

THERMAL AND PHYSIOLOGICAL CONSTRAINTS ON ENERGY ASSIMILATION IN A WIDESPREAD LIZARD (*SCELOPORUS UNDULATUS*)

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Abstract. Thermal constraint on energy assimilation is an important source of life history variation in geographically widespread ectotherms such as the eastern fence lizard (*Sceloporus undulatus*). Fence lizards in southern populations grow faster and produce more offspring per year than do those in northern populations. Biophysical models indicate that this difference in production is the result of thermal constraints on energy assimilation, but they do not exclude intraspecific variation in behavior or physiology. I quantified both thermoregulatory behavior and the thermal sensitivity of metabolizable energy intake (MEI) in lizards from New Jersey (NJ) and South Carolina (SC) populations of *Sceloporus undulatus*. In the laboratory, I conducted feeding trials to estimate MEI at body temperatures experienced by field-active lizards (20°, 30°, 33°, and 36°C). I also measured preferred body temperature (T_p) of lizards in a thermal gradient. In the field, I estimated the accuracy of thermoregulation by lizards. Both NJ and SC lizards exhibited a maximal MEI at their T_p (33°C), but lizards from SC had a significantly higher MEI at this temperature than lizards from NJ. Although lizards in both populations thermoregulated within 2°C of T_p , lizards in SC could maintain T_p for a longer duration on a daily and annual basis. Therefore, lizards in SC could assimilate more energy because they had a higher maximal MEI during activity and were active for longer durations than lizards in NJ. Geographic variation in the life history of *S. undulatus* may be caused by differentiation of physiology between populations, as well as by differences in the thermal environments of populations.

Key words: digestion; energy assimilation; energy budgets; geographic variation; metabolizable energy intake; life history; preferred body temperature; reptiles; *Sceloporus undulatus*; thermal sensitivity of performance; thermoregulation.

INTRODUCTION

Although life history theory has emphasized the allocation of available energy to growth and reproduction (e.g., Gadgil and Bossert 1970, Schaffer 1974), energy acquisition plays an equally important role in the manifestation of life histories (Tuomi et al. 1983, Jönsson 1997). The ability to harvest and assimilate resources constrains the set of possible life histories (Congdon 1989, Dunham et al. 1989, Kersten and Visser 1996). Furthermore, the trade-off between time spent acquiring food and that spent in pursuit of other resources affects the allocation decisions of organisms (Blackenhorn et al. 1995). Resource availability, climate, predation risk, and the social environment influence the rate of energy acquisition, thus determining the amount of energy available for allocation to growth and reproduction (Dunham et al. 1989). Therefore, variation in energy acquisition by individuals is a potentially widespread mechanism underlying the patterns of life history observed among natural populations.

In ectotherms, body temperature (T_b) exerts a major influence on the acquisition of energy. A succession of

behavioral and physiological processes (including detection, capture, ingestion, digestion, and absorption of food) determines the rate of energy assimilation. Many of these processes are sensitive to T_b (Greenwald 1974, Stevenson et al. 1985, Waldschmidt et al. 1986, Van Damme et al. 1991, Beaupre et al. 1993, Ayers and Shine 1997). Typically, such processes proceed best over a certain range of body temperatures and proceed relatively poorly at temperatures outside this range (Huey 1982). However, two factors cause the rate of energy assimilation to be particularly sensitive to T_b . First, processes involved in energy acquisition occur sequentially. Each upstream process (e.g., ingestion) limits all downstream processes (e.g., digestion, absorption), and vice versa. Second, not all processes are equally sensitive to T_b (Huey 1982, Stevenson et al. 1985, Van Damme et al. 1991). Consequently, the rate of energy assimilation, which relies on the concerted performance of multiple behavioral and physiological processes, should be more sensitive to T_b than any single process involved. Estimates of thermal sensitivities of performance support this notion. Performance breadths for locomotion usually span a range of 10–20°C (Bennett 1980, Hertz et al. 1983, Crowley 1985, van Berkum 1986, Huey et al. 1989, Van Damme et al. 1989), whereas those for energy assimilation span ranges of only 5–10°C (Dutton et al. 1975, Waldschmidt et al. 1986, Van Damme et al. 1991, Beaupre

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et al. 1993, Ji et al. 1995, 1996). Precise regulation of T_b is required for the rate of energy assimilation to be maximized.

Given the profound influence of body temperature on the rate of energy assimilation, it is not surprising that the thermal environment has been invoked frequently as the cause of geographic variation in the life histories of ectotherms (e.g., Grant and Dunham 1990, Partridge et al. 1994, Beaupre 1995, Sorci et al. 1996; for reviews, see Partridge and French 1996, Atkinson and Sibly 1997). Although many ectotherms are capable of thermoregulation (Casey 1981, Avery 1982, Bartholomew 1982, Peterson et al. 1993), climate limits the duration for which individuals can maintain their preferred body temperatures (Porter et al. 1973, Grant and Dunham 1988, Bashey and Dunham 1997). All other things being equal, an individual that is able to maintain its preferred body temperature for a longer time period should assimilate more energy. Thermal constraints on energy assimilation may limit the growth and reproduction of individuals. Indeed, laboratory studies have demonstrated that ectotherms grow faster when reared at higher temperatures (reviewed by Atkinson 1994) or given increased access to radiative heat (Sinervo and Adolph 1989, 1994, Autumn and DeNardo 1995). Because the opportunity for thermoregulation varies with altitude and latitude, the potential for growth and reproduction varies geographically.

Divergence in behavior or physiology is an additional factor that can contribute to geographic variation in life histories. Intraspecific variation in the growth rates of individuals may result from adaption to local environments. For example, individuals in cooler environments typically grow more slowly than those in warmer environments, but may grow fastest when all populations are reared in a "common garden" environment (reviewed by Arendt 1997). Presumably, a difference in growth observed in a controlled laboratory setting represents divergence in the underlying behavior or physiology. In some cases, higher rates of consumption lead to faster growth (e.g., Billerbeck et al. 2000). In other cases, faster growth results from higher growth efficiency (e.g., Imsland et al. 2000, Jonassen et al. 2000). Even in the absence of genetic divergence, maternal and environmental factors during embryonic development may have long-term effects on the behavior and physiology involved in energy acquisition (Joanen et al. 1987, Burger 1989, Qualls and Shine 1996, Roosenburg and Kelley 1996).

Further consideration of the behavioral and physiological processes that influence energy assimilation would identify additional factors that contribute to geographic variation in the life histories of ectotherms. Both field and laboratory studies are necessary to determine the relative contribution of environmental, behavioral, and physiological constraints on growth. Laboratory studies can identify divergence in behavior and physiology between populations. Field studies can de-

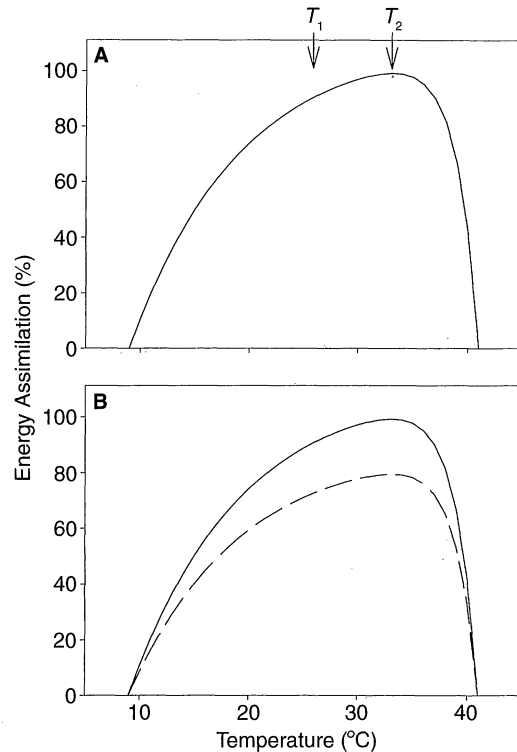


FIG. 1. A larger energy budget can result from (A) an average body temperature that is closer to the optimum temperature for energy assimilation (T_2 vs. T_1), or (B) a higher rate of energy assimilation at all body temperatures. Rates of energy assimilation are depicted in relative terms, as percentages of the maximum.

fine the thermal constraints on behavior and physiology at different localities. The results of these studies can be integrated to explain intraspecific variation in energy budgets. Specifically, relatively fast growth can result from either of two mechanisms: (1) individuals maintain a T_b that is closer to the thermal optimum for energy assimilation (Fig. 1A); or (2) individuals have a physiology that allows them to assimilate more energy at a given T_b (Fig. 1B). Importantly, these two mechanisms are not mutually exclusive.

The eastern fence lizard, *Sceloporus undulatus*, provides an excellent opportunity to study the consequences of an organism's thermal ecology for its life history. *Sceloporus undulatus* ranges over two-thirds of the United States, and life histories differ by as much as twofold between populations (summarized by Tinkle and Dunham 1986, Smith et al. 1996). Lizards in southern populations grow faster and produce more offspring per year than do those in northern populations. Theoretical and empirical work has linked geographic variation in the life history of *S. undulatus* to thermal environments. Grant and Porter (1992) used a biophysical model and climate data to estimate the opportunity for thermoregulation in 11 populations. Annual activity time was correlated with the reproductive

output of females. Additionally, laboratory and field experiments support the notion that the growth of lizards in some populations is limited by thermal constraints on energy assimilation. Supplemental feeding of lizards in New Jersey did not result in faster growth relative to control lizards (Niewiarowski 1995). Moreover, *S. undulatus* matures in 4–5 mo when permitted access to basking sites for 14 h/d, but requires 1–2 yr to mature under natural conditions (Ferguson and Talent 1993).

Although thermal constraints on energy assimilation may be a major source of life history variation in *S. undulatus*, there is some evidence that either behavioral or physiological divergence among populations has occurred. Lizards in South Carolina (SC) grow faster and have a higher reproductive output than lizards in New Jersey (NJ) (Tinkle and Ballinger 1972, Niewiarowski 1994). One is tempted to attribute the greater annual production of SC lizards to their relatively warm environment. However, laboratory studies have shown that lizards from SC gain mass more rapidly than lizards from NJ, even when reared under identical thermal conditions (Niewiarowski 1995). Also, lizards from New Jersey do not grow faster when transplanted to the relatively warm environment of Nebraska (Niewiarowski and Roosenburg 1993). Thus, the life history variation in *S. undulatus* may be caused by divergence in behavior or physiology, as well as geographic variation in the thermal environment.

With this in mind, I used a threefold approach to investigate environmental, behavioral, and physiological constraints on energy assimilation in *S. undulatus*. First, I quantified the thermal sensitivity of energy assimilation by lizards from NJ and SC. Second, I measured thermoregulation in the laboratory and field to assess the consequences of behavior for energy acquisition. Third, I estimated daily and annual constraints on energy acquisition, based on climate data and laboratory measures of energy assimilation. This integration of laboratory and field studies established that both physiological and environmental factors may be important causes of geographic variation in the life history of *S. undulatus*.

METHODS

Thermal sensitivity of energy assimilation

I quantified the thermal sensitivity of energy assimilation in *Sceloporus undulatus* through feeding trials conducted in the laboratory. These trials included lizards from Lebanon State Forest (Burlington County, New Jersey, USA) and the Savannah River Site (Aiken County, South Carolina, USA). All lizards were transported to the University of Pennsylvania, but lizards from NJ were kept in cloth bags for 2 d to mimic the conditions experienced by lizards from SC during transport. Each individual was housed in a 6-L plastic terrarium. Terraria were kept in programmable incu-

bators (Model 818, Precision Scientific, Chicago, Illinois, USA) on a 14:10 light cycle and at a temperature of 33°C during photophase and 20°C during scotophase. Lizards were offered vitamin-dusted crickets, *Acheta domestica*, and water daily.

I measured metabolizable energy intake (MEI) because it is the quantity of energy that can be allocated to maintenance, growth, and reproduction. By definition, MEI is the energy absorbed minus dietary nitrogen (Kleiber 1961). I estimated MEI of lizards as follows:

$$\text{MEI} = C - F - U$$

where C is energy consumed, F is energy lost as feces, and U is energy lost as uric acid. When using this equation to compute MEI, it is assumed that uric acid production is an adequate estimate of dietary nitrogen (i.e., the nitrogen flux of an individual is in equilibrium). This is likely to be a valid assumption because feeding trials lasted ≥ 10 d.

Feeding was conducted at four temperatures: 20°, 30°, 33°, and 36°C. The temperatures 30–36°C span the range of body temperatures of NJ and SC lizards during activity, and 20°C approximates the T_b of NJ lizards at night (Niewiarowski 1992). Feeding trials commenced within 1 wk of collection, and lizards were maintained at their respective treatment temperature for 2 d to allow acclimation to experimental conditions. Because feeding could only be carried out at two temperatures simultaneously, the number of individuals used in each group varied according to the availability of newly captured lizards. In 1995, 48 lizards from NJ were maintained at each of two temperatures, 20° and 33°C (however, 15 of the lizards at 33°C were eliminated from the study because of an incubator malfunction). In 1996, 20 lizards from each population were maintained at 33°C, and 13 and 14 lizards from SC and NJ, respectively, were maintained at 30° and 36°C. A total of 175 lizards, ranging in body mass from 2 g to 12 g, were used in the experiment. Average body mass, 5.4 ± 1.6 g (all descriptive statistics are mean and 95% confidence interval), did not differ significantly among temperature groups ($MS = 8.83$, $F_{2,42} = 1.19$, $P = 0.31$) or between populations ($MS = 8.2$, $F_{1,42} = 2.2$, $P = 0.15$). The sex ratio, 45 males to 55 females, did not deviate significantly from 50:50 ($\chi^2 = 1.0$, $df = 1$, $P = 0.32$).

At the onset of each feeding trial, I measured the passage time of a single marked food item. During the 2-d acclimation period, lizards were fasted to clear their guts of food. After acclimation, each lizard was fed a cricket injected with 100 μL of a slurry containing an indigestible, UV-fluorescent powder (Scientific Marking Materials, Seattle, Washington, USA). The powder associates with feces rather than uric acid (Beaupre et al. 1993), so it provides a reliable estimate of passage time. Lizards that refused to accept a marked cricket within 2–3 d were removed from the experiment. Ter-

riaria were checked for feces at 4-h intervals. If feces were present, the lizard was transferred to an identical clean terrarium and was returned to the incubator immediately. Feces were examined for appearance of the marker. The time at which the first marked feces were discovered was recorded as the passage time for the cricket, and determined the onset of the feeding trial.

Each day, lizards were offered crickets that had been weighed to the nearest 0.1 mg. Lizards were allowed to consume crickets *ad libitum*, except for 15 NJ lizards at 33°C that were restricted to one cricket daily to ensure a broad range of food consumption. Feces and uric acid were collected daily and frozen. Each trial lasted a minimum of 10 d, after which a second marked cricket was fed to each lizard. Passage time was determined a second time and the trial was ended after the appearance of the second marker. By examining feces for markers, I was certain that all feces and urate that I collected were generated from food that was consumed between the first and second marked crickets.

For each lizard, I calculated total consumption of food and production of feces and uric acid during the feeding trial. Energy ingested as food was calculated using a regression model, obtained as follows. Thirty crickets were weighed, dried at 55°C, and weighed again. Linear regression was used to determine the relationship between wet mass and dry mass of crickets (dry mass = 0.25(wet mass); $F_{1,28} = 178.4$, adjusted $r^2 = 0.86$, $P < 0.001$). Dry mass consumed was converted to energy consumption (hereafter referred to as consumption), using an energy density of 25.6 kJ/g (Waldschmidt et al. 1986). Amounts of energy lost as feces and uric acid were determined directly. Feces and uric acid were dried at 55°C and weighed. A subset of samples was combusted for bomb calorimetry (Phillipson 1964). Energy density of feces was not affected by temperature ($MS = 2.28$, $F_{2,12} = 0.48$, $P = 0.63$), and the average energy density of 19.7 kJ/g dry mass was used to calculate feces production. An average energy density of 11.0 kJ/g was used to calculate caloric content of uric acid.

Analysis of covariance (ANCOVA) was used to determine effects of temperature (30°, 33°, and 36°C) and population (NJ and SC) on consumption, passage time, feces production, urate production, and MEI. Because of the incomplete design, data on digestion at 20°C were not included in analyses. Lizards fed a restricted diet were excluded from comparisons of consumption and metabolizable energy intake between populations. Body mass was used as a covariate in all analyses. Consumption was used as an additional covariate in analyses of feces and urate production. Comparison of feces production by ANCOVA allows one to determine whether apparent digestibility coefficients (ADC) differ between NJ and SC lizards without having to analyze ratios (Beaupre and Dunham 1995).

Prior to analyses, data were examined for violations of the assumptions of ANCOVA. First, data were log

transformed to reduce heteroscedasticity. Levene's test was used to assess whether variances were homogeneous among groups. A chi-square goodness-of-fit test was used to examine the assumption of normality. Finally, slopes of the relationship between covariates and dependent variables were examined for homogeneity among treatment groups.

When main effects and interactions were significant, I made unplanned comparisons among means and produced a predictive equation for the dependent variable. Tukey's honest significant difference (hsd) test was used to make pairwise comparisons of group means. Multiple linear regression was used to construct predictive models. Results of ANCOVA were used as a criterion for inclusion in regression models; if a variable had no significant effect on the dependent variable in ANCOVA, it was excluded from the model.

Thermoregulatory behavior

I measured the T_p of lizards from NJ and SC in the spring and summer of 1997. Lizards from NJ and SC were collected on mornings and transported to laboratories at the University of Pennsylvania and Savannah River Site, respectively. Each individual was placed in a thermal gradient at 1500 on the day of collection. A thermal gradient consisted of a 38-L aquarium with a 250-W ceramic heating element (PEARLCO, RAM Network, Reseda, California, USA) positioned above one end. The substrate was ~3 cm of fine sand. Aquaria were kept in a room with an ambient temperature of 24°C, resulting in a stable temperature gradient that ranged from 26° to 38°C (operative temperatures were measured with copper models). A combination of natural and fluorescent lighting was used. Fluorescent lights were turned off at 1800 and lizards remained undisturbed until 0800 the following morning, when the fluorescent lights were turned on. At 1000 and 1400, T_p was measured with a quick-reading cloacal thermometer (T-4000, Miller and Weber, Queens, New York, USA). Lizards were not disturbed prior to or between measures of T_p . Most lizards had food in their stomach and large intestine when placed in the gradient, and all lizards defecated during the morning that T_p was measured. Thus, T_p was measured under fed conditions, which reflects the physiological state of field-active lizards. Analysis of covariance with repeated measures was used to examine the within-subjects effect of time of day (morning vs. afternoon), and the among-subjects effects of season (spring vs. summer) and population on T_p . Body mass was used as a covariate. Unplanned comparisons were made with Tukey's honest significant difference test.

From 1996 to 1998, I measured T_b of field-active lizards in NJ and SC. I walked transects at each study plot in the morning (0800–1200) or afternoon (1400–1800). Most measurements were obtained during the breeding season (April–June), when *S. undulatus* is most conspicuous. Upon sighting a lizard, I attempted

to capture it with the least amount of disturbance. Body temperature was not recorded if excessive chasing (≥ 1 min) was required. Otherwise, T_b was measured to $\pm 0.1^\circ\text{C}$ with a cloacal thermometer, and the time and date were noted. I used ANOVA to examine the effects of time of day (0800–0900, 0900–1000, etc.) and population on T_b . Only data collected on sunny days are presented.

I used the methods outlined by Hertz et al. (1993) to evaluate the accuracy of thermoregulation in *S. undulatus*. The accuracy of thermoregulation (d_b) is the average absolute deviation of T_b from the preferred range (i.e., set point range). This index provides a means of comparing the extent to which body temperatures of NJ and SC lizards correspond to their preferred body temperatures. I defined the set point range as the temperatures bounded by the lower and upper quartiles of T_p . Average d_b was determined for each hour, and a t test was used to compare the hourly means of NJ vs. SC lizards. Prior to analysis, the Shapiro-Wilks' W test was used to assess the normality of the distributions of T_b .

Activity time and energy budgets

I used a biophysical model to estimate the maximum duration of daily and annual activity of lizards in NJ and SC. The model combines the microclimate program of McCullough and Porter (1971) and the ectotherm program of Grant and Porter (1992) to estimate the number of hours per day that an individual can maintain its T_b within a preferred range. All model parameters were specified as in Adolph and Porter (1996), except that monthly air temperatures and relative humidities for NJ and SC sites were obtained from the National Climate Data Center (Asheville, North Carolina, USA). The programs calculate thermal properties of both the environment and a lizard in that environment. For example, the microclimate program outputs the intensity of solar radiation and a soil temperature profile for each hour of the day. The ectotherm program uses output from the microclimate model to determine how many hours of the day an ectotherm can maintain its T_p (hereafter referred to as daily activity time). Because climate data used by the microclimate program are average monthly values, daily activity time is calculated for an average day of each month of the year.

I used the model output to estimate the maximum duration of activity for a year (hereafter referred to as annual activity time). In doing so, I adjusted daily activity times calculated by the model for overestimation of activity. For example, an individual can attain its T_p above the surface in winter months, but the soil temperature is too cold to induce surface activity. Because *S. undulatus* burrows during inactivity, I reasoned that the soil temperature must reach a threshold before individuals will initiate activity on a given day. The lowest T_b values recorded for a lizard active on the surface were 20.8° and 20.0°C for NJ and SC lizards, respec-

tively. Therefore, I assumed that lizards would not become active each day until surface soil temperature reached a minimum of 20°C . For each month, I totaled the number of hours that a lizard could achieve T_p per day after the onset of activity. By summing these hours over an entire year, I arrived at an estimate of annual activity time.

Data on MEI field-active T_b , and activity time were used to estimate energy budgets of NJ and SC lizards. To calculate energy budgets from maximum annual activity, it was necessary to make the following assumptions: (1) lizards were active if they could maintain their T_p ($\pm 1^\circ\text{C}$); (2) the rate of MEI observed in the laboratory was equivalent to the maximum rate of energy assimilation in natural populations; (3) during months in which activity was predicted, lizards maintained T_p during activity and a T_b of 20°C during inactivity (Niewiarowski 1992); and (4) food was not limiting in either NJ or SC. The fourth assumption is supported by the results of food supplementation experiments conducted in the NJ population (Niewiarowski 1995). Even if this assumption were not valid for both populations, my calculations would still define maximum values for daily and annual energy budgets.

RESULTS

Thermal sensitivity of energy assimilation

Consumption was strongly affected by body mass and temperature (Table 1). Not surprisingly, consumption was positively correlated with body mass ($MS = 4245$, $F_{1,41} = 47.1$, $P < 0.000001$). Although the percentage of lizards that completed the feeding trials (44%) did not differ among temperatures ($\chi^2 = 0.58$, $df = 3$, $P = 0.90$), consumption per lizard was highly dependent on temperature ($MS = 1028$, $F_{2,41} = 11.4$, $P = 0.0001$). For lizards that were fed ad libitum, consumption differed significantly among 20° ($94 \pm 16 \text{ J}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$), 30° ($270 \pm 74 \text{ J}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$), and 33°C ($511 \pm 73 \text{ J}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$), but did not differ significantly between 33° and 36°C ($421 \pm 56 \text{ J}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$). Lizards from NJ and SC did not differ in their consumption ($MS = 54.0$, $F_{1,41} = 0.60$, $P = 0.44$), and no interaction between temperature and population was observed ($MS = 54.3$, $F_{2,41} = 0.60$, $P = 0.55$). Digestive data for 1995 and 1996 were pooled because no significant differences in consumption ($MS = 0.02$, $F_{1,23} = 0.47$, $P = 0.50$), feces production ($MS = 0.04$, $F_{1,23} = 0.74$, $P = 0.40$), or urate production ($MS = 0.001$, $F_{1,23} = 0.02$, $P = 0.88$) of NJ lizards were found between years.

A relatively short passage time for food must have contributed to greater consumption at high temperatures. Passage time decreased significantly with increasing temperature ($MS = 0.14$, $F_{2,50} = 7.22$, $P = 0.002$). Passage time for a single cricket was 122 ± 18 h at 20°C , 47 ± 9 h at 30°C , 35 ± 5 h at 33°C , and 27 ± 5 h at 36°C . Passage time did not vary within individuals ($t = 0.81$, $df = 39$, $P = 0.42$), and was not

TABLE 1. Regression analyses of the effects of temperature (T), consumption (C), and body mass (M) on passage time, feces production, and urate production in the lizard *Sceloporus undulatus*.

Variable	Model	df	F	P	Adjusted
Passage time (h)	$-20.59(T) + 0.26(T^2) + 428.86$	2, 1	10 889	0.007	0.99
Feces (kJ)					
20°C	$0.13(C) + 0.34$	1, 18	26.13	0.000	0.57
30°C	$0.14(C) + 0.19$	1, 9	43.89	0.000	0.81
33°C (NJ)	$0.06(C) + 0.87(M) - 1.37$	2, 22	31.44	0.000	0.72
33°C (SC)	$0.07(C) + 0.10(M) + 0.43$	2, 6	10.77	0.010	0.71
36°C	$0.24(C) - 1.56$	1, 11	47.97	0.000	0.80
Uric acid (kJ)					
20°C	$0.03(C) + 0.10(M) - 0.06$	2, 17	30.06	0.000	0.75
30°C	$0.11(C) + 0.30$	1, 9	74.52	0.000	0.88
33°C	$0.06(C) + 0.30(M) + 0.004$	2, 31	102.94	0.000	0.86
36°C	$0.09(C) + 0.68$	1, 11	161.21	0.000	0.93

Notes: Only variables that were significant in the ANCOVA were included in the models. Consumption and body mass were expressed in kJ and g, respectively.

affected by consumption ($MS = 0.01$, $F_{2,50} = 0.58$, $P = 0.56$). Passage time did not differ between NJ and SC lizards ($MS = 0.008$, $F_{1,50} = 0.43$, $P = 0.51$), and no interaction between temperature and population was observed ($MS = 0.02$, $F_{2,50} = 0.85$, $P = 0.43$). The relationship between temperature and passage time was nonlinear, and a second-order regression model described 99% of the variation in passage time (Table 1).

Metabolizable energy intake was extremely sensitive to temperature ($MS = 813$, $F_{2,41} = 12.4$, $P < 0.0001$), and the pattern of sensitivity was consistent between populations (no interaction effect: $MS = 50.0$, $F_{2,41} = 0.76$, $P = 0.47$). Metabolizable energy intake at 33°C was significantly greater than MEI at 30° and 36°C (Fig. 2). Unplanned comparisons revealed that the MEI of SC lizards (34.7 ± 6.8 kJ) was significantly greater than that of NJ lizards (23.2 ± 6.1 kJ) at 33°C (Tukey's hsd test, $P < 0.05$). Thus, MEI for both NJ and SC lizards was maximized at 33°C, but maximum MEI of SC lizards was greater than that of NJ lizards.

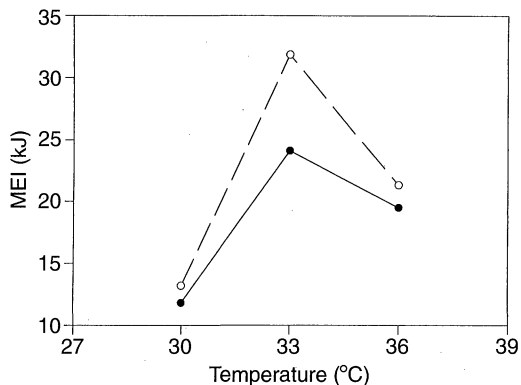


FIG. 2. Metabolizable energy intake (MEI) was very sensitive to body temperature in the fence lizard, *Sceloporus undulatus*. At 33°C, the MEI of lizards from South Carolina (open circles) was significantly greater than that of lizards from New Jersey (solid circles). Data are adjusted means derived from ANCOVA.

The difference in maximum MEI between NJ and SC lizards resulted from a higher efficiency of digestion or absorption by SC lizards. ANCOVA was used to compare feces and urate production by NJ and SC lizards at each temperature, because slopes of the relationships between covariates and dependent variables were not homogeneous among temperatures (see Table 1). Data for 1995 and 1996 were pooled because no significant difference in feces production of NJ lizards was found between years ($MS = 0.04$, $F_{1,23} = 0.74$, $P = 0.40$). After adjusting for body mass and consumption, feces production by NJ lizards at 33°C (4.68 kJ) was significantly greater ($MS = 0.25$, $F_{1,30} = 22.8$, $P < 0.0001$) than that of SC lizards at the same temperature (2.75 kJ). This result supports the conclusion that digestion or absorption by SC lizards was more efficient at 33°C. In fact, ADC of SC lizards at 33°C was higher than that of NJ lizards (Tables 2 and 3). However, no significant difference in feces production was observed between populations at 30° ($MS = 0.00$, $F_{1,7} = 0.04$, $P = 0.84$) or 36°C ($MS = 0.04$, $F_{1,9} = 2.36$, $P = 0.16$). Urate production, adjusted for body mass and consumption, did not differ significantly between populations at 30° ($MS = 0.00$, $F_{1,7} = 0.20$, $P = 0.67$), 33° ($MS = 0.00$, $F_{1,30} = 1.65$, $P = 0.21$), or 36°C ($MS = 0.00$, $F_{1,9} = 2.13$, $P = 0.18$). Therefore, the greater MEI of SC lizards at 33°C was caused mainly by a higher ADC.

Thermoregulatory behavior

Preferred body temperatures of NJ and SC lizards were always very close to the thermal optimum for MEI. Preferred body temperature did not differ significantly between NJ and SC lizards (Table 4), with the average T_p of NJ lizards being 32.8°C ($n = 31$) and that of SC lizards being 32.9°C ($n = 26$). The T_p of NJ lizards was significantly higher in the summer ($34.0 \pm 1.0^\circ\text{C}$, $n = 11$) than in the spring ($31.5 \pm 1.0^\circ\text{C}$, $n = 21$), but no seasonal effect on the T_p of SC lizards was found ($32.6 \pm 1.2^\circ\text{C}$ and $33.2 \pm 0.8^\circ\text{C}$ for spring and

TABLE 2. Results of feeding trials in *Sceloporus undulatus* from New Jersey held at constant temperatures.

Treatment	<i>n</i>	Duration (d)	Mass (g)	<i>C</i> (kJ)	<i>F</i> (kJ)	<i>U</i> (kJ)	ADC† (%)	MEC† (%)
20°C	20	14 ± 1	4.6 ± 0.7	6.4 ± 2.0	1.0 ± 0.3	0.6 ± 0.2	82 ± 6	71 ± 8
30°C	3	13 ± 1	3.2 ± 6.6	9.1 ± 8.3	1.1 ± 0.8	1.2 ± 0.6	87 ± 10	72 ± 18
33°C								
ad libitum	15	14 ± 1	4.8 ± 1.0	29.7 ± 7.3	3.4 ± 0.9	3.2 ± 0.7	88 ± 3	77 ± 4
restricted	10	15 ± 0	4.0 ± 1.5	20.6 ± 5.2	3.3 ± 2.0	2.3 ± 0.9	86 ± 5	75 ± 6
36°C	8	12 ± 1	6.5 ± 4.5	32.5 ± 18.8	5.6 ± 4.1	3.6 ± 1.7	84 ± 4	72 ± 5

Note: Consumption (*C*), feces production (*F*), and urate production (*U*) of lizards are reported as mean and 95% confidence interval.

† Apparent digestibility coefficient (ADC) and metabolizable energy coefficient (MEC) are reported for comparison with other studies.

summer, respectively; *n* = 13 in each season). Time of day did not influence the *T_p* of lizards from either population.

Field body temperatures corresponded well with preferred body temperatures. Lizards in both populations maintained a relatively high and constant *T_b* throughout the day (Fig. 3; effect of time: *ms* = 9.17, *F*_{8,461} = 1.49, *P* = 0.16). Overall, the average *T_b* of NJ lizards (34.0 ± 0.3°C, *n* = 243) was higher than that of SC lizards (33.1 ± 0.4°C, *n* = 242), but body temperatures of NJ and SC lizards did not differ significantly at any specific hour (Tukey's *hsd* test, all *P* > 0.05). Although *T_p* of NJ lizards varied significantly between spring and summer, there was a remarkable similarity between average *T_b* of NJ lizards in spring (33.8°C) and summer (34.0°C). Lizards in New Jersey thermoregulated more accurately (*t* = -2.58, *df* = 16, *P* = 0.02) than those in South Carolina (*d_b* = 0.8 ± 0.3°C and 1.5 ± 0.4°C for NJ and SC lizards, respectively). Even so, lizards from both populations maintained body temperatures that were very close to *T_p* (Fig. 4).

Activity time and energy budgets

Activity times predicted by the biophysical model were in accord with activities observed in the field (Table 5). The model predicted that daily activity time of SC lizards in spring would be 2 h longer than daily activity time of NJ lizards, and I observed that SC lizards were active for 1.5 h longer. Also, the model predicted no difference in daily activity time in summer; a difference of only 0.2 h was observed. Although there were discrepancies between predicted and observed activity (particularly in summer), daily activity predicted by the model was always equal to or greater than that observed in the field. This result is consistent with the notion that the model calculated the maximum

duration of activity by a lizard. Additionally, annual activity times corresponded well to qualitative expectations. Lizards in SC were predicted to become active in March and cease activity in November, whereas lizards in NJ were predicted to become active in April and cease activity in October. These patterns of annual activity were observed in the SC and NJ populations of *S. undulatus* during this study. Given the qualitative match between activity predicted by the biophysical model and activity observed in the field, I considered activity times predicted by the model to be useful for estimating energetics of field-active lizards in these populations.

Annual energy budgets of SC lizards were ~60% larger than those of NJ lizards because of their longer activity time at *T_p* and greater MEI (Table 5). Lizards in SC were active for a longer daily duration in spring, but observed activity was similar between NJ and SC lizards in summer (Table 5). Daily energy budgets for SC lizards were 28% and 16% larger than NJ lizards in spring and summer, respectively (Table 5). The combined effects of an additional 1.5 h of activity and a higher digestive efficiency account for the greater difference in daily MEI in spring, whereas digestive efficiency accounts for most of the difference in daily MEI in summer. Maximum annual activity at *T_p* is the same for juvenile and adult lizards (model output was not sensitive to body size in the range considered), but was greater for SC lizards (2632 h) than for NJ lizards (1864 h). Based on these annual activity times, estimates of annual MEI for NJ and SC juveniles were 104 kJ and 165 kJ, respectively, whereas those for NJ and SC adults were 310 kJ and 495 kJ, respectively. The longer annual activity time and the higher digestive efficiency of SC lizards each account for a large per-

TABLE 3. Results of feeding trials in *Sceloporus undulatus* from South Carolina held at constant temperatures.

Treatment	<i>n</i>	Duration (d)	Mass (g)	<i>C</i> (kJ)	<i>F</i> (kJ)	<i>U</i> (kJ)	ADC† (%)	MEC† (%)
30°C	8	13 ± 1	6.0 ± 2.5	19.4 ± 8.0	2.4 ± 1.0	2.4 ± 0.9	88 ± 2	75 ± 2
33°C	9	12 ± 1	6.5 ± 0.8	42.0 ± 7.7	3.2 ± 0.5	4.1 ± 0.6	92 ± 1	82 ± 1
36°C	5	13 ± 0	6.7 ± 4.3	31.8 ± 13.9	4.1 ± 2.7	3.3 ± 1.2	87 ± 4	77 ± 3

Note: Consumption (*C*), feces production (*F*), and urate production (*U*) are reported as mean and 95% confidence interval.

† Apparent digestibility coefficient and metabolizable energy coefficient are reported for comparison with other studies.

TABLE 4. ANCOVA for the effects of population, season, and time of day on the preferred body temperature of *Sceloporus undulatus*.

Source	df	MS	F	P
A) Between-subjects effects				
Population	1, 52	3.04	0.41	0.52
Season	1, 52	41.85	6.61	0.02
Population × Season	1, 52	7.45	2.78	0.10
B) Within-subjects effects				
Time of day	1, 53	7.45	1.30	0.26
Time × Population	1, 53	5.33	0.93	0.34
Time × Season	1, 53	2.45	0.43	0.52
Time × Population × Season	1, 53	2.64	0.46	0.50

centage of the difference between the energy budgets of SC and NJ lizards.

DISCUSSION

Metabolizable energy intake is a function of consumption, apparent digestibility, and urate production, each of which covaried with temperature in a unique way. In *Sceloporus undulatus*, the combination of these variables resulted in a nonlinear relationship between temperature and MEI, with MEI increasing from 30° to 33°C, but decreasing from 33° to 36°C (Fig. 2). Temperature exerts much of its effects on MEI by influencing the propensity to feed. As reported for other species (e.g., Dutton et al. 1975, Waldschmidt et al. 1986, Van Damme et al. 1991), I found that consumption increased nonlinearly with increased temperature. Two mechanisms may be responsible for the greater consumption at higher temperatures. First, temperature influences the performance of activities associated with feeding (Bennett 1990). For example, sprint speed in-

creased and capture and handling time decreased with increasing T_b in *Lacerta vivipara* (Van Damme et al. 1991). Speed of striking and success at capturing prey increased with increasing T_b in the gopher snake *Pituophis catenifer* (Greenwald 1974). Furthermore, performance seems to have an asymptotic relationship with temperature, similar to that observed for consumption; no significant variation in capture and handling time was noted above 30°C in *L. vivipara* (Van Damme et al. 1991). It is possible that temperature-induced constraints on locomotion contributed to the significant difference in consumption between lizards at 20° and 30°C. It is more likely, however, that passage time limits consumption at low temperatures. Because ingestion is limited by gut capacity, an environment that favors rapid passage of food would allow a higher rate of feeding. The shorter passage time at 33°C relative to 30°C was associated with greater consumption. However, lizards did not consume more food at 36°C

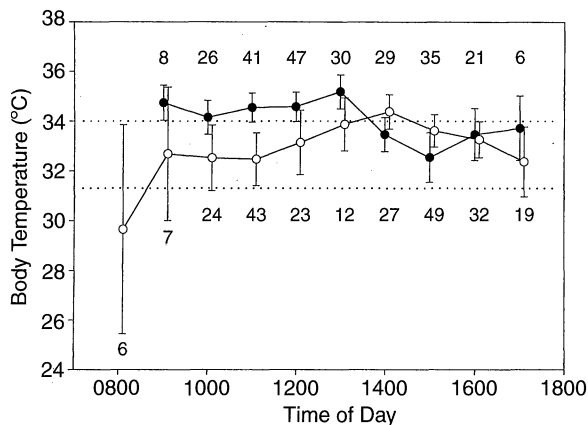


FIG. 3. Fence lizards in New Jersey (solid circles) and South Carolina (open circles) maintained relatively high and constant body temperatures from morning until evening. Error bars denote the 95% confidence intervals of the means. The dotted lines mark the upper and lower bounds of the set point range (central 50% of preferred body temperatures). The top and bottom rows of numbers contain sample sizes for lizards from New Jersey and South Carolina, respectively. Field body temperatures did not differ significantly between populations at any time period (Tukey's hsd test, all $P > 0.05$).

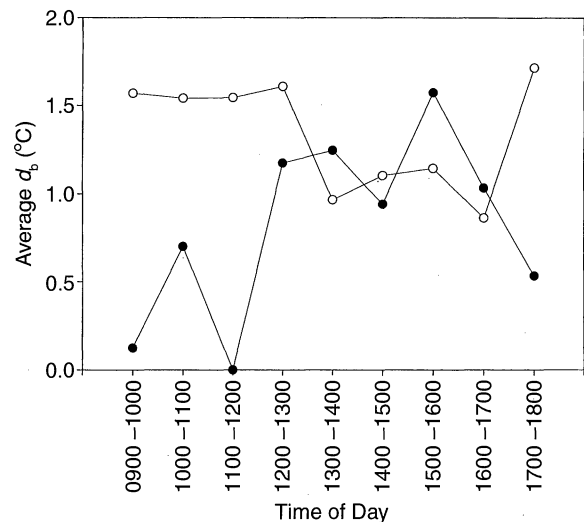


FIG. 4. Fence lizards in New Jersey (solid circles) thermoregulated more accurately than did lizards in South Carolina (open circles). Accuracy of thermoregulation (d_b) was defined as the average absolute deviation between field body temperature and the set point range (central 50% of preferred body temperatures).

TABLE 5. Duration of daily activity in New Jersey (NJ) and South Carolina (SC) populations of *Sceloporus undulatus* based on earliest and latest observations in the field.

Season	Observed activity (h)				Estimated activity			Daily MEI† (J)	
	n	Earliest	Latest	Duration	Time of day		Duration (h)	Juvenile	Adult
					Earliest	Latest			
Spring									
NJ	10	1024	1706	6.7	1100	1800	7	431	1292
SC	28	0930	1739	8.2	0900	0900	9	551	1653
Summer									
NJ	36	0920	1753	8.6	0800	2000	12	499	1498
SC	9	0841	1728	8.8	0800	2000	12	580	1740

Notes: For comparison, the maximum daily activity estimated by a biophysical model (Grant and Porter 1992) is reported. For spring and summer, the number of days on which observations were made (*n*) is given.

† Observed activity was used to calculate daily MEI for a 3-g juvenile and a 9-g adult. For details, see *Methods: Activity time and energy budgets*.

than at 33°C, even though passage time at 36°C was even shorter.

Thermoregulatory behavior is thought to be influenced by the thermal sensitivity of physiological performance (Bennett 1980, Huey and Bennett 1987, Huey et al. 1989). Because the resting metabolic rate of *S. undulatus* is relatively insensitive to temperature (Angilletta 2001), net energy assimilation is maximized at the thermal optimum for MEI. If individuals prefer a body temperature that is close to the thermal optimum for MEI, then thermoregulatory behaviors should enhance energy acquisition in natural populations (van Marken Lichtenbelt et al. 1997). In *S. undulatus*, the close match between the T_p and the thermal optimum for MEI suggests that lizards place a premium on physiological processes that pertain to energy acquisition. Moreover, individuals in both populations used behavioral thermoregulation to enhance MEI. Even though average air temperature in South Carolina was consistently 5–10°C warmer than that in New Jersey (National Climate Data Center, unpublished data), field body temperatures of SC and NJ lizards did not differ significantly. During activity, lizards maintained a T_b within 2°C of T_p (Fig. 4). Consequently, average T_b of field-active lizards corresponded extremely well to the thermal optimum for MEI. Similar field body temperatures have been observed in other populations of *S. undulatus*. In Nebraska, the T_b of *S. undulatus* averaged 33.7 ± 0.3°C (P. H. Niewiarowski, personal communication). In southwestern Utah, *S. undulatus* had an average T_b of 32.7°C (Grover 1996). The homogeneity of field body temperatures among populations indicates that lizards can thermoregulate accurately in a wide range of thermal environments. In fact, behavioral compensation for altitudinal or latitudinal variation in the thermal environment is common (Hertz 1981, Hertz and Huey 1981, Adolph 1990, Díaz 1997, Schwarzkopf 1998). In this case, the high accuracy of thermoregulation allows lizards in different environments to assimilate energy at a relatively high rate. Because ec-

otherms grow faster when permitted to thermoregulate (reviewed by Waldschmidt et al. 1987, Sinervo and Adolph 1989, 1994, Autumn and DeNardo 1995), many species may prefer body temperatures that enhance energy assimilation.

The life history of *S. undulatus* varies considerably among populations, and much of this variation is believed to be induced by the thermal environment (Niewiarowski 1994). Maximum activity time predicted through biophysical modeling is correlated with age at maturity, adult body size, and annual reproductive output (Grant and Porter 1992, Adolph and Porter 1993, 1996). Experimental evidence corroborates the predictions of biophysical models. Niewiarowski (2001) estimated that lizards in Nebraska (NE) can maintain T_p for up to 3 h longer than lizards in NJ each day, and that this difference in activity time corresponds to a larger annual production budget for NE lizards. Niewiarowski and Roosenburg (1993) transplanted hatchlings from NE to NJ, and observed slow growth in transplanted hatchlings relative to hatchlings that remained in NE. However, hatchlings transplanted from NJ to NE did not grow faster than those that remained in NJ. Similarly, “common garden” studies have revealed apparently genetic bases for intraspecific variation in life histories of *Sceloporus* lizards (Sinervo 1990, Ferguson and Talent 1993, Sinervo and Adolph 1994, Niewiarowski 1995). Genetic divergence in behavior and physiology among populations may be just as important as environmental factors in producing geographic variation in the life history of *S. undulatus* (Niewiarowski 1994).

The relatively high annual production of *S. undulatus* in South Carolina results, in part, from more opportunities for thermoregulation. Specifically, the energy budgets of SC lizards would exceed those of NJ lizards if SC lizards are either active at a T_b that is closer to the T_p (i.e., higher accuracy of thermoregulation) or maintain their T_p for a longer period of time. The former scenario is unlikely because the thermoregulation in *S.*

undulatus is extremely accurate. The latter scenario is very plausible. Despite the high accuracy of thermoregulation in *S. undulatus*, the temporal and spatial availability of suitable microclimates should influence the energetics and life history of this species. Energetic benefits of increased activity time may be mediated by a longer duration of activity at the thermal optimum on a daily and seasonal basis, rather than by differences in the accuracy of thermoregulation during activity. Daily and annual activity times for NJ and SC lizards indicate that intraspecific variation in the energetics of *S. undulatus* is affected by differences in activity time among populations. Lizards from South Carolina had a longer daily activity time in spring; presumably, the same is true for fall. The longer daily activity time of SC lizards in spring would result in a daily MEI that is 28% greater than that of NJ lizards (Table 5). Additionally, lizards in SC become active one month earlier and cease activity one month later than lizards in NJ (see *Results*). The greater duration of annual activity by SC lizards can account for up to 38% more metabolizable energy per year. Given that lizards thermoregulate accurately at a T_p that maximizes MEI, these differences in activity time would account for the greater annual production of SC lizards.

Intraspecific variation in digestive physiology may play a significant role in producing geographic variation in the growth and reproduction of *S. undulatus*. Metabolizable energy intake of SC lizards at 33°C was significantly greater than that of NJ lizards. The difference in MEI resulted from the higher ADC of SC lizards, because the production of feces at 33°C was greater for NJ lizards than it was for SC lizards. Because feces production was adjusted for body mass and consumption before comparison, the difference in feces production between populations was due to divergence in physiology between populations. Differences in ADC between populations have been documented previously (e.g., Beupre and Dunham 1995, Khokhlova et al. 1997, Kirkwood and Robertson 1997), but in this case there is a clear link between differentiation of digestive physiology and a difference in the energy budgets of individuals in these populations. As a result of the difference in ADC at 33°C, the MEI of lizards from SC was 32% greater than that of NJ lizards (Fig. 2). Furthermore, the higher rate of MEI for SC lizards at T_p amplifies the effect of the longer activity season in SC on the difference between energy budgets of NJ and SC lizards. For example, a NJ lizard in the SC environment would assimilate 39% more energy per year than a NJ lizard in the NJ environment. However, a SC lizard in the SC environment would assimilate 60% more energy per year than a NJ lizard in the NJ environment. Therefore, digestive physiology partially explains the greater annual growth and reproduction exhibited by lizards in SC.

Why is the digestive efficiency of SC lizards higher than that of NJ lizards? One possible explanation is

that the higher digestive efficiency of SC lizards is actually a consequence of a "fast growth" strategy (Arendt 1997). Growth hormone increases intestinal mass and absorption capacity in vertebrates (Stevens et al. 1999, Stevens and Devlin 2000), so fast growth should be associated with relatively high digestive efficiency. Therefore, the relatively fast growth of SC lizards caused by longer daily activity at T_p may enhance digestive performance and further amplify differences in growth between populations. Why does natural selection not favor the evolution of increased digestive efficiency in NJ lizards to compensate for the shorter activity season? There is some evidence that a fixed strategy of slow growth has been favored in the NJ population (Niewiarowski 2001). First, hatchling lizards transplanted from NJ to NE do not grow faster even though the NE environment permits an additional 2 h of activity at T_p per day (Niewiarowski and Roosenburg 1993). Also, hatchlings from NJ that are reared in the laboratory with unlimited food and exposure to a heat source for 14 h/d do not grow faster than hatchlings in the natural population (Niewiarowski 1995). Slow growth would be associated with lower levels of growth hormone; therefore, one might expect the digestive performance of NJ lizards to be relatively poor. Although a significant difference in fecal production was detected only at 33°C, SC lizards tended to have a higher ADC than NJ lizards at 30° and 36°C as well (Tables 2 and 3). It is possible that the apparent digestibility in SC lizards is generally higher than that in NJ lizards, but that low statistical power prevented me from detecting significant differences at all temperatures. Additional studies to determine whether growth in body length or mass is related to enhanced digestive performance in lizards would help to evaluate the plausibility of this mechanism for differences in ADC between populations.

My conclusions about the relative contributions of environmental and physiological constraints on energy assimilation to the difference in annual production between populations of *S. undulatus* are based on estimates of energy assimilation by field-active lizards. Thus, it is necessary to consider potential sources of error in these estimates. Data on digestibility are likely to be accurate for lizards feeding on adult insects, the major prey of both NJ and SC lizards (M. J. Angilletta, Jr., *unpublished data*), because measures of digestive performance were made within one week of capture. However, the use of lab measures of MEI to estimate energy assimilation in nature relies on several assumptions. First, I assumed that neither population of *S. undulatus* was food limited. Although results of supplemental feeding studies support this assumption for NJ lizards (Niewiarowski 1995), there is no direct evidence to support the same assumption for SC lizards. However, food limitation of SC lizards would not contribute to greater annual production by SC lizards; therefore, thermal and physiological constraints on di-

gestion would be even more important to understanding intraspecific variation in annual production if SC lizards were food limited and NJ lizards were not. Second, I assumed that body temperature during inactivity was 20°C for lizards in both populations. This assumption is almost certainly violated. Soil temperatures in SC are warmer than those in NJ, but this difference is usually a few degrees (e.g., minima for soil temperatures in NJ and SC during June are 17.7°C and 21.5°C, respectively). By assuming the same nighttime body temperature for NJ and SC lizards, I may have overestimated energy assimilation by NJ lizards, although the very low passage rate at 20°C (122 ± 18 h for a single cricket) would minimize the magnitude of error caused by this violation. Third, I assumed that digestive performance at constant temperatures can be used to predict performance under the diel cycles of temperature experienced by individuals in nature. Although there are no data to evaluate the validity of this assumption, variation in temperature should not alter my conclusions qualitatively. Lizards in both populations experienced similar diel cycles of temperature, so the relative difference in energy assimilation should be accurate.

The absolute values of estimated energy budgets in *S. undulatus* are comparable to those for similar-sized lizards. For three species of iguanian lizards, Congdon et al. (1982) reported annual MEI of adults that ranged from 215 to 465 kJ. In comparison, I estimated annual MEI to be 310 kJ and 495 kJ for adults of *S. undulatus* from NJ and SC, respectively. My values of annual energy assimilation for juveniles of *S. undulatus* are certain to be underestimates because I assumed a constant body mass of 3 g, whereas juveniles are growing rapidly during the year. However, my estimates for juveniles compare favorably to those calculated for adults of smaller species of lizards. For example, Nagy (1983) used a combination of lab and field methods to estimate annual energy assimilation in adults of *Uta stansburiana* (body mass = 2.6–3.3 g). Nagy's values of 132–149 kJ for *U. stansburiana* are similar to my estimates of 104 and 165 kJ for juveniles of *S. undulatus* from NJ and SC, respectively. Given these considerations, conclusions that I have drawn from comparison of energy budgets in *S. undulatus* should be valid.

The role of physiology in generating geographic variation in life histories is less understood than that of the environment, perhaps because data on the extent of physiological divergence between populations are rarely available (Garland and Adolph 1991). Environmental factors, such as temperature and food availability, have been posited to be the proximate causes of geographic variation in the life history of *S. undulatus* (Niewiarowski 1994). In fact, biophysical models used to draw inferences about the proximate causes of life history variation in *S. undulatus* assume that no divergence in physiology among populations has occurred (Grant and Porter 1992, Adolph and Porter 1993,

1996). I have demonstrated that both environmental and physiological factors determine energy assimilation in *S. undulatus*. A difference in digestive efficiency between populations compounds the effect of the thermal environment. This result underscores the importance of considering multiple causality when investigating ecological phenomena (Quinn and Dunham 1983). A more complete understanding of the proximate causes of life history variation will aid efforts to explain the evolution of life histories in *S. undulatus* and other geographically widespread ectotherms.

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LITERATURE CITED

- Adolph, S. C. 1990. Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology* **71**: 315–327.
- Adolph, S. C., and W. P. Porter. 1993. Temperature, activity, and lizard life histories. *American Naturalist* **142**:273–295.
- Adolph, S. C., and W. P. Porter. 1996. Growth, seasonality, and lizard life histories: age and size at maturity. *Oikos* **77**: 267–278.
- Angilletta, M. J., Jr. 2001. Variation in metabolic rate between populations of a geographically widespread lizard. *Physiological and Biochemical Zoology* **74**:11–21.
- Arendt, J. D. 1997. Adaptive intrinsic growth rates: an integration across taxa. *Quarterly Review of Biology* **72**:149–177.
- Atkinson, D. 1994. Temperature and organism size—a biological law for ectotherms? *Advances in Ecological Research* **25**:1–58.
- Atkinson, D., and R. M. Sibly. 1997. Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends in Ecology and Evolution* **12**: 235–239.
- Autumn, K., and D. F. DeNardo. 1995. Behavioral thermoregulation increases growth rate in a nocturnal lizard. *Journal of Herpetology* **29**:157–162.
- Avery, R. A. 1982. Field studies of body temperatures and thermoregulation. Pages 93–166 in C. Gans and F. H. Pough, editors. *Biology of the Reptilia*. Volume 12. Academic Press, New York, New York, USA.
- Ayers, D. Y., and R. Shine. 1997. Thermal influences on foraging ability: body size, posture and cooling rate of an

- ambush predator, the python *Morelia spilota*. *Functional Ecology* **11**:342–347.
- Bartholomew, G. A. 1982. Physiological control of body temperature. Pages 167–211 in C. Gans and F. H. Pough, editors. *Biology of the Reptilia*. Volume 12. Academic Press, New York, New York, USA.
- Bashey, F., and A. E. Dunham. 1997. Elevational variation in the thermal constraints on and microhabitat preferences of the greater earless lizard *Cophosaurus texanus*. *Copeia* **1997**:725–737.
- Beaupre, S. J. 1995. Effects of geographically variable thermal environment on bioenergetics of mottled rock rattlesnakes. *Ecology* **76**:1655–1665.
- Beaupre, S. J., and A. E. Dunham. 1995. A comparison of ratio-based and covariance analyses of a nutritional data set. *Functional Ecology* **9**:876–880.
- Beaupre, S. J., A. E. Dunham, and K. L. Overall. 1993. The effects of consumption rate and temperature on apparent digestibility coefficient and passage time in canyon lizards (*Sceloporus merriami*) from two populations. *Functional Ecology* **7**:273–280.
- Bennett, A. F. 1980. The thermal dependence of lizard behaviour. *Animal Behaviour* **28**:752–762.
- Bennett, A. F. 1990. Thermal dependence of locomotor capacity. *American Journal of Physiology* **250**:R253–R258.
- Billerbeck, J. M., E. T. Schultz, and D. O. Conover. 2000. Adaptive variation in energy acquisition and allocation among latitudinal populations of the Atlantic silverside. *Oecologia* **122**:210–219.
- Blackenhorn, W. U., R. F. Preziosi, and D. J. Fairbairn. 1995. Time and energy constraints and the evolution of sexual size dimorphism—to eat or to mate? *Evolutionary Ecology* **7**:369–381.
- Burger, J. 1989. Incubation temperature has long-term effects on behaviour of young pine snakes (*Pituophis melanoleucus*). *Behavioral Ecology and Sociobiology* **24**:201–207.
- Casey, T. M. 1981. Behavioral mechanisms of thermoregulation. Pages 79–114 in B. Heinrich, editor. *Insect thermoregulation*. John Wiley, New York, New York, USA.
- Congdon, J. D. 1989. Proximate and evolutionary constraints on energy relations in reptiles. *Physiological Zoology* **62**:356–373.
- Congdon, J. D., A. E. Dunham, and D. W. Tinkle. 1982. Energy budgets and life histories of reptiles. Pages 233–271 in C. Gans and F. H. Pough, editors. *Biology of the Reptilia*. Volume 13. Academic Press, New York, New York, USA.
- Crowley, S. R. 1985. Thermal sensitivity of sprint-running in the lizard *Sceloporus undulatus*: support for a conservative view of thermal physiology. *Oecologia* **66**:219–225.
- Díaz, J. A. 1997. Ecological correlates of the thermal quality of an ectotherm's habitat: a comparison between two temperate lizard populations. *Functional Ecology* **11**:79–89.
- Dunham, A. E., B. W. Grant, and K. L. Overall. 1989. The interface between biophysical ecology and the population ecology of terrestrial vertebrate ectotherms. *Physiological Zoology* **62**:335–355.
- Dutton, R. H., L. C. Fitzpatrick, and J. L. Hughes. 1975. Energetics of the rusty lizard *Sceloporus olivaceus*. *Ecology* **56**:1378–1387.
- Ferguson, G. W., and L. G. Talent. 1993. Life-history traits of the lizard *Sceloporus undulatus* from two populations raised in a common laboratory environment. *Oecologia* **93**:88–94.
- Gadgil, M., and W. H. Bossert. 1970. Life historical consequences of natural selection. *American Naturalist* **104**:1–24.
- Garland, T., and S. C. Adolph. 1991. Physiological differentiation of vertebrate populations. *Annual Review of Ecology and Systematics* **22**:193–228.
- Grant, B. W., and A. E. Dunham. 1988. Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology* **69**:167–176.
- Grant, B. W., and A. E. Dunham. 1990. Elevational covariation in environmental constraints and life histories of the desert lizard, *Sceloporus merriami*. *Ecology* **71**:1765–1776.
- Grant, B. W., and W. P. Porter. 1992. Modeling global macroclimatic constraints on ectotherm energy budgets. *American Zoologist* **32**:154–178.
- Greenwald, O. E. 1974. Thermal dependence of striking and prey capture by gopher snakes. *Copeia* **1974**:141–148.
- Grover, M. C. 1996. Microhabitat use and thermal ecology of two narrowly sympatric *Sceloporus* (Phrynosomatidae) lizards. *Journal of Herpetology* **30**:152–160.
- Hertz, P. E. 1981. Adaptation to altitude in two West Indian anoles (Reptilia: Iguanidae): field thermal biology and physiological ecology. *Journal of Zoology, London* **195**:25–37.
- Hertz, P. E., and R. B. Huey. 1981. Compensation for altitudinal changes in the thermal environment by some *Anolis* lizards on Hispaniola. *Ecology* **62**:515–521.
- Hertz, P. E., R. B. Huey, and E. Nevo. 1983. Homage to Santa Anita: thermal sensitivity of sprint speed in agamid lizards. *Evolution* **37**:1075–1084.
- Hertz, P. E., R. B. Huey, and R. D. Stevenson. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *American Naturalist* **142**:796–818.
- Huey, R. B. 1982. Temperature, physiology, and the ecology of reptiles. Pages 25–74 in C. Gans and F. H. Pough, editors. *Biology of the Reptilia*. Volume 12. Academic Press, New York, New York, USA.
- Huey, R. B., and A. F. Bennett. 1987. Phylogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards. *Evolution* **41**:1098–1115.
- Huey, R. B., P. H. Niewiarowski, J. Kaufmann, and J. C. Herron. 1989. Thermal biology of nocturnal ectotherms: is sprint performance of geckos maximal at low body temperatures? *Physiological Zoology* **62**:488–504.
- Imsland, A. K., A. Foss, G. Nævdal, T. Cross, S. W. Bonga, E. V. Ham, and S. O. Stefánsson. 2000. Countergradient variation in growth and food conversion efficiency of juvenile turbot. *Journal of Fish Biology* **57**:1213–1226.
- Ji, X., W. Du, and P. Sun. 1996. Body temperature, thermal tolerance and influence of temperature on sprint speed and food assimilation in adult grass lizards, *Takydromus septentrionalis*. *Journal of Thermal Biology* **21**:155–161.
- Ji, X., X. Zheng, Y. Xu, and R. Sun. 1995. Some aspects of thermal biology of the skink (*Eumeces chinensis*). *Acta Zoologica Sinica* **41**:268–274.
- Joanen, T., L. McNease, and M. W. J. Ferguson. 1987. The effects of egg incubation temperature on post-hatching growth of American alligators. Pages 533–537 in G. J. W. Webb, S. C. Manolis, and P. J. Whitehead, editors. *Wildlife management: crocodiles and alligators*. Surrey Beatty and Sons, Sydney, Australia.
- Jonassen, T. M., A. K. Imsland, R. Fitzgerald, S. W. Bonga, E. V. Ham, G. Nævdal, M. O. Stefánsson, and S. O. Stefánsson. 2000. Geographic variation in growth and food conversion efficiency of juvenile Atlantic halibut related to latitude. *Journal of Fish Biology* **56**:279–294.
- Jönsson, K. I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* **78**:57–66.
- Kersten, M., and W. Visser. 1996. The rate of food processing in the oystercatcher: food intake and energy expenditure constrained by a digestive bottleneck. *Functional Ecology* **10**:440–448.
- Khokhlova, I. S., M. Kam, and A. A. Degen. 1997. A small

- gerbil that maximizes intake of energy from low-energy food. *Journal of Mammalogy* **78**:158–162.
- Kirkwood, R., and G. Robertson. 1997. The energy assimilation efficiency of emperor penguins, *Aptenodytes forsteri*, fed a diet of Antarctic krill, *Euphausia superba*. *Physiological Zoology* **70**:27–32.
- Kleiber, M. 1961. *The fire of life: An introduction to animal energetics*. John Wiley, New York, New York, USA.
- Marken Lichtenbelt, W. D. van, J. T. Vogel, and R. A. Weseligh. 1997. Energetic consequences of field body temperatures in the green iguana. *Ecology* **78**:297–307.
- McCullough, E. C., and W. P. Porter. 1971. Computing clear day solar radiation spectra for the terrestrial ecological environment. *Ecology* **52**:1008–1015.
- Nagy, K. A. 1983. Ecological energetics. Pages 24–54 in R. Huey, E. R. Pianka, and T. W. Schoener, editors. *Lizard ecology: studies of a model organism*. Harvard University Press, Cambridge, Massachusetts, USA.
- Niewiarowski, P. H. 1992. Ecological and evolutionary sources of geographic variation in individual growth rates of the lizard *Sceloporus undulatus* (Iguanidae). Dissertation. University of Pennsylvania, Philadelphia, Pennsylvania, USA.
- Niewiarowski, P. H. 1994. Understanding geographic life history variation in lizards. Pages 31–49 in L. J. Vitt and E. R. Pianka, editors. *Lizard ecology: historical and experimental perspectives*. Princeton University Press, Princeton, New Jersey, USA.
- Niewiarowski, P. H. 1995. Effects of supplemental feeding and thermal environment on growth rates of eastern fence lizards, *Sceloporus undulatus*. *Herpetologica* **51**:487–496.
- Niewiarowski, P. H. 2001. Energy budgets, growth rates, and thermal constraints: toward an integrative approach to the study of life-history variation. *American Naturalist* **157**:421–433.
- Niewiarowski, P. H., and W. M. Roosenburg. 1993. Reciprocal transplant reveals sources of geographic variation in growth rates of the eastern fence lizard, *Sceloporus undulatus*. *Ecology* **74**:1992–2002.
- Partridge, L., B. Barrie, K. Fowler, and V. French. 1994. Evolution and development of body size in *Drosophila melanogaster* in response to temperature. *Evolution* **48**:1269–1276.
- Partridge, L., and V. French. 1996. Thermal evolution of ectotherm body size: why get big in the cold? Pages 265–292 in I. A. Johnston and A. F. Bennett, editors. *Animals and temperature: phenotypic and evolutionary adaptation*. Cambridge University Press, Cambridge, UK.
- Peterson, C. R., A. R. Gibson, and M. E. Dorcas. 1993. Snake thermal ecology: the causes and consequences of body-temperature variation. Pages 241–314 in R. A. Seigel and J. T. Collins, editors. *Snakes: ecology and behavior*. McGraw-Hill, New York, New York, USA.
- Philipson, J. 1964. A miniature bomb calorimeter for small biological samples. *Oikos* **15**:130–139.
- Porter, W. P., J. W. Mitchell, W. A. Beckman, and C. B. DeWitt. 1973. Behavioral implications of mechanistic ecology. *Oecologia* **13**:1–54.
- Qualls, C. P., and R. Shine. 1996. Reconstructing ancestral reaction norms: an example using the evolution of reptilian viviparity. *Functional Ecology* **10**:688–697.
- Quinn, J., and A. E. Dunham. 1983. On hypothesis testing in ecology and evolution. *American Naturalist* **122**:602–617.
- Roosenburg, W. M., and K. C. Kelley. 1996. The effect of egg size and incubation temperature on growth in the turtle, *Malaclemys terrapin*. *Journal of Herpetology* **30**:198–204.
- Schaffer, W. M. 1974. Selection for optimal life histories: the effects of age structure. *Ecology* **55**:291–303.
- Schwarzkopf, L. 1998. Evidence of geographic variation in lethal temperature but not activity temperature of a lizard. *Journal of Herpetology* **32**:102–106.
- Sinervo, B. 1990. The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution* **44**:279–294.
- Sinervo, B., and S. C. Adolph. 1989. Thermal sensitivity of growth rate in hatchling *Sceloporus* lizards: environmental, behavioral and genetic aspects. *Oecologia* **78**:411–419.
- Sinervo, B., and S. C. Adolph. 1994. Growth plasticity and thermal opportunity in *Sceloporus* lizards. *Ecology* **75**:776–790.
- Smith, G. R., J. W. Rowe, and R. E. Ballinger. 1996. Intraspecific life history variation in *Sceloporus undulatus*: a factor analysis. *Transactions of the Nebraska Academy of Sciences* **23**:85–90.
- Sorci, G., J. Clobert, and S. Belichon. 1996. Phenotypic plasticity of growth and survival in the common lizard *Lacerta vivipara*. *Journal of Animal Ecology* **65**:781–790.
- Stevens, E. D., and R. H. Devlin. 2000. Intestinal morphology in growth hormone transgenic Coho salmon. *Journal of Fish Biology* **56**:191–195.
- Stevens, E. D., G. N. Wagner, and A. Sutterlin. 1999. Gut morphology in growth hormone transgenic Atlantic salmon. *Journal of Fish Biology* **55**:517–526.
- Stevenson, R. D., C. R. Peterson, and J. S. Tsuji. 1985. The thermal dependence of locomotion, tongue flicking, digestion, and oxygen consumption in the wandering garter snake. *Physiological Zoology* **58**:46–57.
- Tinkle, D. W., and R. E. Ballinger. 1972. *Sceloporus undulatus*: a study of the intraspecific comparative demography of a lizard. *Ecology* **53**:570–584.
- Tinkle, D. W., and A. E. Dunham. 1986. Comparative life histories of two syntopic sceloporine lizards. *Copeia* **1986**:1–18.
- Tuomi, J., T. Hakala, and E. Haukioja. 1983. Alternative concepts of reproductive effort, costs of reproduction, and selection in life-history evolution. *American Zoologist* **23**:25–34.
- van Berkum, F. H. 1986. Evolutionary patterns of the thermal sensitivity of sprint speed in *Anolis* lizards. *Evolution* **40**:594–604.
- Van Damme, R., D. Bauwens, A. M. Castilla, and R. F. Verheyen. 1989. Altitudinal variation of the thermal biology and running performance in the lizard *Podarcis tiliguerta*. *Oecologia* **80**:516–524.
- Van Damme, R., D. Bauwens, and R. F. Verheyen. 1991. The thermal dependence of feeding behaviour, food consumption and gut-passage time in the lizard *Lacerta vivipara* Jacquin. *Functional Ecology* **5**:507–517.
- Waldschmidt, S. R., S. M. Jones, and W. P. Porter. 1986. The effect of body temperature and feeding regime on activity, passage time, and digestive coefficient in the lizard *Uta stansburiana*. *Physiological Zoology* **59**:376–383.
- Waldschmidt, S. R., S. M. Jones, and W. P. Porter. 1987. Reptilia. Pages 553–619 in T. J. Padian and F. J. Vernberg, editors. *Animal energetics: Bivalvia through Reptilia*. Academic Press, New York, New York, USA.