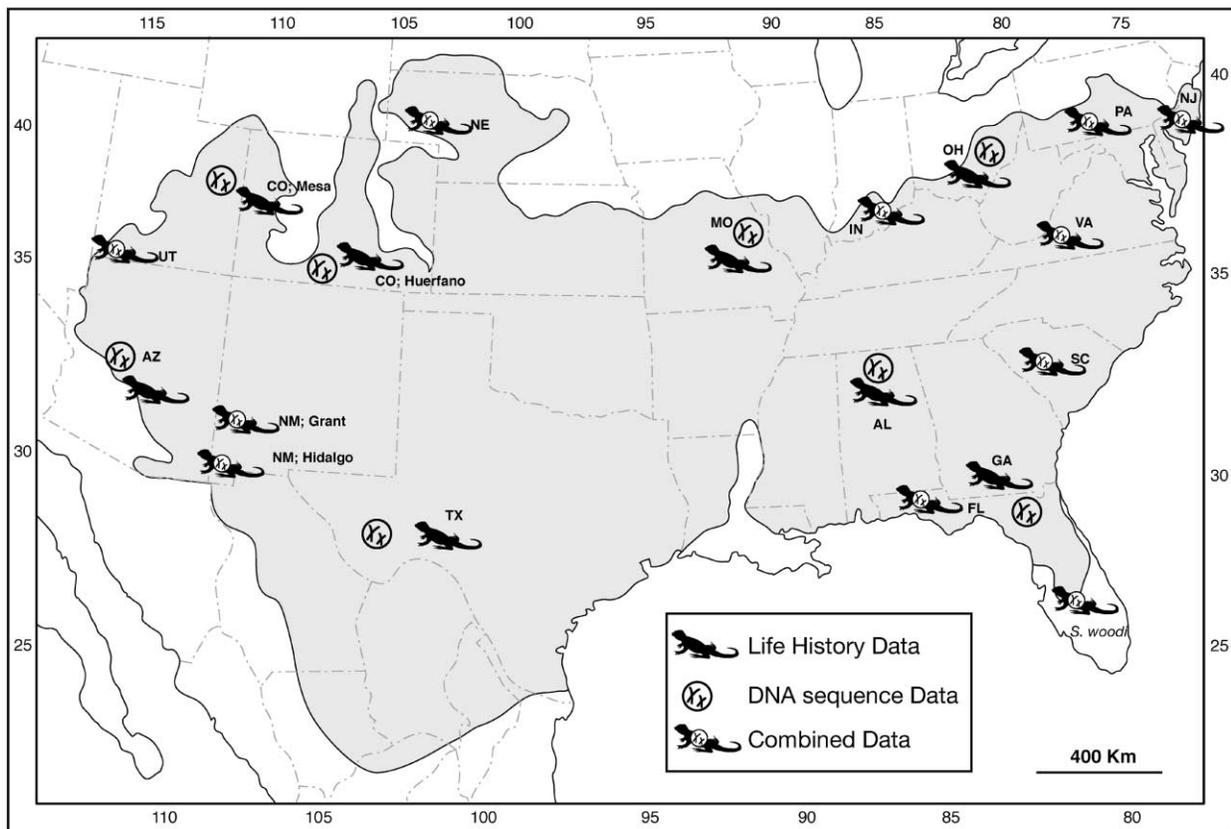
Figure 2: Map showing the locations of populations of *Sceloporus undulatus* (including *Sceloporus woodi*) that were sampled for DNA sequences and life histories. In 11 cases, both types of data were obtained from the same location. In the remaining cases, locations were matched according to proximity and subspecific designations for *S. undulatus*.

that environmental states were passed from generation to generation as were phenotypic states (Garland et al. 1992); this assumption is probably valid because the geographic structure among populations ensures that individuals in a relatively cold environment produce offspring that experience a relatively cold environment. For these reasons, our use of independent contrasts to remove the statistical nonindependence caused by phylogenetic relationships was probably justified. Nevertheless, previous analyses indicated that phylogenetic relationships do not strongly influence variation in the age and size at maturity of *S. undulatus* (Niewiarowski et al. 1994); therefore, we present the results of analyses of raw data in addition to the results of analyses of independent contrasts.

Independent contrasts were based on a phylogeny generated by a Bayesian analysis of 3,688 base pairs of mitochondrial DNA from 57 populations of *S. undulatus* and nine closely related species (Leaché and Reeder 2002). The phylogeny was pruned to remove populations that were not considered in our comparative analyses, and one pop-

ulation in Indiana was added (fig. 3). The maximum parsimony procedure of the computer program PAUP (ver. 4.0b8; Swofford 2001) was used to recalculate branch lengths for the pruned phylogenies. Because the amount of DNA that was sequenced varied among populations, we used a reduced data matrix to avoid artificially inflating branch lengths for those populations for which more data were available. To diagnose the suitability of branch lengths, we examined relationships between absolute values of standardized independent contrasts and their standard deviations (Garland et al. 1992); branch lengths were transformed logarithmically to achieve proper standardization of independent contrasts. Standardized independent contrasts were generated by the computer program COMPARE (ver. 4.5; Martins 2003).

Phylogenetic Comparative Analyses

We used regression analyses to determine whether the body size of *S. undulatus*, estimated by snout-vent length, was
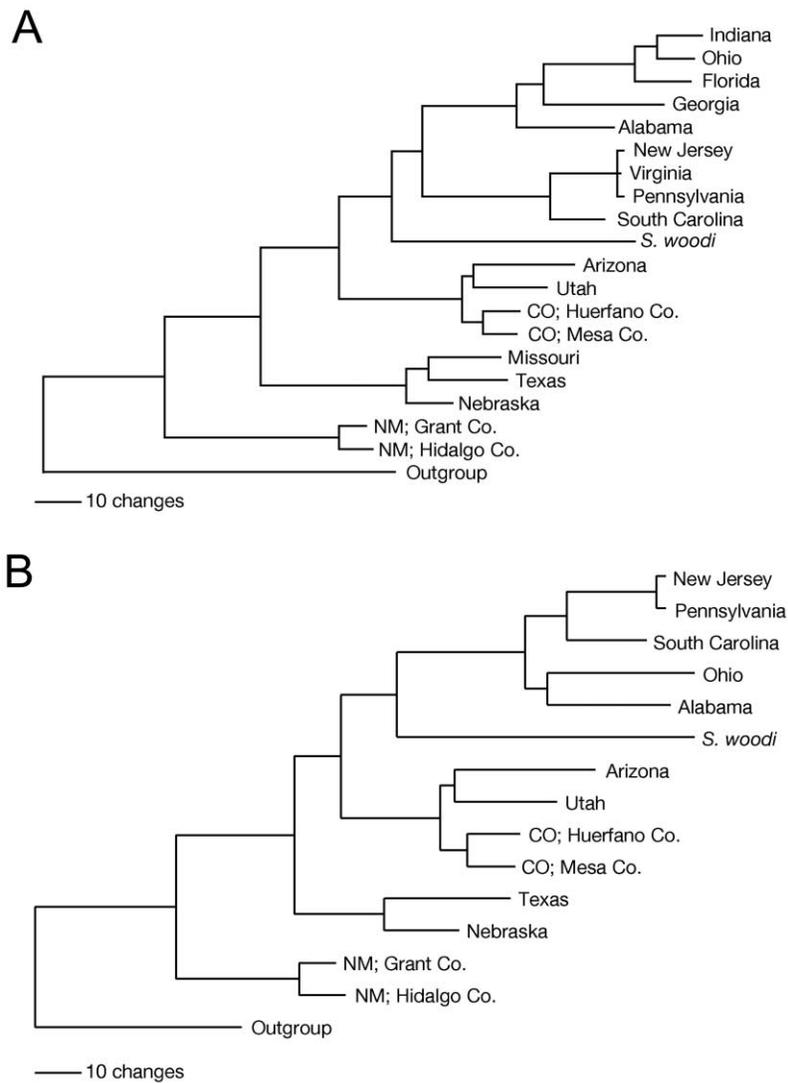
Figure 3: Phylogenetic relationships among the populations of *Sceloporus undulatus* (including *Sceloporus woodi*) that were included in comparative analyses. These relationships are based on data collected by Leaché and Reeder (2002) and additional data for a population in Indiana (GenBank accession number AY728094). Branch lengths for each phylogeny were calculated using the procedure of maximum parsimony. A phylogeny for 19 populations (*A*) was used for analyses of mean body size, and a phylogeny for 14 populations (*B*) was used for analyses of juvenile survivorship and age/size at maturity.

related to either latitude or environmental temperature. Because certain populations of *S. undulatus* were known to be outliers with respect to their life history (see Adolph and Porter 1996), we used robust regression rather than ordinary least squares regression. Robust methods minimize bias in the estimation of parameters when data are not normally distributed while achieving the same degree of statistical efficiency when data are normally distributed. Robust parameters were estimated by the weighted likelihood procedure of Markatou et al. (1998; see also Agos-

tinelli and Markatou 2001). For regressions of independent contrasts, we forced models to intercept the origin (see Garland et al. 1992 for justification). These analyses were performed with R, a statistical software that is freely available (R Development Core Team 2003).

We tested the hypothesis that geographic variation in the body size of *S. undulatus* is a by-product of the coadaptation of life-history traits (Ashton et al. 2000). Based on life-history theory, we predicted that age and size at maturity would be positively related to juvenile survi-
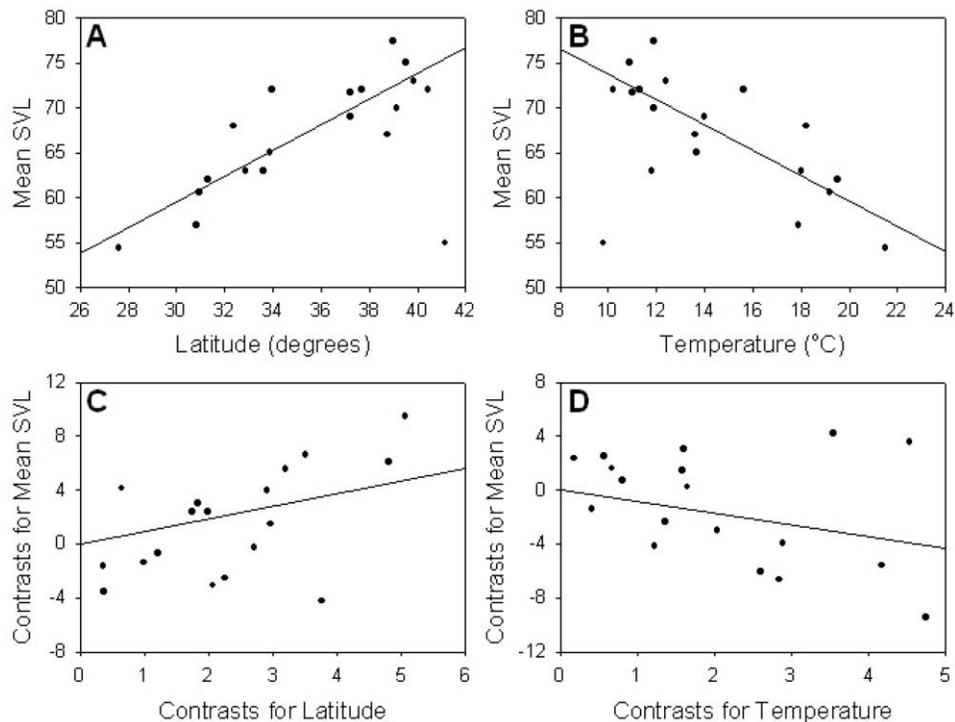
Figure 4: Mean body size of *Sceloporus undulatus*, measured as snout-vent length (*SVL*), was related to latitude (*A*) and environmental temperature (*B*). Analyses of independent contrasts yielded similar results (*C, D*). In both sets of analyses, females at higher latitudes tended to be larger than those at lower latitudes, and females in colder environments tended to be larger than those in warmer environments.

vorship. We used principal components analysis (PCA) to describe the covariation among these life-history variables. This analysis was performed using the correlation matrix to avoid weighting variables by their variance; for the PCA of independent contrasts, correlations were forced to intercept the origin (Garland et al. 1992). We used diagnostic tests suggested by McGarigal et al. (2000) to establish that our data met the assumptions of PCA. To detect a potential violation of the assumption of multivariate normality, we assessed the skewness, kurtosis, and normality of the scores for principal components and examined normal probability plots for the variables and scores. To ensure that the variables met the assumption of linearity, we inspected a scatter plot of scores for the first two principal components (PC1 vs. PC2). The broken-stick criterion was used to decide whether the second principal component was worth interpreting (Jackson 1993). After interpreting the principal components, we evaluated our hypothesis by regressing scores from the first principal component—a linear combination of the three life-history variables—onto latitude, environmental temperature, and potential activity.

Results

Consistent with results of a previous analysis (Ashton and Feldman 2003), our regression analyses indicated that *Sceloporus undulatus* follows Bergmann's rule (fig. 4). The mean body size of adult females was positively related to latitude ($\beta = 1.42 \pm 0.20$ [SE], $F = 50.92$, df $= 1, 15.4$, $P < .001$, $r^2 = 0.77$) and was negatively related to environmental temperature ($\beta = -1.41 \pm 0.27$, $F = 27.17$, df $= 1, 15.3$, $P < .001$, $r^2 = 0.64$). Similarly, independent contrasts for mean body size were positively related to independent contrasts for latitude ($\beta = 0.93 \pm 0.29$, $F = 9.74$, df $= 1, 16.4$, $P = .01$, $r^2 = 0.37$) and were negatively related to independent contrasts for environmental temperature ($\beta = -0.87 \pm 0.34$, $F = 5.88$, df $= 1, 16.3$, $P = .03$, $r^2 = 0.26$).

Principal components analyses of raw data and independent contrasts each revealed a primary axis (PC1) that described the majority of the variation in juvenile survivorship, age at maturity, and size at maturity (table 2). These principal components support our prediction that delayed maturation at a relatively large body size is associated with a high probability of survival as a juvenile.

Table 2: Principal components describing the covariation among life-history traits of *Sceloporus undulatus*

Variable	Raw data		Independent contrasts	
	PC 1	PC 2	PC 1	PC 2
Size at maturity	−.85	.50	.72	.63
Age at maturity	−.91	−.09	.90	.02
Juvenile survivorship	−.87	−.39	.67	.70
Eigenvalue	2.31	.42	1.76	.88
% of variance	77.1	13.9	58.8	29.5
Cumulative	77.1	91.0	58.8	88.3

In the analysis of raw data, all three variables loaded almost equally on PC1, which described more than 75% of the variation. In the analysis of independent contrasts, age at maturity loaded more heavily than size at maturity and juvenile survivorship, but PC1 still described about 60% of the variation.

Because PC1 of both analyses was easily interpreted and described the majority of the variation, we used the scores for these axes to test the hypothesis that latitudinal and thermal clines are a by-product of the coadaptation of life-history traits (fig. 5). Principal component scores derived from raw data were negatively related to latitude ($\beta = -0.22 \pm 0.02$, $F = 86.48$, df = 1, 10.4, $P < .001$, $r^2 = 0.89$) and were positively related to environmental temperature ($\beta = 0.23 \pm 0.04$, $F = 24.50$, df = 1, 10.3, $P < .001$, $r^2 = 0.70$), indicating that individuals at higher latitudes and individuals in colder environments were more likely to survive as juveniles and delay maturation until reaching a relatively large body size. Principal component scores derived from independent contrasts were positively related to independent contrasts for latitude ($\beta = 0.39 \pm 0.07$, $F = 29.77$, df = 1, 11.5, $P < .001$, $r^2 = 0.72$) and were negatively related to independent contrasts for environmental temperature ($\beta = -0.26 \pm 0.08$, $F = 9.33$, df = 1, 10.9, $P = .01$, $r^2 = 0.46$), which agree with the relationships observed in our analyses of raw data (note that factor loadings from PCAs of raw data and contrasts were of the opposite sign). We found mixed support for our hypothesis that geographic variation in the life history was related to potential activity; principal component scores derived from raw data were positively related to potential activity ($\beta = 0.0013 \pm 0.0005$, $F = 5.77$, df = 1, 11.0, $P = .04$, $r^2 = 0.34$), but scores derived from independent contrasts were not significantly related to independent contrasts for potential activity ($\beta = -0.0019 \pm 0.0010$, $F = 3.23$, df = 1, 11.2, $P = .10$, $r^2 = 0.22$).

Discussion

The pattern of covariation in *Sceloporus undulatus* is consistent with the idea that a Bergmann's cline is a by-product of adaptive covariation among life-history traits. Life-history theory predicts that, with all else being equal, delayed maturation at a larger body size is favored in environments where the increment in fecundity or the survivorship between opportunities for reproduction is relatively high (Stearns 1992). Because fecundity is highly correlated with body size in sceloporines (Tinkle and Ballinger 1972; Ballinger 1973; Ballinger and Congdon 1981; Tinkle and Dunham 1986; Tinkle et al. 1993), the benefits of increased fecundity can be assessed indirectly through the potential for growth. A greater increment in fecundity through delayed maturation is unlikely to be a sufficient explanation for the Bergmann's cline because the growth of *S. undulatus* is slower in colder environments. Nevertheless, a higher juvenile survivorship might have favored delayed maturation in colder environments. Lizards at higher latitudes and lizards in colder environments tended to have higher survivorships and delayed maturation until reaching larger body sizes than did lizards at lower latitudes and lizards in warmer environments, respectively (fig. 5). Furthermore, variation in the survivorship of juveniles can explain the one population in which lizards exhibit an exceptional life history; in Nebraska, *S. undulatus* exhibits early maturation at a small body size even though this location is at the northern limit of this species' range (fig. 5A, 5B). The life history of lizards in Nebraska is reconciled by the fact that juveniles in this population suffer a relatively high rate of mortality during the winter (Ballinger et al. 1981). Similar to *S. undulatus*, the survivorship of *Sceloporus jarrovi* was associated with environmental temperature along an altitudinal gradient such that juveniles at high altitude were more likely to survive annually than were lizards at low altitude (Ballinger 1979). This comparative evidence suggests that clinal variations in body sizes of some sceloporines is a consequence of the natural selection of age and size at maturity.

Importantly, we must consider the possibility that arguments based on the relationship between juvenile survivorship and age/size at maturity confuse cause and effect. In other words, survivorships of juveniles might have been higher in colder environments because individuals in these environments adopted particular strategies of growth and maturation (i.e., slow growth and delayed maturation). A comparative analysis, such as ours, cannot be used to distinguish between these two scenarios. Ideally, we should like to know the component of survivorship that is driven by the behavior and physiology of individuals versus the component that is driven by the external environment. Theory predicts the covariation between rates of juvenile
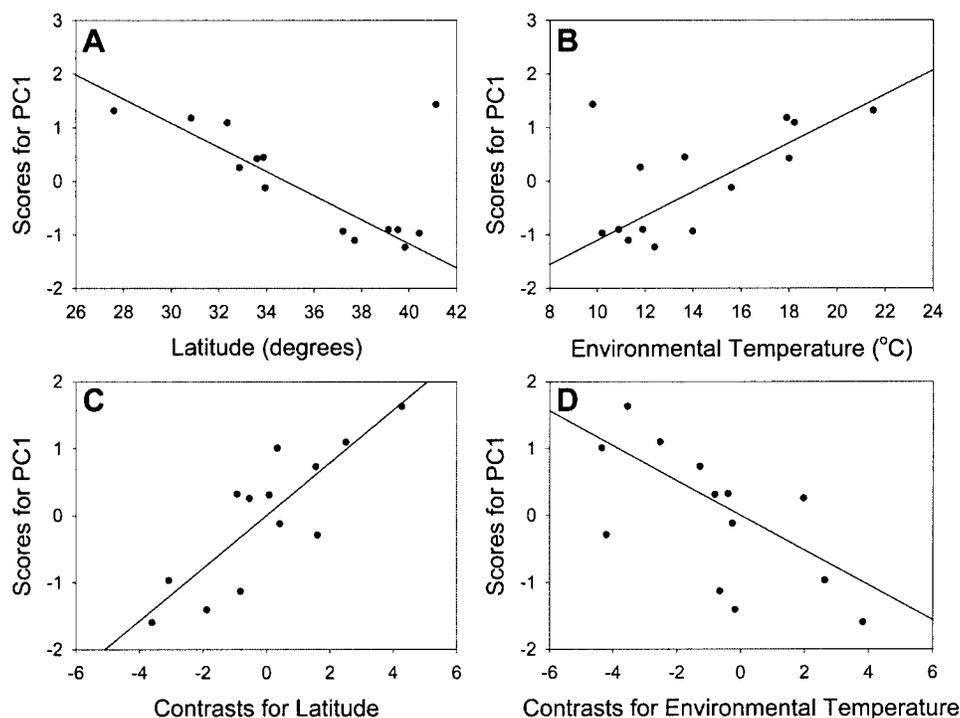
Figure 5: Principal components representing linear combinations of juvenile survivorship, age at maturity, and size at maturity were related to latitude (*A*) and environmental temperature (*B*). Analyses of independent contrasts yielded similar results (*C, D*). Note that the factor loadings from analyses of raw data and independent contrasts were of the opposite sign (table 2), which explains the opposite signs of relationships between raw data (*A, B*) and relationships between independent contrasts (*C, D*). In both sets of analyses, females at higher latitudes and females in colder environments exhibited a higher survivorship as juveniles, an older age at maturity, and a larger size at maturity.

mortality and age/size at maturity should be causally related because optimal rates of intrinsic mortality are positively correlated with rates of extrinsic mortality (Stearns 2000). Therefore, the evolution of life histories reduces probabilities of survival in environments where those probabilities are already low (Gasser et al. 2000; Stearns et al. 2000), which should bolster a negative relationship between temperature and survivorship rather than obscure it. Thus, we infer that Bergmann's clines in *S. undulatus* arise out of geographic variation in extrinsic mortality because that is one aspect of life-history theory that has been explored experimentally. Yet, we lack selection experiments that have tested causality in the other direction (i.e., selection of strategies of growth and maturation that cause variation in juvenile survivorship). In particular, we are unaware of experiments in which earlier or later ages at maturity are selected in different thermal environments. Such experiments would enable one to estimate changes in survivorship associated with strategies of maturation while identifying effects of temperature on survivorship that might be independent of age at maturity.

Interestingly, the life history of *S. undulatus* was more strongly related to latitude than it was to environmental temperature (see figs. 4, 5). We draw this conclusion from the facts that the estimated effects of latitude were greater than the estimated effects of environmental temperature, and that environmental temperature decreased by less than 1°C per degree of latitude ($\beta = -0.89$; $F = 63.91$, df $= 1, 17$, $P < .001$, $r^2 = 0.79$). Much of the evidence presented in favor of Bergmann's rule consists of latitudinal clines in body size rather than thermal clines, with the assumption being that environmental temperature is closely related to latitude (see Ashton 2001*a*, 2002*a*; Belk and Houston 2002). A statistical explanation for the difference in strength between these relationships is that environmental temperature is bound to be measured with less accuracy than latitude. However, we believe that a biological explanation is also plausible. Life histories are influenced by many factors—both abiotic and biotic—that can covary with latitude; temperature is only one of these factors. Temperature varies both latitudinally and altitudinally, but other factors could be more strongly associated with latitude than with altitude. Important biotic factors include the numbers of predators and competitors, which

should be fewer at higher latitudes because of the decrease in the diversity of species with increasing latitude (Currie 1991). At any particular latitude, temperature might serve more as a reliable indicator of the intensity of biotic interactions than as a direct source of mortality (Perrin 1988; Sibly and Atkinson 1994). This view is consistent with a recent analysis that shows the direct effect of temperature on survivorship to be relatively weak (Angilletta et al., in press). Nevertheless, the thermal adaptation of body size observed in the laboratory (Partridge et al. 1994) supports the hypothesis that temperature has some direct effect on the evolution of life histories.

Predation is an obvious source of mortality that varies among populations. Both the frequencies of activity and the rates of movement by lizards and their predators should influence the rate of mortality (Werner and Anholt 1993). Lizards in warmer environments have higher frequencies of activity (Angilletta 2001*a*; Niewiarowski 2001) and therefore are exposed to predators for a longer duration. For these reasons, we hypothesize that predation plays an important role in producing differences in juvenile survivorship among populations of *S. undulatus*. Directly quantifying predation is often impractical (Wilson 1991), but the intensity of predation in *S. undulatus* has been estimated by the frequency of tail loss. Vinegar (1975) compared the life histories of *S. undulatus* in two populations in New Mexico and found that a higher frequency of tail loss by juveniles was associated with a lower survivorship. However, Tinkle and Ballinger (1972) noted that a high frequency of tail loss is not always associated with low survivorship in *S. undulatus*. In fact, a summary of data for seven populations (Tinkle 1972; Tinkle and Ballinger 1972; Vinegar 1975) indicates no relationship between the frequency of tail loss and juvenile survivorship ($t = -0.90$, $P = .40$, $r^2 = 0.12$). Since the frequency of tail loss can be an inaccurate estimate of the intensity of predation (Turner et al. 1982; Jaksic and Greene 1984; Wilson 1991), behavioral indices of the relative risk of predation (Cooper 2000; Downes and Adams 2001; Martín and López 2001) are probably more useful for evaluating hypotheses about the role of predators in causing geographic variation in survivorship.

Contrary to our hypothesis, Ashton and colleagues (Ashton et al. 2000; Ashton 2001*b*) hypothesized that greater risks of predation in colder environments favor relatively large body sizes. The discrepancy between their hypothesis and ours is explained by assumptions about size-dependent risks of predation. If the risk of predation is higher in colder environments for small individuals but not for large individuals, then natural selection could produce variation in life history that is consistent with Bergmann's rule. However, if the risk of predation is higher in colder environments for individuals of all sizes, natural selection should favor early maturation at a relatively small body size in cold environments, a pattern that violates Bergmann's rule. Therefore, one must clearly distinguish between size-dependent and size-independent risks when discussing predation as a cause of Bergmann's rule. The scenario proposed by Ashton and colleagues is based on the assumption that a latitudinal gradient in the risk of predation is experienced primarily by small individuals rather than individuals of all sizes. Given these two distinct scenarios, studies of size-specific rates of mortality along latitudinal transects (e.g., Wilson 1991) will be necessary to evaluate the role of predation in generating Bergmann's clines.

Competition can also lead to geographic variation in survivorship. Higher densities of populations and greater diversities of species in warmer environments could enhance intra- and interspecific competition. To assess the impact of intraspecific competition in a population of *S. undulatus* in Arizona, Tinkle and Dunham (1986) examined the relationship between population density and the annual survivorship of juveniles; the survivorship of juveniles was low during years when density was high, suggesting that intraspecific competition does cause mortality. If competition is an important source of geographic variation in survivorship, population density should be negatively correlated with juvenile survivorship. Using data for 11 populations of *S. undulatus* (Tinkle 1972; Tinkle and Ballinger 1972; Vinegar 1975; Jones and Ballinger 1987; Tinkle and Dunham 1986; G. Hokit, unpublished data), we observed no correlation between population density and juvenile survivorship ($t = 0.88$, $P = .40$, $r^2 = 0.08$). Geographic variation in the abundance of resources could explain why densities within populations are correlated with survivorship but densities among populations are not.

Environments at higher latitudes tend to be more seasonal, and seasonal variation in temperature and other aspects of the environment can have a major influence on survivorship. Ashton (2001*b*) hypothesized that differences in seasonality generate disparate latitudinal clines in two species of rattlesnakes, *Crotalus viridis* and *Crotalus oreganus*. Lower survivorship during hibernation in northern populations was suggested as the cause of a Bergmann's cline in *C. viridis*, whereas a lack of strong seasonality throughout the range of *C. oreganus* was suggested as an explanation for a reversed cline in body size. Ashton's hypothesis is based on the assumption that larger individuals survive hibernation better than smaller individuals. Several observations suggest that this hypothesis does not account for the majority of geographic variation in the life history of *S. undulatus*. First, juvenile survivorship tends to be higher in colder environments, except in the extremely cold environment of Nebraska. Second, a principal

component describing the life history of *S. undulatus* was only weakly related to potential activity, which is a reasonable measure of the seasonality of an environment. Finally, one would only expect the evolution of larger body sizes in more seasonal environments if survival during winter was size dependent (Conover 1992). The relationship between body size and survival during winter in most populations of *S. undulatus* is unknown, but large hatchlings were not more likely than small hatchlings to survive hibernation in the relatively cold environment of New Jersey (Niewiarowski 1992). If juveniles are less likely to survive winter in more seasonal environments, irrespective of their body size, natural selection would favor early maturation at a relatively small body size, which is a pattern that contradicts Bergmann's rule. Indeed, in Nebraska, where only 22% of juveniles survive the winter, individuals mature early at a relatively small body size (Jones and Ballinger 1987).

Conclusions

Ultimately, a general explanation for latitudinal and thermal clines in body size will reside in life-history theory (Roff 1986). Therefore, theories proposed to explain Bergmann's rule should explicitly address the costs and benefits of particular body sizes in different thermal environments. To date, most of the explanations proposed for Bergmann's clines have been based solely on the potential benefits of attaining a relatively large body size in colder environments (see Blackburn et al. 1999). For example, some biologists suppose that large body size enhances the ability to thermoregulate or resist starvation (Ashton et al. 2000; Ashton and Feldman 2003; Heinze et al. 2003). Others suggest that larger body sizes in colder environments evolved in response to decreased competition or increased predation (Ashton et al. 2000; Ashton 2001b; Ashton and Feldman 2003). Surprisingly, the most obvious benefit of a large body size—a higher fecundity—has not been a prominent feature of explanations for Bergmann's rule. Regardless of which benefits are considered, the primary

cost of attaining a larger body size is a decreased probability of surviving to reproduce.

Using *Sceloporus undulatus* as an example, we argued that Bergmann's clines result not only from the benefits of attaining a larger body size but also from the costs. Individuals at higher latitudes and individuals in colder environments enjoy higher survivorship and thus can expect a greater probability of surviving to reach a given size at maturity. Latitudinal and thermal clines in survivorship might be common among species that follow Bergmann's rule, but we expect the relative importance of different sources of mortality to vary among species. For this reason, a general explanation for Bergmann's clines is unlikely to be based on a single mechanism that applies broadly across taxa. Even within *S. undulatus*, both abiotic and biotic factors probably play a role in producing a Bergmann's cline. Advances will come partly from detailed studies of the proximate and ultimate mechanisms that produce variation in body size, such as the one presented here. These studies will serve to complement comparative studies that focus on the generality of intraspecific patterns (Ashton et al. 2000; Ashton 2002a, 2002b; Belk and Houston 2002; Ashton and Feldman 2003; Meiri and Dayan 2003). Because comparative studies are incapable of distinguishing cause and effect definitively, disentangling the factors that cause Bergmann's clines will require experiments that test specific hypotheses about the costs and benefits of different life histories. Models that incorporate the relationships among abiotic factors (e.g., temperature), biotic factors (e.g., predators), and the performance of organisms (e.g., survival) would be valuable for designing such experiments and interpreting their outcomes.

Table A1: Environmental and life-historical data for the populations included in the comparative analyses

Population	Latitude (degrees)	Mean temperature (°C)	Potential activity (hours)	Size at maturity (mm)	Mean size (mm)	Age at maturity (months)	Monthly survivorship	Source
Sceloporus undulatus								
Aiken County, S.C.	33.6	18.0	1,955	55	63	12	.83	Tinkle and Ballinger 1972
Baker County, Ga.	31.3	19.5	…	…	62	…	…	Crenshaw 1955
Blount County, Ala.	34.0	15.6	1,804	60	72	12	.87	McKinney 1982
Burlington County, N.J.	39.8	12.4	1,470	60	73	20	.93	Niewiarowski 1994; P. H. Niewiarowski, unpublished data
Grant County, N.M.	32.9	11.8	2,049	53	63	18	.80	Vinegar 1975
Hildago County, N.M.	32.4	18.2	2,109	54	68	12	.75	Vinegar 1975
Hocking County, Ohio	39.5	10.9	1,224	66	75	20	.84	Tinkle and Ballinger 1972
Huerfano County, Colo.	37.7	11.3	2,200	62	72	20.5	.89	Gillis and Ballinger 1992
Huntingdon County, Pa.	40.4	10.2	1,193	62	72	22	.86	J. Matter, unpublished data
Franklin County, Mo.	38.8	13.6	…	…	67	…	…	Marion 1970
Keith County, Nebr.	41.1	9.8	1,836	45	55	9.5	.80	Ballinger et al. 1981; Jones and Ballinger 1987
Mesa County, Colo.	39.1	11.9	2,020	58	70	20.5	.90	Tinkle and Ballinger 1972
Maricopa County, Ariz.	33.9	13.7	1,987	60	65	11.5	.79	Tinkle and Dunham 1986
Monroe County, Ind.	39.0	11.9	…	…	77	…	…	C. E. Oufiero and M. J. Angilletta, Jr., unpublished data
Montgomery County, Va.	37.2	11.0	…	…	72	…	…	C. E. Oufiero and M. J. Angilletta, Jr., unpublished data
Santa Rosa County, Fla.	30.9	19.2	…	…	61	…	…	C. E. Oufiero and M. J. Angilletta, Jr., unpublished data
Schleicher County, Tex.	30.8	17.9	2,815	47	57	12	.79	Tinkle and Ballinger 1972
Washington County, Utah	37.2	14.0	2,415	58	69	22.8	.88	Tinkle 1972

Table A1 (*Continued*)

Population	Latitude (degrees)	Mean temperature (°C)	Potential activity (hours)	Size at maturity (mm)	Mean size (mm)	Age at maturity (months)	Monthly survivorship	Source
Sceloporus woodi								
Highlands County, Fla.	27.6	21.5	2,444	47	54	10.5	.79	Hokit et al. 2001; D. G. Hokit, unpublished data

Note: Environmental temperatures were obtained from the National Climate Data Center (Asheville, N.C.), and life histories were obtained from the sources shown. Monthly survivorships were calculated from ages at maturity and survivorships to maturity (summarized in Smith et al. 1996), assuming that the survivorship of a juvenile was constant in each environment. Potential durations of activity were calculated using a biophysical model (see text for details).

APPENDIX B

Refinement of the Biophysical Model That Estimates Potential Activity

The microclimate model of Porter et al. (1973), which contains the solar radiation model of McCullough and Porter (1971), was modified such that body temperatures in full sun and full shade were calculated for all possible positions (i.e., on the ground and up to 2 m above and below the ground). Before this modification, an animal moving from sun to shade would be affected by its thermal history, with air temperatures above the surface being those of the sunny location. The new procedure assumes no direct solar radiation is absorbed by the shaded ground at any time of the day. This condition even exists in the desert, where a minimal horizontal distance of 30 cm within the shadow of a large, open bush creates relatively low and constant temperatures between the surface and a height of 2 m. Therefore, this procedure provided a better estimate of the potential body temperatures of an animal than the previous procedure.

The ectotherm model of Grant and Porter (1992) was modified such that transients of body temperature were calculated hourly rather than assuming an animal could reach a steady-state temperature each hour. To achieve this result, a full day of hourly steady-state calculations were made to determine the locations and environmental conditions that enable the animal to stay within its preferred range of temperatures. These hourly locations and environmental conditions were then used to calculate hourly transient body temperature for the entire day. This procedure prevented the numerical integrator from becoming unstable while calculating the temporal trajectory of body temperatures; previously, the numerical integrator became unstable whenever an animal suddenly changed its position because its body temperature rose above or fell below the preferred range.

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