

# Variation in Metabolic Rate between Populations of a Geographically Widespread Lizard

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Accepted 8/3/00

## ABSTRACT

In geographically widespread ectotherms, variation in life history phenotypes may be caused by differences in maintenance metabolism of individuals. I estimated daily and annual maintenance metabolism of eastern fence lizards, *Sceloporus undulatus*, from two populations with markedly different life histories; lizards in South Carolina grow faster, mature earlier, and have greater annual reproductive output than lizards in New Jersey. I measured diel cycles of resting metabolic rate (RMR) at four temperatures (20°, 30°, 33°, and 36°C) during spring, summer, and fall. In all seasons, RMR increased significantly from 20° to 33°C but did not differ significantly between 33° and 36°C. Adults from New Jersey had a higher RMR than adults from South Carolina in summer and fall but not in spring. Juveniles from South Carolina had a higher RMR than juveniles from New Jersey in summer but not in spring or fall. Annual maintenance metabolism of New Jersey lizards (53.7 kJ) was greater than that of South Carolina lizards (45.8 kJ), despite the shorter duration of activity in New Jersey. I conclude that the difference in maintenance metabolism between populations contributes to the greater production by *S. undulatus* in South Carolina.

## Introduction

Metabolism is, by far, the largest component of energy budgets of animals. In nature, energy lost to metabolism composes over 80% of annual energy expenditure (e.g., Congdon et al. 1982; Anderson and Karasov 1988; van Marken Lichtenbelt et al. 1993; Green and Ydenberg 1994; Beaupre 1996). Field metabolic rates include energy required to fuel maintenance, growth,

digestion, locomotion, and reproduction (Clarke 1993; Dunham and Beaupre 1998). Energy expenditure related to some processes (e.g., activity, growth, digestion) may be altered in response to energy availability (Wieser 1994, 1998; Secor 1997). However, opportunities to reduce the maintenance component of field metabolic rate depend on available microclimates because standard metabolic rate of an ectotherm is affected greatly by temperature (Bennett and Dawson 1976). Therefore, the obligatory energetic cost of maintenance is a major determinant of the quantity of energy available for activity and production.

Geographic variation in life history traits may be caused, at least in part, by differences in maintenance metabolism among individuals from different populations. Individuals at lower latitudes or altitudes usually experience warmer temperatures throughout the year (e.g., Beaupre 1995), potentially resulting in higher metabolic rates. Climatic differences among sites can cause variation in maintenance metabolism on a seasonal or annual basis (e.g., Beaupre 1996). Further, acclimatization can produce seasonal variation in metabolic rate (Tsuji 1988; Beyer and Spotila 1994). To estimate maintenance costs of individuals in natural populations, diel and seasonal effects on the thermal sensitivity of metabolic rate must be known (e.g., Beaupre 1993; Beaupre et al. 1993). Consequently, laboratory studies that quantify effects of ecological variables on metabolic rate are useful for inferring proximate causes of life history variation (Waldschmidt et al. 1987; Niewiarowski and Waldschmidt 1992).

The eastern fence lizard, *Sceloporus undulatus*, exhibits considerable variation in life history traits among populations (Tinkle and Dunham 1986; Niewiarowski 1994). Individuals in southern populations tend to grow more rapidly and mature earlier than individuals in northern populations (Ferguson and Brockman 1980; Ferguson et al. 1980; Angilletta 1998). For example, females in New Jersey mature at 60 mm snout-vent length in 20 mo, but those in South Carolina mature at 55 mm snout-vent length in only 10 mo (Tinkle and Ballinger 1972; Niewiarowski 1994). Additionally, South Carolina (SC) females have a greater annual reproductive output than New Jersey (NJ) females (Tinkle and Ballinger 1972; Niewiarowski 1994). Based on these data, one can conclude that the annual production budget of lizards in South Carolina is greater than that of lizards in New Jersey.

Differences in production between NJ and SC lizards can be explained by patterns of energy assimilation and energy expenditure of individuals in these two populations (Dunham et al. 1989). That is, lizards in South Carolina may assimilate more

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energy or expend less energy on maintenance than lizards in New Jersey. Others have suggested that intraspecific variation in growth and reproduction of *S. undulatus* is influenced by thermal constraint on annual energy assimilation (Grant and Porter 1992; Adolph and Porter 1993, 1996). However, laboratory studies have shown that hatchlings from South Carolina grow more rapidly ( $\text{g d}^{-1}$ ) than those from other populations, including hatchlings from New Jersey, even when reared in the same environment (Ferguson and Brockman 1980; Niewiarowski 1995). Thus, intraspecific variation in behavior or physiology must contribute to the difference in production between NJ and SC lizards. Indeed, lizards from South Carolina have a greater rate of metabolizable energy intake than lizards from New Jersey at the preferred body temperature (Angilletta 2002). It is not known whether annual maintenance metabolism differs between NJ and SC lizards. In this study, I quantified the effects of temperature, time of day, and season on resting metabolic rates (RMR) of NJ and SC lizards. These data were used to estimate daily and annual maintenance metabolism of lizards in nature and to assess whether energy expenditure, as well as energy assimilation, contributes to geographic variation in the life history of *S. undulatus*.

## Material and Methods

### Animal Collection and Care

Metabolic rates were measured in spring (May), summer (July/August), and fall (October) of 1997. In each season, 15 lizards were collected from each of two populations, one at Lebanon State Forest (Burlington County, N.J.) and the other at the Savannah River Site (Aiken County, S.C.). Samples contained a mixture of sexes and age classes (Table 1). Lizards were immediately transported to the University of Pennsylvania, but those from New Jersey were kept in cloth bags for 48 h to mimic the conditions experienced by lizards from South Carolina during transport. In the laboratory, each individual was housed in a 6-L plastic terrarium and was fed crickets, *Acheta domestica* Linnaeus. After feeding, lizards were placed in an incubator at 33°C for 48 h to allow food to pass through the digestive tract.

### Measurement of Metabolic Rate

Metabolic rates of lizards were measured with a flow-through respirometry system (TR-3, Sable Systems, Henderson, Nev.). Respirometry chambers, 120 mL in volume, were contained in a programmable incubator (model 818, Precision Scientific, Chicago). An opening in the incubator, 5 cm in diameter, was used for incoming and outgoing tubing. Incoming air flowed through columns of soda lime, Drierite, and Ascarite to remove  $\text{H}_2\text{O}$  and  $\text{CO}_2$ . After the absorbent columns, air was pushed at  $150 \text{ mL min}^{-1}$  through 20 m of copper tubing submerged in 38 L of water that was at equilibrium with the incubator temperature. As a result, air entering respirometry chambers was at the same temperature as air in the incubator. Outgoing air was scrubbed of water and entered a mass flowmeter (v1.0, Sable Systems, Henderson, Nev.), a  $\text{CO}_2$  analyzer (model LI-6251, LI-COR, Lincoln, Nebr.), and an oxygen analyzer (model FC-1, Sable Systems, Henderson, Nev.). In between the  $\text{CO}_2$  analyzer and the  $\text{O}_2$  analyzer,  $\text{CO}_2$  was removed from the airstream by soda lime and Ascarite. Before the study, the mass flowmeter was calibrated using a mass-flow controller valve (Sidetrak, Sierra Instruments, Monterey, Calif.) connected to a mass-flow controller electronic unit (v1.0, Sable Systems, Henderson, Nev.).

I measured RMR, as opposed to standard metabolic rate (SMR) because lizards were inactive and postabsorptive but were not always in darkness. Metabolic rate of each lizard was measured at four temperatures (20°, 30°, 33°, and 36°C). Measurements were made at one temperature per day, and the order of temperatures was determined randomly (33°, 20°, 30°, and 36°C). Therefore, the following procedure was repeated daily until measurements had been performed at all temperatures. At 1000 hours, 15 lizards were weighed to the nearest 0.1 mg and were sealed in respirometry chambers. Lizards were allowed to habituate to chambers from 1000 to 1200 hours, during which  $\text{O}_2$  and  $\text{CO}_2$  analyzers were calibrated. From 1200 to 0800 hours the following day, production of  $\text{CO}_2$  and consumption of  $\text{O}_2$  were measured for a period of 2 min every 2.5 h, resulting in eight recordings for each individual. During each 2-min period, the concentrations of  $\text{O}_2$  and  $\text{CO}_2$  in the chamber and the flow rate through the chamber were recorded each second by data acquisition software (Sable Systems International 1991a). Before and after each period, baseline measures

Table 1: Mean body masses  $\pm$  95% confidence intervals of lizards collected from New Jersey and South Carolina populations of *Sceloporus undulatus*

Season	New Jersey		South Carolina	
	Adult	Juvenile	Adult	Juvenile
Spring	7.3 $\pm$ 1.5 (5♂ : 3♀)	1.5 $\pm$ .3 (3♂ : 4♀)	5.9 $\pm$ 1.2 (4♂ : 3♀)	2.4 $\pm$ .7 (4♂ : 4♀)
Summer	8.9 $\pm$ 1.6 (3♂ : 5♀)	3.7 $\pm$ .6 (5♂ : 2♀)	7.0 $\pm$ .8 (4♂ : 3♀)	1.0 $\pm$ .3 (4♂ : 4♀)
Fall	7.0 $\pm$ 1.6 (7♂ : 1♀)	1.0 $\pm$ .2 (3♂ : 4♀)	8.8 $\pm$ 1.6 (2♂ : 3♀)	1.4 $\pm$ .4 (4♂ : 6♀)

Note. Sample sizes are given in parentheses.

of O<sub>2</sub> and CO<sub>2</sub> concentrations were recorded from an empty chamber, identical to those that held lizards. Photoperiod during measurements was 14L : 10D, with photophase beginning at 0600 hours. Thus, the 20-h measurement period spanned both photophase and scotophase. On the following morning, lizards were removed from the chambers, and body temperatures were measured immediately with a quick-reading cloacal thermometer (T-4000, Miller and Weber, Queens, N.Y.). Lizards were placed in 6-L terraria with unlimited access to water from 0800 to 1000 hours, when measures at the next temperature were initiated.

#### *Data Analysis*

Data were analyzed using the computer program DATACAN (Sable Systems International 1991*b*). For each recording, baseline concentrations of CO<sub>2</sub> and O<sub>2</sub> were used to calculate percentage enrichment of CO<sub>2</sub> and percentage depletion of O<sub>2</sub> by the lizard. Rates of CO<sub>2</sub> production and O<sub>2</sub> consumption (mL h<sup>-1</sup>) at each sampling point were calculated as the product of flow rate and percentage enrichment (or -1 × percentage depletion). For calculation of O<sub>2</sub> consumption, flow rate was corrected for the mass of CO<sub>2</sub> removed from the airstream between the CO<sub>2</sub> analyzer and the O<sub>2</sub> analyzer (J. Lighton, personal communication). Rates of CO<sub>2</sub> production and O<sub>2</sub> consumption were averaged for the entire 2-min recording, resulting in a single value of CO<sub>2</sub> production and O<sub>2</sub> consumption (mL h<sup>-1</sup>). Therefore, data for each lizard consisted of eight rates of CO<sub>2</sub> production and O<sub>2</sub> consumption at each of four temperatures.

Respiratory exchange was used to convert CO<sub>2</sub> production at STP (mL h<sup>-1</sup>) to energy expenditure (J h<sup>-1</sup>). O<sub>2</sub> consumption is commonly used to estimate energy expenditure because the error associated with the conversion of CO<sub>2</sub> production to energy expenditure can be as much as 13% if respiratory quotient is unknown (Schmidt-Nielsen 1997). However, measures of CO<sub>2</sub> production can provide more precise estimates of energy expenditure when respiratory quotient is known. Because I scrubbed air of CO<sub>2</sub> before the chambers, the majority of CO<sub>2</sub> in air leaving a chamber was produced by a lizard. Conversely, the O<sub>2</sub> consumed by a lizard composed only a tiny fraction of the O<sub>2</sub> in air entering a chamber. Therefore, measures of CO<sub>2</sub> production have a greater signal-to-noise ratio than those of O<sub>2</sub> consumption, which renders greater power to statistical analyses of metabolic rate. For this reason, CO<sub>2</sub> production was used to estimate energy expenditure, using the appropriate conversion factor for the respiratory exchange that was observed (Nagy 1983). Hereafter, metabolic rate is defined in terms of energy expenditure (J h<sup>-1</sup>).

Because the experimental design involved repeated measures of the metabolic rates of individuals, ANCOVA with repeated measures was used to examine the among-subjects effects of population and season on metabolic rate. Average body mass

(i.e., average of four daily measures for each individual) was used as a covariate because body mass of lizards varied between populations and among seasons (Table 1). Within-subjects effects of temperature and time period were evaluated by MANCOVA, in which repeated measures are treated as dependent variables. Analysis of repeated measures by MANCOVA requires fewer assumptions about the form of the variance-covariance matrix than the univariate test (Potvin et al. 1990). Before employing ANCOVA, I examined data for violations of the assumption that slopes of relationships between body mass and metabolic rate were homogeneous among groups (Sokal and Rohlf 1981). Levene's test was used to determine whether data met the assumption of homogeneity of variances. Pairwise comparisons of means for seasons, temperatures, and time periods were made with Tukey's honest significant difference test. Statistical analyses were performed with Statistica for Windows (StatSoft 1996). In most cases, metabolic rates are reported as mean ± 95% confidence interval, but adjusted means from ANCOVA are reported when making direct comparisons between populations or age classes.

I constructed multiple linear regression models to predict RMR from body mass and temperature. For the purpose of regression analysis, data for time periods were averaged within photophase (1200–1930 hours) and scotophase (1930–0800 hours). I analyzed RMR from each phase (photophase, scotophase) and each season (spring, summer, fall), producing a minimum of six models. Additionally, separate models were computed for populations and age classes if these effects were found to be significant by ANCOVA.

#### *Activity Time and Maintenance Metabolism*

I used a biophysical model to estimate the maximum duration of daily and annual activity of lizards in New Jersey and South Carolina. 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 body temperature within a preferred range. All model parameters were specified as in Adolph and Porter (1996), except that monthly air temperatures and relative humidities for New Jersey and South Carolina sites were obtained from the National Climate Data Center (Asheville, N.C.). The programs calculate thermal properties of both the environment and a lizard in that environment. 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 which hours of the day an ectotherm can maintain its preferred body temperature (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 preferred body temperature above the surface in winter months, but the soil temperature is too cold to induce surface activity. Because *Sceloporus undulatus* burrows during inactivity, I reasoned that the soil temperature must reach a threshold before individuals would initiate activity on a given day. The lowest body temperature that I have recorded for a fence lizard that was active on the surface is 20.8°C (Angilletta 2002). 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 hours that *S. undulatus* could achieve its preferred body temperature ( $33^{\circ} \pm 1^{\circ}\text{C}$ ; Angilletta 2002) per day after the onset of activity. By summing these hours over an entire year, I arrived at an estimate of annual activity time.

Activity times were used to estimate daily and annual maintenance budgets for NJ and SC lizards. I was only able to estimate daily maintenance budgets of juveniles because they gain considerable mass within seasons. Assuming that adults do not grow much between years, I used average mass of adults in this study (7.5 g) to calculate daily and annual maintenance budgets for an adult lizard in each population. To estimate maintenance budgets, it was necessary to make the following assumptions: (1) at a given body temperature, the maintenance metabolic rate of a lizard in its natural environment is equivalent to the RMR observed in the laboratory; (2) during months in which activity was predicted, lizards maintained body temperatures of 20° and 33°C during inactivity and activity, respectively (Niewiarowski 1992; Angilletta 2002); and (3) no energy is expended during months in which lizards cannot be active (i.e., during hibernation).

## Results

Respiratory exchange (RE) was dependent on temperature; lizards metabolized lipid at 20°C ( $\text{RE} = 0.66 \pm 0.08$ ) but primarily metabolized carbohydrate at 30° ( $\text{RE} = 0.92 \pm 0.4$ ), 33° ( $\text{RE} = 0.99 \pm 0.04$ ), and 36°C ( $\text{RE} = 1.05 \pm 0.04$ ). Respiratory exchanges of NJ lizards and SC lizards at each temperature were not significantly different ( $t$ -tests,  $P > 0.05$  for all). Therefore, I assumed that lizards from both populations metabolized 100% lipid at 20°C ( $27.7 \text{ J mL}^{-1} \text{ CO}_2$ ), 73% carbohydrate and 27% lipid at 30°C ( $22.6 \text{ J mL}^{-1} \text{ CO}_2$ ), and 100% carbohydrate at 33° and 36°C ( $20.8 \text{ J mL}^{-1} \text{ CO}_2$ ).

A significant difference in RMR between populations was observed in some seasons. For SC lizards, slopes of relationships between body mass and metabolic rate differed significantly among seasons (spring =  $0.84 \pm 0.11$ , summer =  $0.08 \pm 0.06$ , and fall =  $0.28 \pm 0.06$ ; Fig. 1), so an ANCOVA for each season was used to examine the effects of population and age class on metabolic rate (Table 2). In spring, no differences in

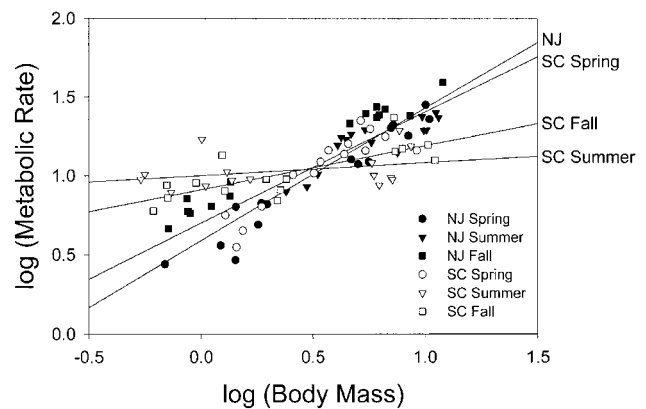


Figure 1. Relationship between body mass and metabolic rate ( $\text{J h}^{-1}$ ) of lizards in New Jersey (NJ) and South Carolina (SC) populations of *Sceloporus undulatus*. Metabolic rate of each individual is the average of metabolic rates at all temperatures and time periods. Regression lines for SC lizards are shown for each season because slopes of the relationship between body mass and metabolic rate for SC lizards differed significantly among seasons.

RMR were observed between populations or age classes (Fig. 2). Metabolic rates of NJ adults were higher than those of SC adults in summer and fall (Fig. 2). However, SC juveniles had a significantly higher RMR than NJ juveniles in summer.

In all seasons, RMR was insensitive to temperature over part of the range (Fig. 3). Metabolic rate of NJ lizards increased significantly from 20° to 33°C but did not differ significantly between 33° and 36°C (Tukey’s test). Metabolic rate of SC lizards was less sensitive to temperature than NJ lizards. In spring and fall, SC lizards had similar metabolic rates over the range of 30°–36°C, but metabolic rate differed significantly between 30° and 36°C in summer (Tukey’s test).

There was a significant diel cycle of RMR in all seasons (Table 2). Metabolic rate decreased significantly between time periods 3 (1700–1930 hours) and 5 (2200–0030 hours) and remained lower for all subsequent time periods (Tukey’s test). Metabolic rate was minimal at time period 6 (0030–0300 hours) and increased significantly between time periods 6 and 8 (0530–0800 hours). The two shifts in metabolic rate coincide with the onset of scotophase (2000 hours) and photophase (0600 hours), respectively. Amplitude of the diel cycle was greater at higher temperatures (Fig. 4). In summer and fall, NJ lizards tended to have higher metabolic rates during photophase (1200–1930 hours) but not during scotophase (significant interactions, Table 2). In spring, lizards from the two populations had similar metabolic rates at all time periods except 0600–0830 hours.

I used ANCOVA to assess seasonal variation in RMR of NJ lizards. Metabolic rate of NJ lizards differed significantly among seasons ( $MS = 4.47$ ,  $F_{2,38} = 28.90$ ,  $P < 0.001$ ); metabolic rate in fall ( $11.8 \text{ J h}^{-1}$ ) was significantly higher than in spring ( $7.6$

Table 2: ANCOVA with repeated measures of the effects of population, age class, temperature, and time period on metabolic rate ( $J h^{-1}$ ) of *Sceloporus undulatus*

Effects	Spring					Summer					Fall				
	df	MS	F	Wilks's $\lambda$	P	df	MS	F	Wilks's $\lambda$	P	df	MS	F	Wilks's $\lambda$	P
Between-subjects:															
Population (pop)	1, 25	.02	.03	...	.856	1, 25	.05	.24	...	.626	<b>1, 25</b>	<b>3.39</b>	<b>23.27</b>	...	<b>.000</b>
Age class (age)	1, 25	.04	.09	...	.766	<b>1, 25</b>	<b>.97</b>	<b>4.77</b>	...	<b>.038</b>	1, 25	.56	3.84	...	.061
Pop $\times$ age	1, 25	.05	.10	...	.748	<b>1, 25</b>	<b>2.37</b>	<b>11.68</b>	...	<b>.002</b>	<b>1, 25</b>	<b>4.49</b>	<b>30.78</b>	...	<b>.000</b>
Within-subjects:															
Temperature (temp)	<b>3, 24</b>	...	...	<b>.06</b>	<b>.000</b>	<b>3, 24</b>	...	...	<b>.08</b>	<b>.000</b>	<b>3, 24</b>	...	...	<b>.03</b>	<b>.000</b>
Time period (time)	<b>7, 20</b>	...	...	<b>.46</b>	<b>.015</b>	<b>7, 20</b>	...	...	<b>.29</b>	<b>.000</b>	<b>7, 20</b>	...	...	<b>.06</b>	<b>.000</b>
Temp $\times$ time	21, 6	...	...	.16	.324	21, 6	...	...	.12	.172	21, 6	...	...	.27	.695
Pop $\times$ temp	3, 24	...	...	.79	.120	<b>3, 24</b>	...	...	<b>.60</b>	<b>.006</b>	3, 24	...	...	.88	.391
Pop $\times$ time	<b>7, 20</b>	...	...	<b>.42</b>	<b>.007</b>	<b>7, 20</b>	...	...	<b>.28</b>	<b>.000</b>	<b>7, 20</b>	...	...	<b>.40</b>	<b>.005</b>
Age $\times$ temp	3, 24	...	...	.75	.072	3, 24	...	...	.79	.121	<b>3, 24</b>	...	...	<b>.62</b>	<b>.008</b>
Age $\times$ time	7, 20	...	...	.69	.297	7, 20	...	...	.84	.788	7, 20	...	...	.74	.451
Pop $\times$ temp $\times$ time	21, 6	...	...	.19	.443	21, 6	...	...	.18	.395	21, 6	...	...	.12	.197
Age $\times$ temp $\times$ time	21, 6	...	...	.17	.366	21, 6	...	...	.09	.092	21, 6	...	...	.31	.791
Pop $\times$ age $\times$ temp	3, 24	...	...	.98	.894	<b>3, 24</b>	...	...	<b>.54</b>	<b>.002</b>	<b>3, 24</b>	...	...	<b>.50</b>	<b>.001</b>
Pop $\times$ age $\times$ time	<b>7, 20</b>	...	...	<b>.49</b>	<b>.025</b>	7, 20	...	...	.66	.224	7, 20	...	...	.76	.516
Pop $\times$ age $\times$ temp $\times$ time	21, 6	...	...	.15	.296	21, 6	...	...	.12	.168	21, 6	...	...	.25	.649

Note. Significant effects are designated by bold typeface.

$J h^{-1}$ ) and summer ( $7.2 J h^{-1}$ ). I could not use ANCOVA to compare RMR of SC lizards among seasons because slopes of relationships between body mass and RMR were heterogeneous. However, RMR of SC lizards did not vary significantly among seasons when compared by ANOVA ( $MS = 0.06$ ,  $F_{2,39} = 0.09$ ,  $P = 0.917$ ). It is likely that the differences in RMR between NJ and SC adults was caused by divergent patterns of seasonal acclimatization. The RMR of NJ lizards increased throughout the year, whereas the RMR of SC lizards did not.

I compared daily and annual maintenance budgets of NJ and SC lizards, calculated from regression models of RMR. On average, temperature and body mass explained 70% of the variation in RMR (Table 3). In all seasons, temperature and body mass were better predictors of RMR during scotophase than RMR during photophase. Based on the biophysical model, annual activity times were 1802 and 2387 hours for NJ and SC lizards, respectively. Assuming that activity of lizards in New Jersey and South Carolina corresponded to the predictions of the model, SC adults had a maintenance expenditure of 45.8 kJ, whereas NJ adults had a maintenance expenditure of 53.7 kJ. Note that the annual activity of SC lizards was estimated to be 32% greater than that of NJ lizards, but annual maintenance expenditure was estimated to be 15% less. The relatively high maintenance expenditure of NJ adults was caused by the significantly higher RMR of NJ adults during summer and fall. Adult lizards in New Jersey have greater daily maintenance expenditures than those in South Carolina (Table 4), and this results in a greater annual maintenance budget.

Daily maintenance expenditure of juveniles was calculated

for three stages along a growth trajectory (1, 1.5, and 3 g; Table 4). At body masses of 1 and 1.5 g, daily maintenance expenditures of SC juveniles was greater than those of NJ juveniles. These differences were mostly driven by longer daily activity times in South Carolina (Table 4). At a body mass of 3 g, the daily maintenance expenditure of NJ juveniles was greater than that of SC juveniles. The difference in daily maintenance metabolism at 3 g was caused by both a longer daily activity time and a higher RMR of NJ lizards (Table 4). The difference in RMR was a consequence of divergent patterns of seasonal acclimatization in NJ and SC lizards because SC juveniles were born in early summer and attained a body mass of 3 g by their first spring, whereas NJ juveniles were born in late summer and did not attain this mass until the following summer (Tables 1, 4).

## Discussion

Metabolic rates for *Sceloporus undulatus* reported here compare favorably with those reported by other investigators. For example, I observed a RMR of  $5.4 \pm 0.9 J g^{-1} h^{-1}$  for lizards at  $33^\circ C$ . Zannoni (1997) reported a RMR of  $5.8 \pm 0.7 J g^{-1} h^{-1}$  and  $5.1 \pm 0.6 J g^{-1} h^{-1}$  for lizards from Nebraska and Ohio populations of *S. undulatus*, respectively. It is important to note that RMR reported here and by Zannoni (1997) are not equivalent to SMR because measurements were made during periods of photophase as well as scotophase. Also, neither study selectively reported minimum rates of metabolism observed, as in many studies of SMR (e.g., Feder and Feder 1981; Tsuji 1988;

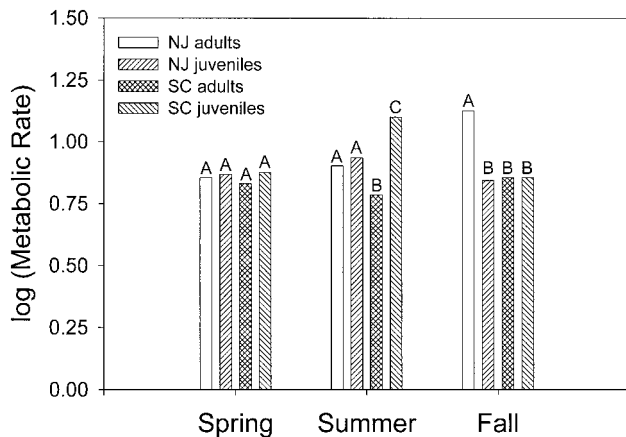


Figure 2. Seasonal metabolic rates ( $\text{J h}^{-1}$ ) of juvenile and adult lizards from New Jersey (NJ) and South Carolina (SC) populations of *Sceloporus undulatus*. Data are adjusted means from ANCOVA. Data for each season were analyzed separately because the assumptions of ANCOVA were not met when all seasons were combined (see text for details). Within seasons, letters indicate the groups whose metabolic rates did not differ significantly (Tukey's test,  $P > 0.05$ ).

Rowe et al. 1998). Therefore, RMR is expected to be slightly greater than SMR (Niewiarowski and Waldschmidt 1992). As expected, allometric equations for SMR of *S. undulatus* at  $35^\circ\text{C}$  predict metabolic rates of  $4.5\text{--}4.6 \text{ J g}^{-1} \text{ h}^{-1}$  (John-Alder 1990; Joos and John-Alder 1990), only 85% of that reported here.

Most important, my regression models seem capable of predicting maintenance expenditure with considerable accuracy. This can be demonstrated by comparing daily maintenance expenditure predicted by regression equations to that determined by the doubly labeled water method. Joos and John-Alder (1990) used doubly labeled water to estimate the daily energy expenditure of adults from a New Jersey population of *S. undulatus*. These animals were maintained in the laboratory with access to an external heat source for  $10 \text{ h d}^{-1}$ . I used regression equations reported in Table 3 to predict daily energy expenditure for an adult lizard under conditions experienced in Joos and John-Alder's (1990) study. I predicted an expenditure of  $31.5 \text{ J g}^{-1} \text{ d}^{-1}$ , which is very close to the  $29.8 \text{ J g}^{-1} \text{ d}^{-1}$  reported by Joos and John-Alder (1990).

Metabolic plateaus, temperature ranges over which metabolic rate is constant, are common in *S. undulatus* and other reptiles (Waldschmidt et al. 1987). For example, SMR of lizards from a Kansas population of *S. undulatus* was independent of temperature, from  $30^\circ$  to  $36^\circ\text{C}$  (Hughes et al. 1982). Likewise, SMR of lizards from a Nebraska population of *S. undulatus* did not differ significantly between  $33^\circ$  and  $36^\circ\text{C}$  (Zannoni 1997). I observed a metabolic plateau from  $30^\circ$  to  $36^\circ\text{C}$  in spring and from  $33^\circ$  to  $36^\circ\text{C}$  in summer and fall (Fig. 3). Failure to find a significant difference between RMR at  $33^\circ$  and  $36^\circ\text{C}$  might have resulted from imprecision in my measures of RMR. How-

ever, given the sensitivity of the FC-1  $\text{O}_2$  analyzer ( $\pm 0.0001\%$ ) and the frequency with which metabolic plateaus have been reported in reptiles (see review by Waldschmidt et al. 1987), it is reasonable to conclude that RMR of *S. undulatus* is relatively insensitive to temperature in the range of  $30^\circ\text{--}36^\circ\text{C}$ . Hughes et al. (1982) claimed that a metabolic plateau at relatively high temperatures is adaptive because it enables *S. undulatus* to ther-

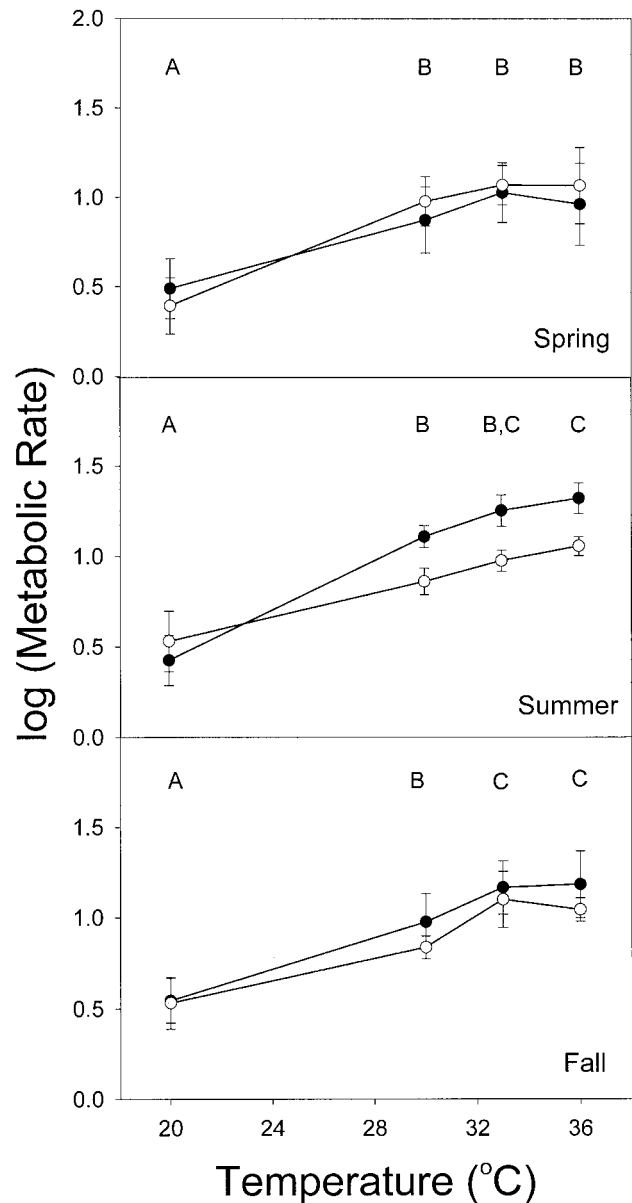


Figure 3. Thermal sensitivities of metabolic rate ( $\text{J h}^{-1}$ ) in lizards from New Jersey (filled circles) and South Carolina (open circles) populations of *Sceloporus undulatus*. Error bars represent 95% confidence intervals. Letters denote temperatures at which metabolic rate did not differ significantly (Tukey's test,  $P > 0.05$ ).

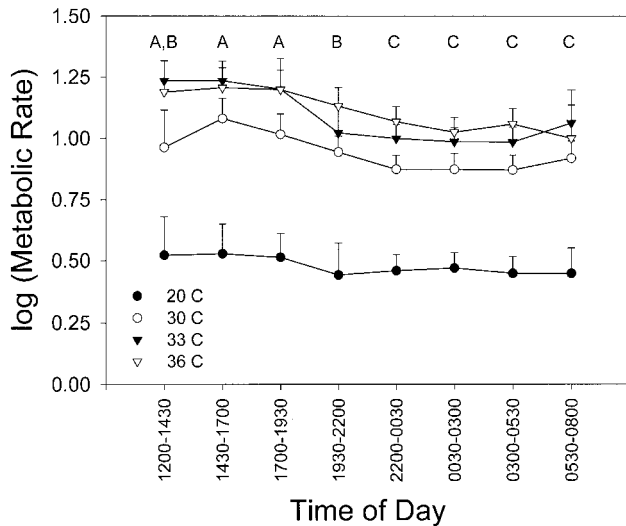


Figure 4. Diel variation in the metabolic rate of *Sceloporus undulatus* at four temperatures: 20°, 30°, 33°, and 36°C. Error bars represent 95% confidence intervals and are unidirectional for clarity. Letters denote time periods at which metabolic rate did not differ significantly (Tukey's test,  $P > 0.05$ ).

moregulate at higher temperatures while maintaining energetic homeostasis. Accordingly, the temperature range of a metabolic plateau should match the range of body temperatures during activity (Peterson et al. 1993). Lower and upper quartiles for field body temperatures of NJ lizards are 32.7° and 35.5°C, respectively, while those for SC lizards are 31.9° and 35.2°C (Angilletta 2002). Thus, the metabolic plateau that I observed matches well with body temperatures experienced by NJ and SC lizards during activity.

Lizards typically exhibit diel cycles of metabolic rate such that metabolic rate is highest during time periods when lizards are active (Waldschmidt et al. 1987). For example, diurnal lizards have maximal metabolic rates between 1000–1800 hours and minimal metabolic rates between 2000–0600 hours (Waldschmidt et al. 1987). In contrast, nocturnal geckos exhibit a peak in metabolic rate around 2100 hours and a minimum metabolic rate between 1000–1600 hours (Waldschmidt et al. 1987). *Sceloporus undulatus* exhibited a marked diel cycle of RMR, similar to those of other diurnal lizards. Metabolic rate was maximal at 1200–1930 hours and decreased significantly at the onset of scotophase (Fig. 4).

The primary cause of the diel cycle of RMR observed in this study was probably an environmental cue, rather than a circadian rhythm. Natural photoperiod differs between sites and among seasons, but I used the same experimental photoperiod for NJ and SC lizards in all seasons. Therefore, a circadian rhythm of metabolic rate would not necessarily correspond to the experimental photoperiod. Although circadian rhythms in

metabolic rate exist in reptiles (Underwood 1992), the diel shift in RMR that I observed was linked too closely to the onset scotophase (2000 hours) to be considered circadian. Furthermore, stress induced by handling is not a good explanation for the diel cycle. First, lizards were allowed to habituate to the chamber for 2 h before measurements. Second, RMR did not decrease significantly until the onset of scotophase each day. Finally, the difference in RMR between photophase and scotophase appears to be as pronounced on the fourth day of measurements (36°C) as it was on the first day (33°C; Fig. 4). The most plausible explanation for diel variation is that RMR was affected by the photoperiod used in the experiment. Much of the decrease in RMR during scotophase may be caused by lower levels of mentation. Brain tissue accounts for a substantial proportion of SMR in vertebrates (Rolfe and Brown 1997). The absence of light probably reduced metabolic activity of the nervous system, especially if lizards slept during scotophase.

The seasonal variation in RMR that I observed is different from that observed by other investigators. Tsuji (1988) hypothesized that acclimatization of metabolic rate would differ among populations at different latitudes. Specifically, Tsuji (1988) predicted that lizards in California would exhibit an increase in metabolic rate in fall because of their moderately seasonal environment, but lizards in Washington would exhibit a decrease in metabolic rate in fall because of their strongly seasonal environment. As predicted, SMR of *Sceloporus occidentalis* in California increased significantly from September to November, whereas SMR of *S. occidentalis* in Washington peaked in May or June and decreased significantly by September (Heusner and Jameson 1981; Tsuji 1988). Beyer and Spotila (1994) reported seasonal variation in RMR of *S. undulatus* that is consistent with Tsuji's (1988) hypothesis; adult males from the strongly seasonal environment of New Jersey had higher RMR in spring than in summer and fall. In contrast, my measures of RMR for *S. undulatus* do not support Tsuji's (1988) hypothesis. I observed a higher RMR of NJ lizards in fall than in spring and summer.

The discrepancy in patterns of acclimatization observed in sceloporine lizards is not surprising because seasonal acclimatization is a complex phenomenon driven by a multitude of metabolic processes (Clarke 1993). Metabolic rate of a resting ectotherm depends on tissue synthesis (Wieser 1994), food intake (Niewiarowski and Waldschmidt 1992; Secor and Diamond 1997), and physiological state (Guillette 1982; Beuchat and Vleck 1990; John-Alder 1990; Angilletta and Sears 2000). Beyer and Spotila (1994), like Tsuji (1988), only examined adult males, which may incur higher metabolic rates due to changes in physiological state associated with heightened levels of aggression or territorial defense (McKinney and Marion 1985; Marler et al. 1995). I examined a mixture of sexes and age classes (Table 1); therefore, the mechanisms that caused the acclimatization response observed in my study may be different from those that produced patterns observed by other investi-

Table 3: Regression models of resting metabolic rate ( $\log J h^{-1}$ ) of *Sceloporus undulatus*

Season	Photoperiod	Model	<i>P</i>	Adjusted <i>r</i> <sup>2</sup>
Spring:				
NJ and SC	Photophase	$RMR = .04(T) + .90(\log M) - .91$	.000	.61
	Scotophase	$RMR = .03(T) + .90(\log M) - .64$	.000	.76
Summer:				
NJ	Photophase	$RMR = .07(T) + .57(\log M) - 1.43$	.000	.73
	Scotophase	$RMR = .05(T) + .54(\log M) - .89$	.000	.82
SC juveniles	Photophase	$RMR = .04(T) + .10(\log M) - .57$	.000	.62
	Scotophase	$RMR = .06(T) + .27(\log M) - .96$	.000	.82
SC adults	Photophase/scotophase	$RMR = .01(T) + .71(\log M) - .10$	.002	.34
Fall:				
NJ adults	Photophase	$RMR = .06(T) + .56(\log M) - .85$	.000	.87
	Scotophase	$RMR = .04(T) + .47(\log M) - .44$	.000	.89
NJ juveniles and SC	Photophase	$RMR = .03(T) + .30(\log M) - .25$	.000	.55
	Scotophase	$RMR = .04(T) + .34(\log M) - .56$	.000	.69

Note. Body mass (*M*) and temperature (*T*) are independent variables. Values for mass are in grams and those for temperature are in degrees Celsius. NJ = New Jersey; SC = South Carolina.

gators. Clearly, simple hypotheses cannot adequately explain patterns of acclimatization in ectotherms, and studies should be designed to examine hypotheses that incorporate multiple causality at a biochemical level (Clarke 1993).

Intraspecific variation in metabolic rate has been found in most major groups of vertebrate ectotherms (see review by Garland and Adolph 1991). At least one conclusion can be drawn from the available data; individuals that inhabit stronger seasonal climates tend to have higher metabolic rates. For certain, my data for *S. undulatus* are consistent with this notion. I found that adult lizards from New Jersey had a higher RMR than adult lizards from South Carolina in two of three seasons (Fig. 2). Although average body mass of NJ adults was greater than that of SC adults, the difference in RMR persisted after adjusting metabolic rates for body mass. Likewise, SMR in *S. occidentalis* was higher for lizards from Washington than lizards from California (Tsuji 1988). Also, the rate of O<sub>2</sub> consumption by male *S. occidentalis* was positively correlated with altitude of the source population (Jameson et al. 1977). Such intraspecific variation in RMR has important implications for understanding the proximate causes of geographic variation in life history because maintenance metabolism directly affects production efficiency (Calow and Townsend 1981).

The greater annual production of SC lizards may be caused by a higher rate of energy assimilation, a lower rate of energy expenditure, or both. Previously, investigators have proposed that thermal constraint on annual energy assimilation is the primary cause of life history variation in *S. undulatus* (Grant and Porter 1992; Adolph and Porter 1993, 1996). Several lines of evidence support the notion that SC lizards assimilate more energy per year than NJ lizards. Lizards in South Carolina experience a warmer environment and are active for a longer duration than lizards in New Jersey; SC lizards become active

in March and remain active into November, but NJ lizards do not emerge until April and cease activity in October (Angilletta 2002). Because lizards in both populations maintain a body temperature during activity that enhances energy assimilation (Angilletta 2002), the longer activity time of SC lizards would allow a greater annual energy budget. Specifically, I estimated that SC lizards can assimilate up to 60% more energy per year than NJ lizards (Angilletta 2002). As predicted, estimated annual activity time is positively correlated with reproductive output of female *S. undulatus* (Grant and Porter 1992; Adolph and Porter 1993).

Table 4: Daily activity time and maintenance metabolism of *Sceloporus undulatus* in South Carolina and New Jersey

Population	Activity (h)	Maintenance (J)	
		Juvenile	Adult
New Jersey:			
Spring	7	48 (1.5 g)	205
Summer	12	198 (3.0 g)	333
Fall	8	72 (1.0 g)	428
South Carolina:			
Spring	9	99 (3.0 g)	226
Summer	12	88 (1.0 g)	148
Fall	10	90 (1.5 g)	149

Note. Maintenance metabolism was calculated using regression equations for resting metabolic rate, activity time, and field body temperatures (see text for details). A constant body mass of 7.5 g was assumed for adult lizards, but body masses of juveniles were based on average masses in each season. The body mass used to calculate maintenance metabolism of juveniles for each season is given in parentheses.

Conversely, very little is known about the contribution of variation in energy expenditure to geographic patterns of life history in *S. undulatus*. Because lizards in South Carolina are often active at relatively high body temperatures (32°–35°C) for a longer duration each day, it is presumed that their daily maintenance expenditure is greater than that of lizards in New Jersey. However, RMR of NJ adults was higher than that of SC adults in summer and fall. As a result, lizards in New Jersey had a greater daily maintenance expenditure in these seasons, despite shorter daily activity times (Table 4). The greater daily maintenance cost of NJ lizards impacted the annual maintenance budget. A NJ adult expended an estimated 53.7 kJ yr<sup>-1</sup>, whereas a SC adult expended only 45.8 kJ. The lower maintenance cost of SC lizards necessarily results in a higher production efficiency. Thus, the greater reproductive output of SC lizards is partly a product of physiological differentiation between populations.

My results highlight the importance of considering multiple causality of ecological phenomena (Quinn and Dunham 1983). Intraspecific variation in life history phenotypes of *S. undulatus* results from differences in energy assimilation and energy expenditure between populations. Similar physiological mechanisms are likely to operate in other species that are geographically widespread. Undoubtedly, a genuine understanding of the proximate causes of geographic variation in the life histories of ectotherms will not be achieved by formulating simple causal hypotheses but will compel an integrative approach designed to tease apart the relative contribution of multiple mechanisms.

### Acknowledgments

I thank M. Angilletta, Sr., R. Estes, and D. Kling for field assistance. A. Dunham and J. Congdon provided logistical support, advice, and encouragement. Discussions with P. Niewiarowski facilitated design and execution of the study. W. Porter kindly assisted in the use of his computer programs to calculate activity times. Lizards in New Jersey were collected with permission from the New Jersey Department of Environmental Protection, Division of Fish, Game, and Wildlife. All work was conducted with the approval of the University of Pennsylvania Institutional Animal Care and Use Committee. Financial support was received from the University of Pennsylvania Research Foundation and a Sigma Xi grant-in-aid of research. Previous versions of the manuscript were improved by J. Congdon, J. McNair, L. Rome, and R. Winters.

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