

## Body Size Clines in *Sceloporus* Lizards: Proximate Mechanisms and Demographic Constraints<sup>1</sup>

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**SYNOPSIS.** Although most species of animals examined to date exhibit Bergmann's clines in body size, squamates tend to exhibit opposing patterns. Squamates might exhibit reversed Bergmann's clines because they tend to behaviorally regulate their body temperature effectively; the outcome of this thermoregulation is that warmer environments enable longer daily and annual durations of activity than cooler environments. Lizards of the genus *Sceloporus* provide an opportunity to understand the factors that give rise to contrasting thermal clines in body size because *S. undulatus* exhibits a standard Bergmann's cline whereas *S. graciosus* exhibits a reverse Bergmann's cline. Interestingly, rapid growth by individuals of both species involves adjustments of physiological processes that enable more efficient use of food. Patterns of adult body size are likely the evolutionary consequence of variation in juvenile survivorship among populations. In *S. undulatus*, delayed maturation at a relatively large body size is exhibited in cooler environments where juveniles experience higher survivorship, resulting in a Bergmann's cline. In *S. graciosus*, high juvenile survivorship is not consistently found in cooler environments, resulting in no cline or a reversed Bergmann's cline, *i.e.*, geographic patterns in body size aren't necessarily produced by natural selection. Thus, discerning the mechanistic links between the thermal physiology of an organism and environment-specific rates of mortality will be critical to understanding the evolution of body size in relation to environmental temperature.

### INTRODUCTION

Understanding the causal basis of geographic variation in body size has been the focus of much work in life-history evolution since the field's inception (Stearns, 1992; Roff, 2001). The relationship between variation in thermal environments and the resultant variation in growth and body size has been of particular interest to evolutionary ecologists (Atkinson, 1994; Atkinson and Sibly, 1997; Angilletta and Dunham, 2003). The focus on the thermal environment has been largely due to the fact that temperature influences the biology of organisms across multiple levels of organization from biochemical processes (Hochachka and Somero, 2002) to organismal performance (Huey and Stevenson, 1979; Huey, 1991; Willmer, 1991; Angilletta *et al.*, 2002; Angilletta *et al.*, 2003), all of which contribute directly or indirectly to growth. One of the major patterns that has emerged is Bergmann's rule, the tendency for animals to exhibit larger body size in cooler climates (Blackburn *et al.*, 1999; Ashton, *in review*). Nearly 70–80% of animal taxa examined to date have exhibited this pattern (invertebrates: Arnett and Gotelli, 1999; Chown and Gaston, 1999; birds: Ashton, 2002a; Meiri and Dayan, 2003; mammals: Ashton *et al.*, 2000; Freckleton *et al.*, 2003; Meiri and Dayan, 2003; amphibians: Ashton, 2002b; Morrison and Hero, 2003; turtles: Ashton and Feldman, 2003). While there has been a concentrated effort to document Bergmann's rule and, to some extent, understand the mechanisms that produce it, exceptions to Bergmann's rule have largely been ignored. For in-

stance, as a group, the squamate reptiles (snakes and lizards) tend to exhibit larger body size in warmer climates, with over 70 percent of squamates exhibiting reversed Bergmann's clines (Ashton and Feldman, 2003). Inspection of the processes responsible for body size patterns in nonconforming groups may lend considerable insight toward a more general understanding of the factors that affect the evolution of body size (Chown and Gaston, 1999; Ochocinska and Taylor, 2003; Atkinson, 1995).

Why do we see a reversed Bergmann's size cline in most species of lizards and snakes? One reason might be that many squamates are active behavioral thermoregulators, that is, the body temperatures of individuals are not simply caused by a passive response to environmental heat fluxes, but rather are caused by the selection of specific thermal conditions within an environment (Hertz *et al.*, 1993). Thus, individuals inhabiting warmer environments don't necessarily exhibit higher body temperatures than individuals inhabiting cooler environments (Huey *et al.*, 2003). In fact, they often exhibit similar body temperatures across habitats that differ with regard to thermal environments (Adolph, 1990; Andrews, 1998). The outcome of such thermoregulatory behavior is that environmental temperatures simply modulate the duration of activity for individuals occurring in contrasting thermal environments (Fig. 1). Therefore, in squamates, selection on life histories imposed by the thermal environment would most likely manifest itself through differences in the duration of activity, on both a daily and seasonal basis, and not necessarily through variation in body temperatures that are experienced during activity. Where there is a high premium for growth under limited time, selection might favor modifications in physiology that enhance the efficiency of growth (Weiser, 1991, 1994; Koehn, 1991) (although strategies may

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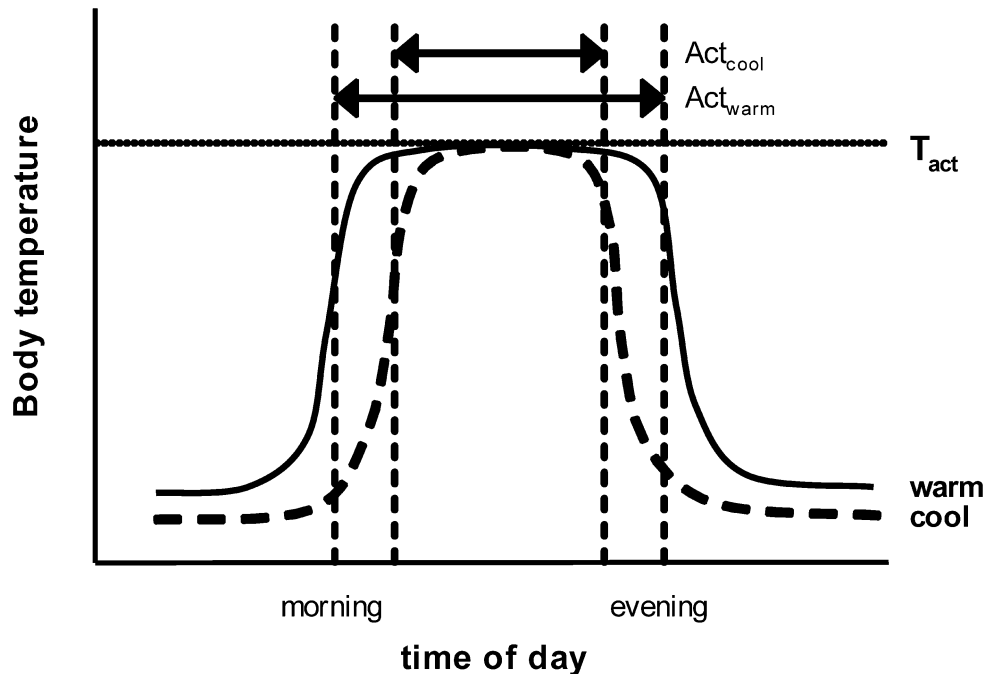


FIG. 1. Because squamates often thermoregulate within a narrow range of temperatures, variation of environmental temperature affects the time that an individual can be active at a preferred body temperature. As environmental temperatures increase early in the day, an animal can bask until it reaches its preferred body temperature for activity ( $T_{act}$ ). During the middle of the day, the animal must move among microhabitats to maintain its  $T_{act}$ . As environmental temperature decreases at the end of the day, the individual can bask to maintain  $T_{act}$  for as long as possible before retreating into a refuge. As illustrated, warmer environments simply offer longer potential periods of activity ( $Act_{warm}$ ) than do cooler environments ( $Act_{cool}$ ) as long as suitable habitat exists to facilitate thermoregulation.

incur costs such as decreased survivorship or smaller adult body size). Indeed, many examples demonstrate a tradeoff between fast growth and reduced metabolic expenditure (Koehn, 1991; Hawkins and Day, 1996; Bayne, 2000). Alternatively, selection may act on physiology by selecting on the average temperatures that an animal experiences or on the modal extremes (*i.e.*, retreat site temperatures and temperatures for activity). Evidence for the former strategy will be discussed later in this paper. Little, if any, evidence has been documented for the latter strategy in squamates.

The coupling of thermoregulation with the thermal sensitivity of physiological performance of individuals suggests a null model of body size against which to compare size clines observed in nature. If we assume that food is not limiting in a given environment, then growth and body size are determined by physiological constraints on the assimilation of consumed energetic resources and their subsequent allocation to growth (Congdon, 1989; Adolph and Porter, 1993, 1996). The range of body temperatures over which lizards are generally active tends to maximize the amount of assimilated energy (Angilletta *et al.*, 2001a, b). Indeed, several studies have documented differences in the size of the energy budget for individuals from different populations that correspond to differences in seasonal activity in those populations (Tinkle *et al.*, 1993; Angilletta, 2001a; Niewiarowski, 2001). For example, juvenile fence lizards (*Sceloporus undulatus*) in New Jersey experience 8% less activity annually than do

fence lizards in Nebraska. This reduction in activity corresponds to a 7% reduction in the size of energy budgets for fence lizards from NJ versus those from NE (Niewiarowski, 2002), supporting the notion that the longer an individual is active, the greater is its potential for growth (and subsequently, large body size). So, as a null model, we should expect that daily growth would be higher in warmer environments that enable a longer duration of activity, and in general, lizards should exhibit a reversed Bergmann's size cline (Adolph and Porter, 1993, 1996).

Deviations from the reverse Bergmann's size clines within squamates are likely to arise either when the environment limits somatic growth in warmer environments (through resource limitation or process limitation [Congdon, 1989; Dunham *et al.*, 1989]) or when age-specific mortality schedules select for a specific body size, or growth rate, in a particular environment, *i.e.*, body size is a result of evolutionary tradeoffs (Case, 1978; Stearns and Koella, 1986; Arendt, 1997). Resource limitation exists when an individual cannot acquire sufficient resources from the environment to support maximal growth. Such a situation can arise either when material resources (*e.g.*, food or water) is limited in the environment (Dunham, 1978) or when a behavioral response to some environmental stimulus, such as the presence of a predator, prevents or discourages an individual from foraging (Downes [2001]; reviewed by Lima and Dill [1990], and Lima [1998]). Even when resources are available in the environment

(and those resources are consumed), process limitation may prevent maximal growth (Congdon, 1989). For instance, growth rates of *S. merriami* at high elevation (Maple Canyon) in Big Bend National Park (TX) are limited by the rate at which food items pass through the gut due to prolonged exposure to cool nighttime temperatures (Dunham *et al.*, 1989). So, although there is plentiful food in the environment, lizards cannot take advantage of it due to thermal constraints on ingestion and assimilation. Finally, patterns of body size that do not track environmental resources (such as Bergmann size clines) can be produced by mortality schedules that favor earlier reproduction in warmer environments than in cooler environments. For instance, classical models of life history evolution predict that when juvenile mortality is high, fast growth is favored (Stearns, 1992, 2000). Often, fast growth incurs the cost of maturing at a relatively smaller adult body size. Because longer potential periods of activity, such as those found in warmer environments, can produce higher rates of mortality (Wilson, 1991), selection may produce faster growing lizards that achieve smaller adult body sizes, resulting in a Bergmann size cline. As we illustrate later in this manuscript, these types of evolutionary tradeoffs are a likely causative factor that contributes to the Bergmann size cline observed in *S. undulatus*.

To understand when we should, or should not, expect to observe a Bergmann size cline in a particular species of squamate, the costs and benefits derived from behavioral thermoregulation should be considered. The benefits of thermoregulation are obvious: relatively high rates of physiological performance in general, and rapid growth in particular. The costs of thermoregulatory behavior are a harder to discern, largely because they are generated through realized or perceived penalties on survivorship. Huey and Slatkin (1976) were the first to formalize a cost-benefit analysis of thermoregulatory behavior in lizards (though the model can be applied to ectotherms in general). Their model simply posits that animals should maintain a range of temperatures that maximize lifetime reproductive success (*i.e.*, the product of survival and fecundity). Fecundity is affected mainly by the time that lizards experience suitably elevated body temperatures that maximize the net rate of energy assimilation. Survival is affected mainly by choosing temperatures that minimize exposure to predators, overheating, or desiccation. Thus, a balance must be realized such that the duration and precision of thermoregulation maximizes lifetime reproductive success.

#### *SCELOPORUS* AS A MODEL SYSTEM

Lizards of the genus *Sceloporus* are a model system for studying the evolution of life histories in response to variation in environmental resources, particularly the thermal environment. *Sceloporus* comprises over 70 species of relatively small-bodied lizards found in North America from Panama to the northern United States (Sites *et al.*, 1992). Across this broad geograph-

ical range, sceloporines are found from sea level to over 4,000 meters in elevation throughout a variety of biomes ranging from extreme deserts to temperate and subalpine forests. The habitat of a given species can be highly generalized to highly specialized and includes rocky outcroppings, sand dunes, forest understories, and riparian zones. Such a broad distribution, both in terms of geography and habitat, enables the investigation of covariation between life history and thermal conditions.

Although sceloporines encounter a wide range of thermal environments, they exhibit a small and surprisingly consistent range of body temperatures (Bogert, 1949*a, b*; Andrews, 1998). Across all temperate species and lowland tropical species (<1,500 m), body temperature averages 35°C and does not vary latitudinally. Within temperate species, no consistent pattern of variation in body temperature is associated with elevation, but tropical species tend to exhibit lower body temperatures at higher elevation, with species at high elevations (>1,500 m) averaging 31.5°C. The consequence of such narrow ranges of selected body temperatures is that the duration of daily and seasonal activity varies in a predictable manner in response to variation in thermal environments (Adolph and Porter, 1993). As stated earlier, our null (non-adaptationist) expectations are that, within a given species, larger body size would be produced in individuals from populations that are found at more southern latitudes or low elevations that experience longer periods of activity than in individuals from populations found at more northern latitudes or high elevation that experience shorter periods of annual activity.

Body size within *Sceloporus* does vary greatly within and among species. Although adult body size varies over tenfold among species, from 4 grams to 60+ grams, no consistent thermal clines are apparent (Fig. 2). Within species, several patterns of geographic variation in body size do emerge. Bergmann's size clines are exhibited in at least four species (Ashton, 2003, Angilletta *et al.*, 2004; Leaché, unpublished data)—*S. undulatus*, *S. jarrovi*, *S. virgatus*, and *S. occidentalis*—and a reversed Bergmann's pattern is observed in *S. graciosus* (Sears, 2004). No regular clinal pattern is seen in most species in *Sceloporus*, although it should be noted that body size data for multiple populations are unavailable for most species. Contrasting the availability of resources, variation in physiological performance of individuals, and variation in demographic parameters for populations of species that exhibit different body size clines offers a unique opportunity to understand the proximate and evolutionary underpinnings of body size.

Indeed, an understanding of the proximate factors that determine the life histories of sceloporines is beginning to emerge from the intensive study of several species. In particular, studies of *S. undulatus* and *S. graciosus* have given new insight to the environmental factors that drive patterns of body size in *Sceloporus*. In the following section, we present an overview of

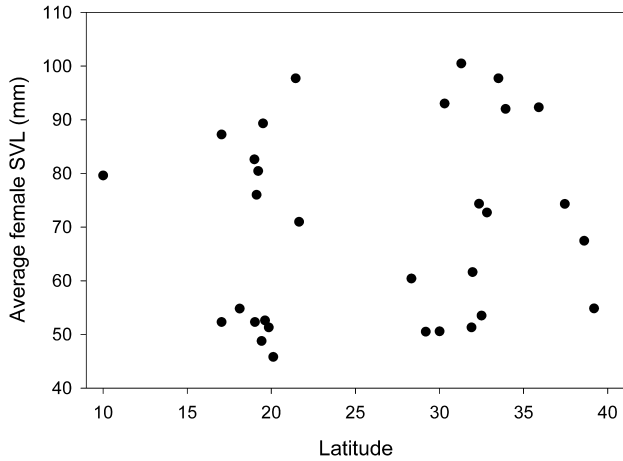


FIG. 2. The mean body size (expressed as snout-vent length [SVL]) of an adult female *Sceloporus* is not related to the latitude where the study population is found. Similarly, no elevational cline in body size exists (data not shown). When multiple records were available for multiple populations of a single species, both body size and latitude were averaged to create a single plotted datum. Sources of data can be obtained from the authors.

these studies in an attempt to generate a general understanding of size variation. Differences in body size between *S. graciosus* and *S. undulatus* seems to be driven by different combinations of resource limitation and rates of mortality among populations.

#### PATTERNS OF BODY SIZE IN *SCELOPORUS GRACIOSUS*

The sagebrush lizard (*S. graciosus*) is an example of a species that exhibits a distinct reverse Bergmann's size cline across its range (Sears, 2004). Sagebrush lizards are small (5–10 g for mature adults) yet long-lived lizards for their size (up to 6 years, Dunham and Miles, 1985) that are found throughout the western United States from the state of Washington to Baja California, and from the west coast through the Rocky Mountains. Sagebrush lizards appear to be adapted to cool climates throughout their geographic range; they are found near sea level at northern latitudes and on mountaintops (over 3,000 meters above sea level) at the southern extent of their range. Depending on their location, sagebrush lizards are saxicolous, arboreal, or generalize among different habitat types including sand dunes. Over their geographic range, annual activity of sagebrush lizards varies twofold, from 4 to 8 months. The consequence of this variation is that the maximum body size of adult lizards increases with annual activity (Fig. 3). For example, the activity season of sagebrush lizards from Mt. Rose (CA) is 60% longer than that of lizards from Kolob Mesa (UT) (Tinkle *et al.*, 1993). Accordingly, the energy budgets of lizards from Mt. Rose are approximately 60% larger than are those of lizards from Kolob Mesa, but the proportion of resources allocated to growth is similar for both populations. Therefore, lizards from Mt. Rose likely achieve larger body sizes than lizards from Kolob Mesa due to longer periods of time over which to for-

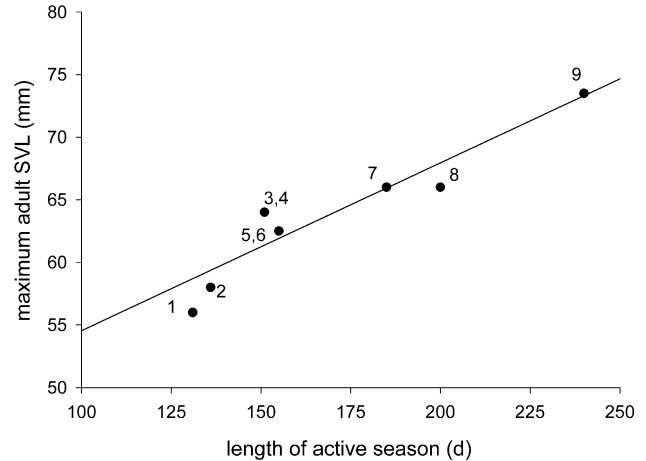


FIG. 3. The maximum size (expressed as snout-vent length [SVL]) of *Sceloporus graciosus* increases with the annual duration of activity. The locations of populations are as follows: 1) Yellowstone National Park, WY, 2) Butte Co., CA, 3) Nevada and Placer Co., CA, 4) Napa Co., CA, 5) Kolob Mesa, CA, 6) Salt Lake Co., UT, 7) Utah Co., UT, 8) Los Angeles Co., CA, and 9) Contra Costa Co., CA. Reproduced from Sears (2004).

age. In further support of this argument, sagebrush lizards from CA, when reared in the laboratory with unlimited food over activity periods similar to those observed in nature (6–12 hr), grew larger the longer that they were allowed to maintain elevated body temperatures necessary for activity (Sinervo and Adolph, 1994). Interestingly, for a duration of activity (15 hr) that was typically longer than that observed in nature, lizards grew to a size smaller than did those experiencing 12 hr of activity.

Oddly, within a more localized geographic area over an elevational gradient, sagebrush lizards tend to be of similar adult size, even though seasonal activity varies among locations (Fig. 4). For example, individuals from three populations along an elevational gradient, ranging from 1,700 m to 2,250 m above sea level, in Zion National Park (UT), all achieve similar maximal body sizes (to approximately 65 mm SVL) despite large differences in annual activity (Sears, in press). Lizards at high elevation experience nearly two additional months in brumation while overwintering than do lizards at the lowest elevation at which sagebrush lizards are found within the park. In terms of annual activity, lizards from the highest site experience conditions that restrict activity by approximately 400 fewer hours per year than lizards at the lowest elevations. Even more peculiar is that, despite having a shorter duration of daily and annual activity, sagebrush lizards at high elevation exhibit higher rates of intrinsic growth. During the late May and early June, lizards from high elevation weigh 70% less and are 20% shorter than lizards from both of the populations at lower elevations. However, these differences are nearly absent by late summer, and disappear by the time that lizards reach their second growing season.

Although sagebrush lizards along an elevational gra-

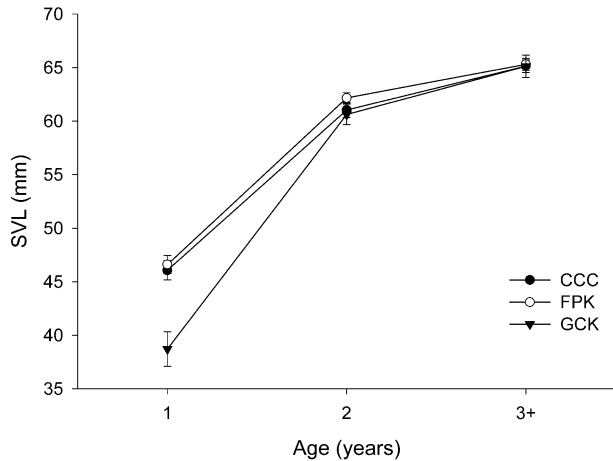


FIG. 4. Over an elevational gradient in Zion National Park, the adult body size of *Sceloporus graciosus* does not vary among populations (Sears, 2004). Lizards at Goose Creek Knoll (GCK, 2,255 m) can be active for 2,420 per year, whereas lizards at Firepit Knoll (FPK, 1,961 m) and Clear Creek Canyon (CCC, 1,752 m) can only be active for 2,205 hours and 1,988 hours per year, respectively (Sears, in press). Interestingly, despite fewer hours of activity to acquire resources, lizards at GCK start their first year of activity at a smaller size, but grow faster to reach the same sizes as lizards at FPK or CCC by the age of maturity. Adapted from Sears and Angilletta (2003). Means and 95% CI are plotted.

dient at Zion National Park exhibit different growth rates in the field, differences in growth rate disappeared when lizards were reared in the laboratory under shared conditions (Sears and Angilletta, 2003). Gravid females from each of the three populations in UT were brought into the laboratory, where their eggs were collected and incubated under identical thermal and hydric conditions. Hatchlings were then reared under identical conditions of temperature and photoperiod, and were allowed to consume food *ad libitum*. Half of the lizards from each population were supplemented with additional water. After controlling for the amount of food that was consumed by each individual, growth rates were similar for lizards from all populations and were not affected by water supplementation. Furthermore, individual rates of food consumption were not different among populations. Thus, variation in growth rates observed in free-ranging lizards is influenced by variation in environmental conditions in the field, or acclimation to those conditions, and is not likely caused by genetic divergence. Interestingly, Sinervo and Adolph (1994) also failed to show differences in growth rate for sagebrush lizards that were collected from two elevationally distinct sites in southern CA. Although only two elevational gradients have been studied, apparently the factors underlying geographic patterns of body size in sagebrush lizards are different than those factors underlying local elevational patterns. This discrepancy could be a consequence of gene flow among populations that occur locally over elevational gradients versus the lack of gene flow over larger geographic scales, as in *S. occidentalis* (Adolph, personal communication).

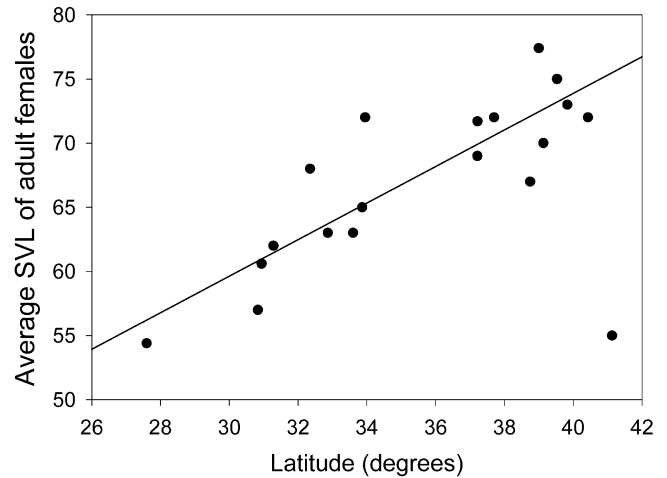


FIG. 5. *Sceloporus undulatus* exhibit a Bergmann size cline for nineteen populations that have been studied within the US. The average SVL of adult females increases with latitude and also decreases with average environmental temperature. Adapted from Angilletta *et al.* (2004).

PATTERNS OF BODY SIZE IN *SCELOPORUS UNDULATUS*

Uncharacteristically for most squamates, the Eastern fence lizard (*S. undulatus*) exhibits a Bergmann size cline over its geographic range (Fig. 5; Angilletta *et al.*, 2004). This phenomenon is particularly interesting because the Eastern fence lizards is one of the most widely distributed species of lizards in North America, ranging throughout the eastern two-thirds of the US and into northern Mexico. Throughout its range, the eastern fence lizard inhabits a diverse range of environments from eastern pine forests, to Midwestern grasslands, and to Western riparian zones and canyon habitats. Regardless of their longitude, lizards from northern latitudes are larger than lizards from southern latitudes. Furthermore, lizards from higher elevation in geographically proximal areas exhibit larger body size than lizards from lower elevations. Thus, lizards in colder environments grow to a larger size despite having less opportunity for activity on both a daily and annual basis. This pattern has been observed independently among four clades within this species (Angilletta *et al.*, 2004). Even more puzzling is that larger lizards from northern populations grow more slowly to reach their adult body size. Such a pattern contrasts the pattern of growth and body size of sagebrush lizard, and therefore, affords a excellent opportunity to investigate how clines in life history can be driven by environmental variables.

Unlike sagebrush lizards, patterns of growth and body size of Eastern fence lizards appear to have been caused by genetic divergence among populations. In a reciprocal transplant of fence lizards between Nebraska and New Jersey (Niewiarowski and Roosenburg, 1993), lizards from New Jersey grew no faster in Nebraska than they did in New Jersey despite having 2–2.5 hours more per day available for activity. In contrast, lizards from Nebraska exhibited a 50% reduction

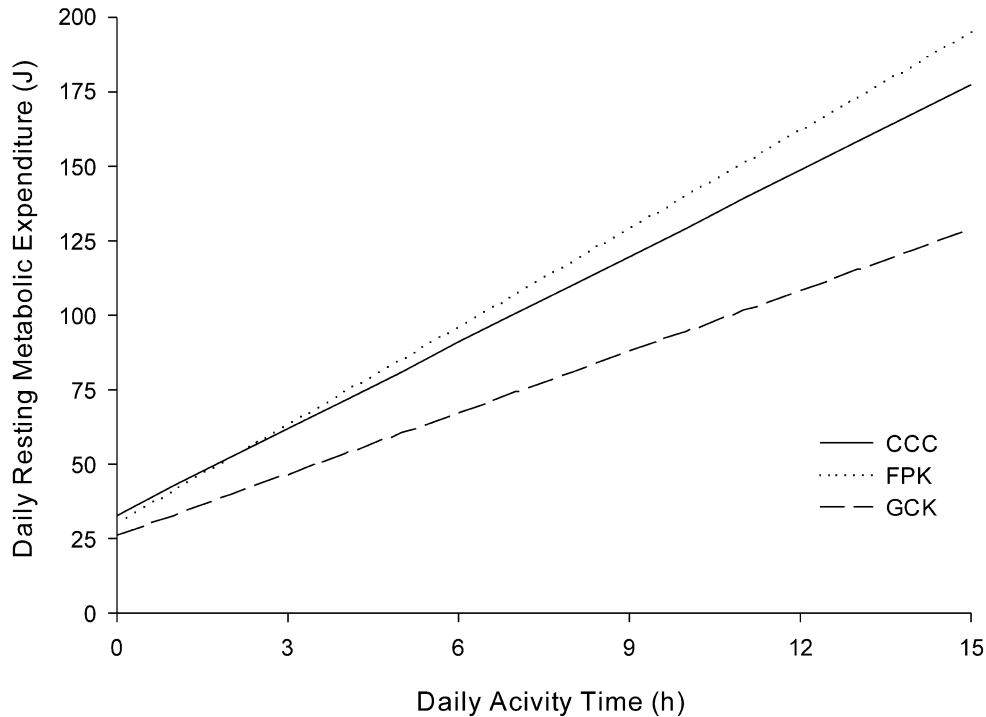


FIG. 6. In *Sceloporus graciosus*, lizards at Goose Creek Knoll (GCK, 2,255 m) in Zion National Park expend less energy on maintenance than do lizards at Firepit Knoll (FPK, 1,961 m) and Clear Creek Canyon (CCC, 1,752 m). As the duration of daily activity increases, so does the magnitude of energetic savings for lizards at high elevation. Resting metabolic expenditure was calculated using rates measured in the laboratory (at temperatures appropriate for activity and inactivity) in combination with estimates of daily activity for an average year.

in growth rate when transplanted to New Jersey. Thus, slow growth of resident lizards in New Jersey would appear to be the result of a flat reaction norm for growth with respect to the thermal environment. Furthermore, lizards from New Jersey did not grow faster when supplemented with additional food either in the field or in the laboratory, suggesting a set trajectory for growth. Other populations of fence lizards have also exhibited intrinsic (likely genetic) differences in growth; fence lizards from Utah grow faster than those from Oklahoma in the field, though the opposite pattern was observed in the laboratory (Ferguson and Talent, 1993). Because food and temperature could not be controlled in the field, this pattern only suggests that genetic differentiation occurred between the two populations and not necessarily that thermal reaction norms for growth have diverged among populations. Regardless, strong evidence exists that a genetic basis for geographic variation in growth rate of *S. undulatus* is the rule rather than the exception.

#### PROXIMATE CAUSATION OF GROWTH AND BODY SIZE IN *SCELOPORUS* LIZARDS

Although different geographic patterns of growth are observed among *S. graciosus* and *S. undulatus*, similar physiological processes generate fast growth in both species. *Sceloporus graciosus* at high elevation exhibits faster rates of growth in a relatively cool environment than lizards from lower elevations and warmer environmental temperatures. *Sceloporus un-*

*dulatus* exhibits faster rates of growth in relatively warmer environments (SC) than in cooler environments (NJ). Regardless of species, fast growth simply results from modifications in the processes of mass balance and energy allocation (Bayne, 2004); organisms consume macromolecules, which are then catabolized to perform cellular work or are anabolized to form somatic and gametic tissues. As discussed earlier, the duration that an individual can forage generally limits energy assimilation in lizards. What further limits growth after ingestion, then, are the rates and efficiencies of the absorption of and expenditure of assimilated resources. Thus, to grow fast, a lizard must either be better at extracting the available energy from their diet or they must reduce expenditure from their total energy budget allowing more potential energy to be available for growth (Bayne, 2004).

Reduced costs of maintenance contribute to fast growth rates of *S. graciosus* from high elevation and of *S. undulatus* from southern latitude. The resting metabolic rates (RMR's) of juvenile and adult *S. graciosus* from the high elevation at Zion National Park were lower than those from lower elevation over a broad range of temperatures (21–37°C). The difference in RMR among individuals from high and low elevations was greatest at temperatures selected for activity. Thus, for a typical day in July, resting metabolic expenditure is 50% higher for lizards at low elevation than for lizards at high elevation (Fig. 6). Incorporating differences in maintenance into an energy budget

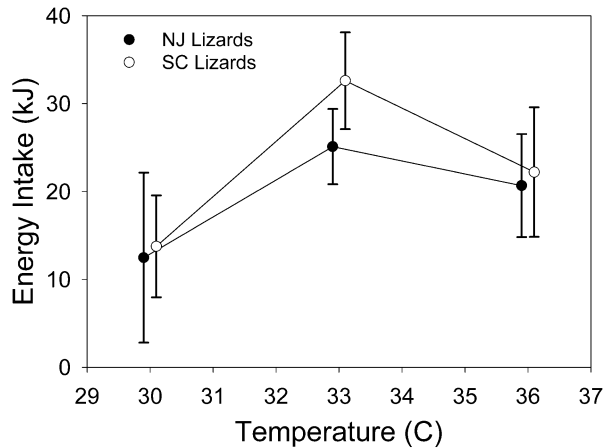


FIG. 7. In *Sceloporus undulatus*, metabolizable energy intake of lizards from SC was greater than that of lizards from NJ during a two week feeding trial. Plotted values are means adjusted for body mass by ANCOVA with 95% confidence intervals. The difference in energy intake was largest at the mean body temperatures during activity. Lizards from SC achieved higher rates of energy intake than lizards from NJ not by consuming more food but by absorbing a greater percentage of the energy in their food. Reproduced from Angilletta 2001a.

analysis, Sears (in review) concluded that lizards from high elevation could potentially allocate 12.5% more energy to growth on a daily basis than lizards from low elevation populations. Interestingly, hatchlings raised in a common environment exhibit no differences in RMR, suggesting that divergent RMR's in field-active lizards is caused by acclimatization to differences in environmental conditions. Similarly, rapidly faster growing juveniles of *S. undulatus* from SC had a lower RMR than juveniles from NJ, which resulted in an annual energy expenditure on maintenance by juveniles in SC that was 15% less than that of juveniles in NJ (Angilletta, 2001b).

Fast growth of individuals in southern populations of *S. undulatus* can also result from more efficient digestion (Angilletta, 2001a). Comparisons of digestive performance between *S. undulatus* from SC and NJ showed that lizards from SC were more efficient at absorbing energy from their diet even though passage rates did not differ between populations. Thus, lizards from SC had a higher rate of energy assimilation than did lizards from NJ. The difference in energy assimilation between populations was observed at the selected body temperature (Fig. 7). When metabolizable energy intake was coupled with patterns of activity in the field, daily energy budgets of lizards in SC were estimated as 28% and 16% larger in spring and summer, respectively, than the daily energy budgets of lizards in NJ. On an annual basis, the energy budget of lizards in SC is 60% larger than that of lizards in NJ. Thus, more efficient digestion along with energetic savings from a lower RMR enables fence lizards in SC to grow more efficiently than fence lizards in NJ. Whether or not fast growing sagebrush lizards exhibit similar modifications of digestive performance as *S.*

*undulatus* is unknown, but *S. graciosus* from ZNP that were grown in a common environment as hatchlings did not exhibit differences in growth efficiency (*i.e.*, lizards grew similarly per amount of consumed food; Sears and Angilletta, 2003). Regardless, the potential exists for the digestive efficiency of free-ranging lizards to differ among populations because of acclimatization to thermally distinct habitats, as did RMR.

#### DEMOGRAPHIC CONSTRAINTS ON GROWTH AND BODY SIZE

The underlying evolutionary mechanisms that cause the contrasting patterns of growth and body size between *S. undulatus* and *S. graciosus* could be linked more to juvenile survivorship in different environments than to the physiological responses of individuals to thermal resources. Life-history theory predicts faster growth in environments that cause lower juvenile survivorship because such a strategy increases the probability of reaching reproductive size before death (Stearns, 2000). In both species, fast growth is exhibited in environments where individuals experience low survivorship as juveniles. For sagebrush lizards at ZNP, the lowest survivorship occurs at high elevation. Because few predators of lizards are present at high elevation than at low elevation, the lower survivorship at high elevation is more likely the consequence of longer winters. This geographic pattern of survivorship differs from that of *S. undulatus*, which experiences lower juvenile survivorship in warmer environments (Angilletta *et al.*, 2004) presumably because of higher intensities of predation and competition. A latitudinal gradient in survivorship can explain the faster growth of juveniles in SC relative to juveniles on NJ.

Additionally, the Bergmann's cline in *S. undulatus* might have been caused by geographic variation in survivorship. Life history theory predicts that lizards should delay maturation until reaching a relatively large body size if, by doing so, they can achieve large gains in fecundity or produce offspring of a higher quality (Stearns and Crandall, 1981; Stearns and Koella, 1986; Stearns, 1992). The major cost of delayed maturation is a decrease in the probability that a lizard will survive to reproduce. We expect large body size to be observed in environments where the benefits of delayed maturation are relatively high and its costs are relatively low. Large size appears to confer both higher benefits and lower costs in colder environments. First, theory predicts that larger offspring should be produced in colder environments (Yampolsky and Scheiner, 1996; Perrin, 1988). Females in northern populations of *S. undulatus* produce larger eggs (Oufiero and Angilletta, in review), and larger body size could be necessary to produce larger eggs because eggs must pass through the pelvic aperture (Congdon and Gibbons, 1987). Second, colder environments confer juveniles with higher survivorships (Angilletta *et al.*, 2004), which also favors delayed maturation at a larger body size. In fact, relatively large body size is only

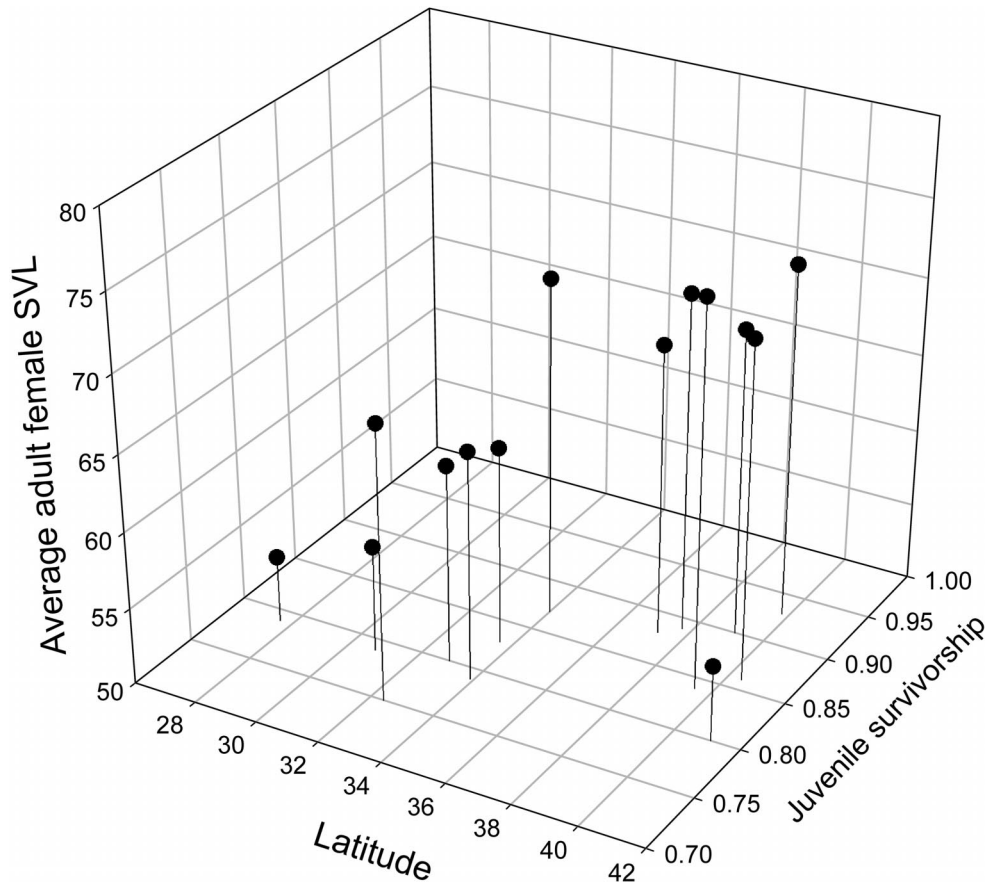


FIG. 8. In *Sceloporus undulatus*, high juvenile survivorship in northern populations appears to favor delayed maturation at a larger body size. For 14 populations, both juvenile survivorship and mean body size increase with increasing latitude. Sources of data are listed in Angilletta *et al.* (2004).

observed in northern populations where survivorship of juveniles tends to be very high (Fig. 8).

In *S. graciosus*, elevational variation in seasonality and survivorship interact to eliminate clinal variation in body size. Among the three populations at ZNP, all females reproduce by the spring of their second summer (Sears, unpublished data). Females from high elevation experience lower survivorship and a shorter activity season; therefore, delayed maturation to a large body size would be disadvantageous because the probability of surviving until the next year is low. Instead, to compensate for a shorter growing season, lizards from high elevation grow faster, likely, to reach as large a size as possible in their second year. Consequently, adult body size does not vary along the elevational gradient at ZNP. Furthermore, survival of juveniles at high elevation is not enhanced by large body size (Sears, unpublished data). Thus, we should expect that large body size should be observed only in populations where juvenile survival is relatively high (favoring delayed maturation as in *S. undulatus*).

#### CONCLUSIONS AND SOME FUTURE DIRECTIONS

Future modeling efforts of life-history evolution must address the more complex issues of how adap-

tation to thermal conditions relates to schedules of mortality and fecundity (Stearns, 2000; Angilletta *et al.*, 2004). Classical models often have made unrealistic assumptions about the organisms they are trying to model. For example, vital rates (fecundity and survival) are assumed to be insensitive to the strategy of energy allocation. However, faster growing lizards may incur higher mortality than slower growing lizards because of more exposure to predators. Thus, a demographic analysis that explores the benefits of large size (mediated by slow or fast growth) may be an inaccurate caricature of potential life histories if vital rates are assumed to remain fixed for different strategies of growth. Models that incorporate mechanistic links between thermal physiology and vital rates will further our understanding of the evolution of geographic variation in body size (Angilletta *et al.*, 2004; Kozlowski, 2004).

Models of life-history evolution are still relatively simplistic and the currently small body of empirical literature that deals with the consequences of variation in life history parameters hampers the formulation and testing of more complex models. Relatively few studies have been conducted that examine the sources of variation (genetic versus environmental) in the body



size of squamates using reciprocal field transplants or common environmental studies of the growth of individuals from different populations (*e.g.*, see Sorci *et al.*, 1996, and Bronikowski, 2000). Furthermore, little is known about the fitness consequences of variation in rates of growth among individuals within populations, about the effects on the survival of offspring that are the consequence of being produced by females of varying size and age, or even about the influence of variation in body size across all life stages on survival and fecundity. Such data are critical if we are to build realistic models of the evolution of body size. The allometric engineering of phenotypes (Sinervo *et al.*, 1992) and molecular determination of reproductive success (Haanel *et al.*, 2003) are promising approaches for exploring the fitness consequences of different body sizes. Though rarely collected, basic long-term demographic studies are still needed to define geographic patterns in many species; for example, survivorship of *S. graciosus* is unknown in most populations. Only when these data are gathered will we be able to piece together a coherent understanding of the evolution of body size in response to thermal resources.

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