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# Energy Budgets, Growth Rates, and Thermal Constraints: Toward an Integrative Approach to the Study of Life-History Variation

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**ABSTRACT:** Variation in thermal constraints on activity has been hypothesized to be an important ecological source of geographic variation in growth rates of juvenile eastern fence lizards *Sceloporus undulatus*. However, most of the evidence to support this hypothesis is either inferential or indirect. In this study, I quantitatively compared thermal constraints on activity and their relationship to growth rates of free-ranging juvenile fence lizards from two extremes of the range of variation in growth rate (Nebraska and New Jersey) used in a reciprocal transplant experiment. I also examined energy allocation made to growth and storage by yearling lizards. Reduced growth rates in New Jersey of normally fast-growing hatchlings from Nebraska were associated with a more stringent thermal constraint on activity corresponding to a 2–3-h shorter predicted daily activity period in New Jersey compared to Nebraska. The thermal constraint on activity was particularly strong (24% less time available in New Jersey compared to Nebraska) during the period when hatchling lizards emerge (August–October). An 8% reduction in total activity time available over the course of a single year was associated with a 7% reduction in the total amount of energy accumulated by lizards in New Jersey. Differences in the total amount of energy available for allocation were also accompanied by differences in how energy was allocated. Lizards from New Jersey had an allocatable energy pool of approximately 40.34 kJ (88% to growth, 12% to storage, and 0% to reproduction). Lizards from Nebraska had an allocatable pool of 43.44 kJ (22% to growth, 18% to storage, and 60% to reproduction). This study joins others in advocating and illustrating an integrative approach to determining the causes and consequences of life-history variation by combining experimental, comparative, and phylogenetic methods in a single system.

**Keywords:** biophysical constraint, eastern fence lizard, geographic variation, growth rate, life history, *Sceloporus undulatus*.

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Species distributed across broad geographic ranges often display extensive variation in life-history phenotypes, and such variation has been the subject of extensive theoretical and empirical work (see Roff 1992; Stearns 1992; Charnov 1993 for recent reviews). Traditionally, most life-history theory begins with the assumption that phenotypic life-history variation has an adaptive basis and then applies either genetic analysis or phenotypic optimization to explain how the variation evolved (Roff 1992). In the past 15 yr, analysis of life-history variation has increased in sophistication and potential realism, owing to explicit consideration of the role of phenotypic plasticity (e.g., Stearns and Koella 1986; Berrigan and Charnov 1994; Atkinson and Sibly 1997). However, incorporation of plasticity in life-history models may be advancing faster than our understanding of how plasticity is generated (*sensu* Travis et al. 1999) and of the consequences that accrue in systems to which models are applied (Gotthard and Nylin 1995; Nylin and Gotthard 1998).

Nowhere is the gap between theoretical implementation and empirical understanding greater than in analyses of growth rate variation. Although most life-history theory has traditionally targeted the evolution of reproductive traits (Arendt 1997), growth is often implicitly modeled since it is assumed to trade off with reproduction (e.g., Stearns and Crandall 1981; Kozłowski and Teriokhin 1999; Roff 2000). Recently, explicit analysis of growth rate variation, especially across environmental gradients (i.e., geographic variation within and among populations or species), has received increased attention in studies ranging from tests of Bergmann's rule (e.g., Atkinson and Sibly 1997; Arnett and Gotelli 1999) to the search for life-history invariants (e.g., Berrigan and Charnov 1994). If there is a common theme developing from studies of growth rate variation, it is that, in spite of tight correlations between growth rate and other life-history traits (Arendt 1997), our understanding of the ecological and evolutionary signifi-

cance of growth rate variation is obscured by phenomena such as countergradient selection (Conover and Schultz 1995; Arendt and Wilson 1999; Billerbeck et al. 2000) and phenotypic plasticity (Nylin and Gotthard 1998).

Given that geographic variation in growth rate has complex sources (Arendt 1997), analyses usually proceed according to an operationally useful but inherently false dichotomy (Trexler and Travis 1990; Sinervo and Svensson 1998; Travis et al. 1999) between genetic ("ultimate") and environmental ("proximate") sources of variation. The dichotomy is false because prediction and understanding require examination of both sources as well as their interaction (Duvall and Beaupre 1998); systems that allow us to study how environmental and genetic sources of variation are integrated will illuminate not only the limitations of the dichotomy but will also suggest the necessary properties of a more comprehensive and synthetic life-history theoretical framework (Bernardo 1993, 1994).

Many study systems have the potential to contribute to building a more integrative theoretical framework, including one of the most extensively studied cases of geographic variation in life-history traits of vertebrate ectotherms, the eastern fence lizard *Sceloporus undulatus*. Comparative studies have documented twofold variation in many life-history traits among 13 populations of *S. undulatus* across its range (Tinkle and Ballinger 1972; Tinkle and Dunham 1986; Gillis and Ballinger 1992). Adaptive hypotheses based on traditional life-history theory have been proposed, tested (e.g., Stearns and Crandall 1981), and also challenged because assumptions about genetic differences remain largely unsubstantiated (Niewiarowski 1994). Furthermore, geographic variation in individual growth rates, reproductive output (Grant and Porter 1992; Adolph and Porter 1993), and age at maturity (Adolph and Porter 1996) are surprisingly well predicted by several nonevolutionary biophysical models driven solely by temperature effects on physiological processes.

Using a reciprocal transplant experiment, Niewiarowski and Roosenburg (1993) demonstrated genetic differences in growth rate plasticity between two populations at the extremes of the range of observed variation in growth rate in the species (Nebraska and New Jersey); Nebraska lizards, which normally grow rapidly, grew half as fast when transplanted to New Jersey, but New Jersey lizards showed no increase in normally slow growth rates when transplanted to Nebraska. Reciprocal transplantation revealed the relative contribution of genes and environments to producing growth rate variation between Nebraska and New Jersey, but this very dichotomy represents the starting rather than the ending point of study. Given what we know about growth rate variation between New Jersey and Nebraska, two central questions not readily addressed by existing theoretical or empirical approaches are, Do the dif-

ferences in plasticity reflect genuine plasticity (McManus and Travis 1998)? and Are current environmental differences related to phenotypic and genetic differences in plasticity? Answers to these questions are at the very heart of moving beyond the genes versus environment dichotomy.

A life history is a heritable set of "rules" that determines age-specific allocations of time and energy that an individual makes over its lifetime (Dunham et al. 1989). The rate at which an individual grows reflects proportional allocation of net assimilated energy (NAE) made to growth, maintenance, storage, and reproduction (Congdon et al. 1982; Dunham et al. 1989; McManus and Travis 1998). Variation in growth rate between populations could reflect either differences in NAE under identical proportional allocations, differences in proportional allocations, or a combination of both. Only the latter two possibilities, requiring an energy budget analysis, represent genuine plasticity (McManus and Travis 1998).

Biophysical modeling (Adolph and Porter 1996) and reciprocal transplant (Niewiarowski and Roosenburg 1993) have implicated temperature, operating through constraints on thermoregulation and activity, as an important source of phenotypic variation in individual growth rate in *S. undulatus*. Thermal constraints have been hypothesized as an important source of geographic life-history variation in free-ranging ectotherms (Tinkle 1972; Tinkle and Ballinger 1972; Levinton and Mohan 1983; Conover and Present 1990; Bernardo 1994) and in laboratory experiments (Avery 1984; Sinervo and Adolph 1989; Sinervo 1990). However, while thermal constraints have been frequently invoked to explain life-history variation in *S. undulatus* (Niewiarowski 1994), they have never been formally estimated.

In this study, I examine proportional allocation of NAE by *S. undulatus* from Nebraska and New Jersey and estimate constraints on activity imposed by their respective thermal environments. This approach allows me to determine whether differences in growth rate plasticity between these two populations result from differences in proportional allocation, and whether thermal constraints on activity are associated with differences in plasticity.

## Material and Methods

### *Study Sites*

Biophysical and energy-budget comparisons were made at a pair of adjacent sites (see Niewiarowski and Roosenburg 1993) in both Nebraska (41°34'N, 101°41'W; 1,000 m) and New Jersey (39°45'N, 74°44'W; 7 m). The Nebraska sites are located in sandhills prairie in Arthur County and include large blowouts irregularly vegetated with grasses

and yucca; a detailed description of this area may be obtained from Keeler et al. (1980) and Ballinger and Jones (1985). In New Jersey, the sites are located in Wharton State Forest in Burlington County. The New Jersey sites are sandy soiled, oak-pitch pine forest associations typical of upland areas in the New Jersey Pine Barrens (Forman 1979).

#### *Characterizing the Biophysical Environment*

I divided the New Jersey and Nebraska lizard activity season of 1989 and 1990 into three, one-trimester sampling periods to estimate seasonal variation in the distribution of microhabitat temperatures. The first trimester commenced with the onset of lizard activity in spring (beginning of April: Ballinger et al. 1981; P. H. Niewiarowski, unpublished data) and extended through May. The second trimester extended through June, July, and August, and the third trimester began in September and ended with the cessation of lizard activity at the end of October (Ballinger et al. 1981; P. H. Niewiarowski, unpublished data). Although the precise dates marking the beginning and end of each trimester are somewhat arbitrary, the sampling intervals were chosen to represent early, middle, and late climatic conditions at each locality.

Sampling of the biophysical environment was conducted for 4 d in the middle of each trimester in both Nebraska and New Jersey. Sampling methods closely followed those outlined in Grant and Dunham (1988) and Grant (1990). I constructed hollow copper models of *Sceloporus undulatus* (Grant 1988), fitted them with thermocouples, painted them to match live lizards visually, and then deployed them along transects that extended through the study sites. A critical assumption of this technique is that copper models realistically estimate the body temperature of a live lizard. I verified this assumption for my models by comparing  $T_e$  (standard operative temperature; Bakken 1980) to  $T_b$  (body temperature) for a sample of lizards in each population. I regularly patrolled the study sites and captured lizards that had been stationary for five or more minutes and quickly recorded their  $T_b$  (using a rapid reading thermometer) on capture (see Grant and Dunham 1988). Immediately subsequent to a lizard's capture, I placed a copper model in the exact perch location of the captured lizard, allowed the model to equilibrate thermally for 2 min, and then recorded the model's temperature. Operative temperature was compared to  $T_b$  by linear regression. In order for  $T_e$ 's to be reliable estimates of  $T_b$ 's,  $T_e$  should explain a high proportion of variance in  $T_b$ .

To estimate the relative availability of thermally suitable microhabitats, a single transect of copper models (Grant

and Dunham 1990) was deployed in a randomly chosen compass direction on each of 4 d in an area of high apparent lizard density at each site. Transects were 37 m long, with models spaced at 1-m intervals, each in a randomly selected compass direction. Standard operative temperature was monitored with a Campbell CR10 data logger that scanned all models once every minute and calculated 15-min averages for each model throughout the course of the day. The substratum on which each model rested was noted and classified according to a classification scheme specific to Nebraska (e.g., yucca, ground) or New Jersey (e.g. ground, tree, log). At hourly intervals, I also walked along the transect of copper models and recorded the type of solar radiation experienced by each model (e.g., full sun, shade, partial sun) as well as the model's orientation with respect to the radiation (e.g., head-on, tail-on, side) and the angle of incidence (e.g. perpendicular, oblique, tangent). In addition to the transect of copper models, I also recorded the substratum and solar radiation characteristics (hereafter, substratum-solar microhabitat types) of 100 additional sample points along two more 50-m transects deployed in the same area as the copper model transect but in different randomly selected compass directions. I used mean temperatures from copper models within a particular substratum-solar microhabitat type to estimate the temperatures of the extra sample points along the transects without copper models and assumed that models within substratum-solar categories provided unbiased estimates of  $T_e$ 's in substratum-solar microhabitats along transects without copper models. This technique allowed me to increase the sample size of the relative frequencies of perch microclimate types and temperatures.

For each trimester sampling period at each locality, I used estimates of substratum-solar microhabitat type temperatures (copper model transects) and estimates of the hourly frequency of these types (copper model plus additional transects) to estimate the temporal distribution of temperatures. These data are presented as hourly estimates of the fractional availability of microhabitats (summed across all substratum and solar categories) falling within the range of observed body temperatures recorded for active lizards in each population (20.0°–40.0°C; P. H. Niewiarowski, unpublished data). I used the range of body temperatures observed in free-ranging lizards as a cutoff because it represents the potential for activity under the full range of behavioral conditions under which lizards are active. I included data only from clear, sunny days (in each trimester at each site) to reduce uncontrolled variation between sampling periods and sites. Consequently, estimates should be considered upper bounds on microhabitat availability and potential activity. Lizards can be active during nonclear days in both populations (P. H. Niewia-

rowski, unpublished data), but my estimates do not address differences during those kinds of climatic conditions.

### *Lizard Activity Patterns*

In order to quantify actual lizard activity, I walked standardized transects of approximately 0.75 km at hourly intervals through the same habitat and at the same time copper models were deployed. During these walks, I recorded observations of lizards active on the surface. For each site and trimester, lizard activity was expressed as the percentage of the maximum number of lizards observed during the walking of any single transect.

### *Energy Allocation*

Net assimilated energy includes energy allocated to production (tissue) as well as that allocated to metabolism. I estimated energy allocated to the production of tissue only and hereafter refer to it as  $NAE_{pro}$ . Furthermore, I categorized  $NAE_{pro}$  as either growth (carcass mass excluding fat bodies) or storage (abdominal fat-body mass). Abdominal fat bodies are a major site for storage lipids in lizards (Derickson 1976b) and have been used to estimate relative energy reserves and general condition of fence lizards (Gillis and Ballinger 1992). Although lizards can store lipids exclusive of fat bodies (Derickson 1976b), there is no reason to expect lizards from Nebraska and New Jersey to differ with respect to storage locations. I assumed that fat-body storage provides a comparable relative index of storage lipids from these two populations.

Absolute and proportional allocation of energy to growth ( $G$ ) and storage ( $S$ ) were estimated for two groups of yearling females collected from both Nebraska and New Jersey in 1989 and 1990. Lizards were collected from each population at the onset and termination of each activity season. I regard differences in  $G$  and  $S$  between initial and final collections as estimates of proportional allocation to  $G$  and  $S$  over a single activity season. Immediately after collection, lizards were autopsied. I removed fat bodies from each lizard, froze the carcass and fat bodies, and then lyophilized fat samples to constant mass. Conversion of dry mass to energy equivalents was accomplished using published values for lean tissue and lipid in *S. undulatus* (Derickson 1976a).

### *Statistical Analyses*

All data were analyzed with SAS/JMP statistical software (SAS Institute 2000). Homogeneity of variances and nor-

malinity were checked before performing ANOVAs, and transformations were made when the raw data did not fit these assumptions. Microhabitat availability data were analyzed qualitatively for trends and quantitatively using logistic regression with Wald effect tests. I ran a fully saturated model separately for each year (sources: time, population, trimester). Reduced models were constructed and tested by removing nonsignificant interaction terms. Qualitative trends in the distribution data were tested by referencing the significance of specific sources in the appropriate reduced models. Energy allocation data were analyzed by ANCOVA, using body mass as a covariate to account for differences in body size (Hayes and Shonkwiler 1996; Packard and Boardman 1999).

## Results

### *Thermal Environment and Lizard Activity Patterns*

Copper model  $T_c$  explained 86% and 91% of the variation in lizard  $T_b$ , in Nebraska and New Jersey, respectively (fig. 1). Estimates of the relative availability of microhabitats with  $T_c$ 's within the range of  $T_b$ 's exhibited by *Sceloporus undulatus* at each locality, along with the mean model temperature and estimates of relative activity, are shown in figures 2 and 3. Restricting attention to estimates of microhabitat availability and mean  $T_c$ 's, time-dependent profiles of relative microhabitat availability are similar between years in both Nebraska and New Jersey. However, these profiles varied substantially between trimesters within a single active season. The most obvious trend in Nebraska was a drastic reduction in the relative availability of suitable microhabitats during the middle of the day in the second trimester when mean model temperatures were equal to or exceeded 50°C (fig. 2). For all three trimesters, microhabitat availability varied significantly with time of day (1989: Wald  $\chi^2 = 33.7$ ,  $df = 9, 18$ ,  $P < .0001$ ; 1990: Wald  $\chi^2 = 93.7$ ,  $df = 9, 18$ ,  $P < .0001$ ), and there was a significant time of day by trimester interaction (1989: Wald  $\chi^2 = 322.5$ ,  $df = 18, 18$ ,  $P < .0001$ ; 1990: Wald  $\chi^2 = 590.0$ ,  $df = 18, 18$ ,  $P < .0001$ ) associated with differences in the hour when microhabitats first became available or ceased to be available (figs. 2, 3). In both cases, initiation and cessation of the potential for activity coincided with average model temperatures of 10°–15°C.

Trends similar to those just described for Nebraska also characterized the profiles of relative microhabitat availability in New Jersey. Two distinctions between these sites were apparent, however. First, in New Jersey, the reduced relative availability of microhabitats during midday of the second trimester was not as drastic as in Nebraska (figs. 2, 3; 1989: time of day  $\times$  population interaction, NS, pop-

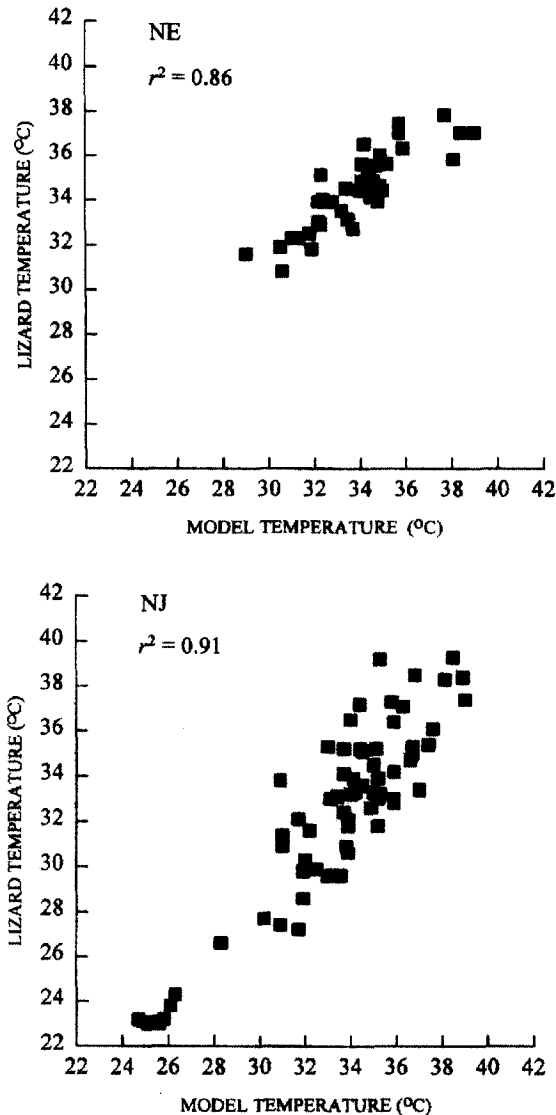


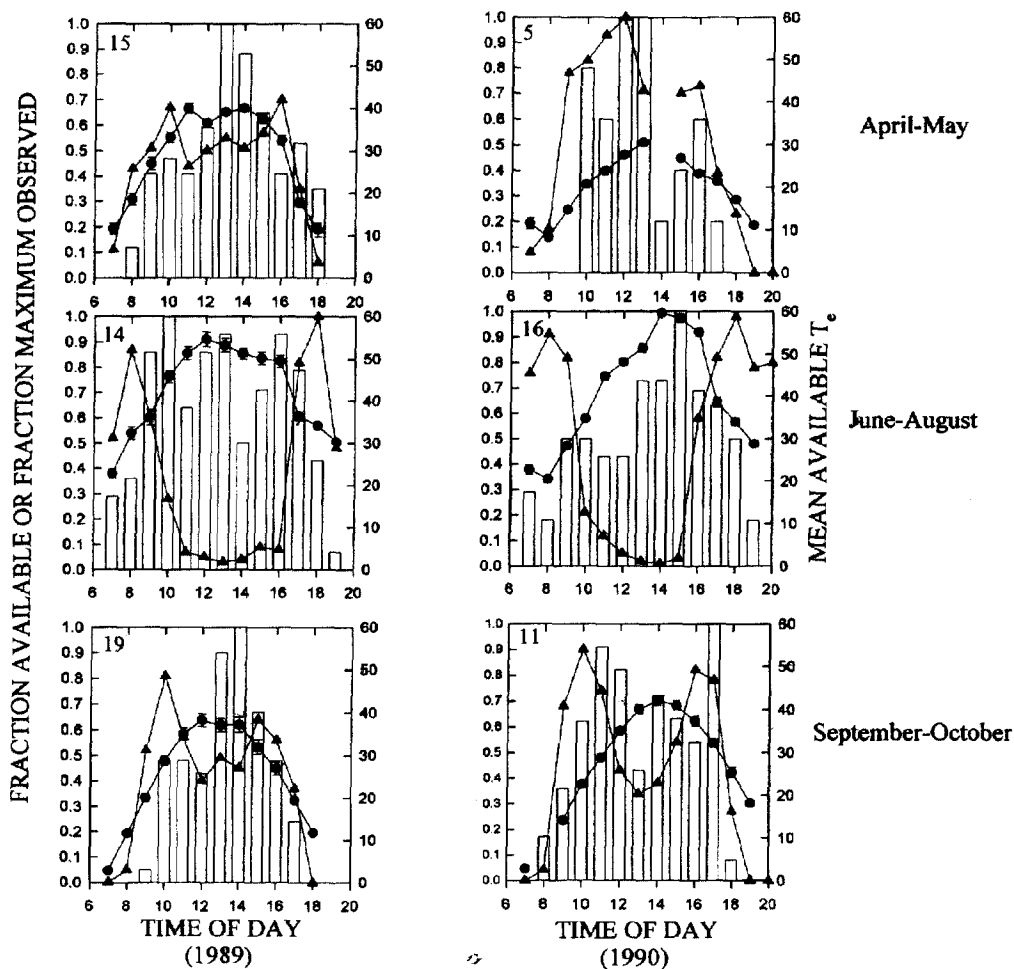
Figure 1: Population-specific regressions of lizard body temperature ( $T_b$ ) on copper model temperature ( $T_e$ ).

ulation Wald  $\chi^2 = 490.8$ ,  $df = 1, 9$ ,  $P < .0001$ ; 1990: time of day  $\times$  population interaction, NS, population Wald  $\chi^2 = 74.3$ ,  $df = 1, 9$ ,  $P < .0001$ ). For example, mean model temperatures peaked between 30°C and 40°C in New Jersey, and relative availabilities still exceeded 35%, while during the corresponding period in Nebraska, only between 1% and 3% of the habitat was available (figs. 2, 3). A second difference was that, during the third trimester, thermally suitable microhabitats were only available between 1000 and 1700 hours compared to approximately 900 and 1800 hours in Nebraska (figs. 2, 3).

Estimates of relative activity levels superimposed on the availability of microhabitats and mean model temperatures (figs. 2, 3) illustrate that the relationship between lizard activity patterns and the thermal environment are complex. For example, high levels of activity were observed in Nebraska even when microhabitat availability estimates were very low (1%–2%, second trimester, middle of the day), but in both Nebraska and New Jersey, availabilities exceeding 5% were not necessarily associated with the initiation of lizard activity at the start of the day. One encouraging pattern that emerged for both study sites in all three trimesters and both years was that activity was not observed when estimates of relative microhabitat availability were 0% (figs. 2, 3). However, *S. undulatus* in Nebraska had a remarkable ability to find suitable microhabitats when they were estimated to be extremely rare (between 1% and 3%, second trimester; fig. 2). In general, approximately 1 h after microhabitats became available and 1 h before they ceased to be available, activity levels equaled or exceeded 40% of the maximum levels observed during any single activity transect (figs. 2, 3). Assuming that *S. undulatus* from both populations were similarly capable of finding suitable microhabitats when rare (1%–5%), I assumed that activity was possible, with respect to thermal opportunities, at any time when the relative availability of microhabitats was  $>0\%$ . Estimates of potential activity day lengths using this criterion and the data presented in figures 2 and 3 are shown in table 1. The potential activity day lengths in Nebraska and New Jersey usually only differed by an hour or less, except during the third trimesters, where they were  $\geq 2$  h greater in Nebraska.

#### Mass and Energy Allocation

Population and date of collection (sample) had significant effects on yearling lizard body size. Nebraska yearlings were heavier than New Jersey yearlings at emergence (contrast,  $t = -5.39$ ,  $P < .0001$ ) but not at the end of the activity season (contrast,  $t = 1.7301$ ,  $P > .087$ ), accounting for a significant population by sample interaction (New Jersey lizards gained mass more rapidly than Nebraska yearlings) and a marginal population effect (table 2). Amount of energy devoted to fat stores corrected for size (body mass as a covariate) was affected by population, sample, size, and their interactions (table 3). Pairwise comparisons showed that Nebraska and New Jersey yearlings did not significantly differ in the proportion of  $NAE_{pro}$  they allocated to fat storage at emergence (Tukey HSD,  $\alpha = 0.05$ ). However, New Jersey yearlings had reduced proportional allocation to storage at the end of the season compared to emergence, as well as lower proportional al-



**Figure 2:** Plots of observed activity level, average copper model temperature, and relative microhabitat availability in Nebraska. Panels show the three sampling trimesers from top to bottom, with 1989 in the left column and 1990 in the right column. Solid triangles show percentage of the habitat available to lizards for activity (see text for description), bars show percentage (of maximum) of lizards active along standardized transects, and solid circles show average  $T_c$  along copper model transects. Number inset in upper left corner of each panel represents the maximum number of lizards seen during any walked transect during the sampling period. Error bars are  $\pm 2$  SE. Gap in microhabitat availability during April–May 1990 was due to a data logger failure.

location compared to Nebraska yearlings at the end of the season (Tukey HSD,  $\alpha = 0.05$ ).

### Discussion

Differences between New Jersey and Nebraska in the potential time available for activity, based on estimates of lizard activity and the distribution of thermally acceptable microhabitats (table 1; figs. 2, 3), support the hypothesis that slow growth rates of Nebraska hatchlings transplanted to New Jersey resulted from a decrease in potential activity time (Niewiarowski and Roosenburg 1993). Interestingly,

differences between populations in estimated activity day length (table 1) were largest (~2–3 h) at the same time of year when the transplant experiment was conducted and hatchlings are active (mid-August–October, third trimester). Estimates of microhabitat availability suggest there is less time during the day when hatchlings can maintain body temperatures ( $T_b$ ) near their average field  $T_b$ . Such a constraint could influence growth rate directly (i.e., limiting physiological processes supporting growth or growth itself) or indirectly (e.g., reduced foraging success).

Analysis of thermally suitable microhabitat availability shows that activity day lengths were on average 2 h shorter in New Jersey during the third trimester. Furthermore, dif-

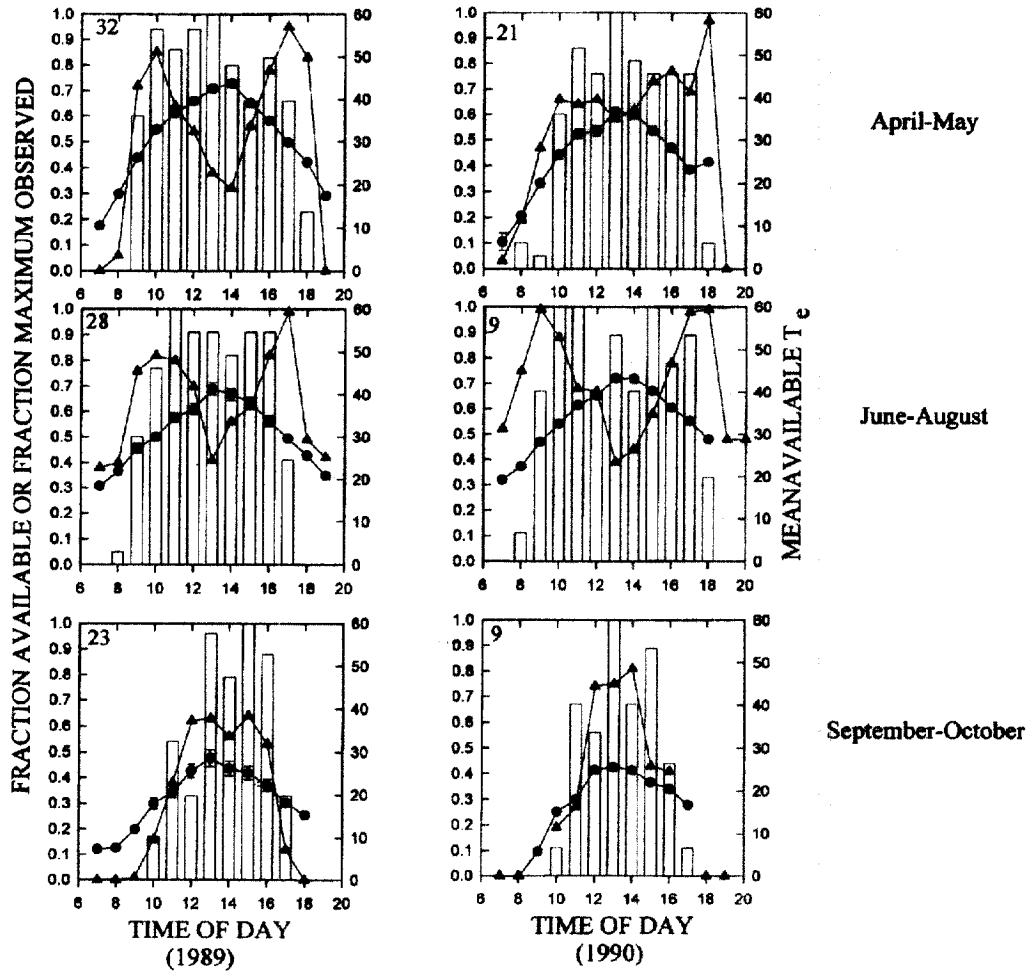


Figure 3: Same as figure 2 but for New Jersey; gap in microhabitat availability during September–October 1990 was due to a data logger failure

ferences in activity day lengths were correlated with differences in both the proportional allocation and absolute availability of  $NAE_{pro}$ . Nebraska yearlings started out the activity season larger (wet mass; tables 2, 4), possibly because of increased activity time the previous trimesters, but by the end of the season, New Jersey yearlings were larger. Even though they were not significantly larger than their Nebraska counterparts, at the end of the activity season, New Jersey yearlings did nevertheless grow significantly faster (table 2; populations  $\times$  sample,  $P < .0001$ ). However, proportional allocation by yearlings to fat-body mass was higher in Nebraska by the end of the activity season, with New Jersey yearlings actually decreasing in relative fat stores (tables 3, 4).

Estimating  $NAE_{pro}$  as total carcass mass ignores allocation to reproduction (i.e., eggs), which is realistic for New Jersey yearlings because they had not yet reached

maturity. However, yearlings from Nebraska produce two or three clutches of eggs (Jones and Ballinger 1987), which is allocation not included in the two-point sampling regime I used. Assuming that each yearling allocated mass and energy equivalent to the average for two clutches (Jones and Ballinger 1987), estimated  $NAE_{pro}$  of Nebraska yearlings can be compared to the measured  $NAE_{pro}$  of New Jersey yearlings. Such a comparison reveals that  $NAE_{pro}$  of Nebraska yearlings, including mass and energy from two average-sized clutches, actually appears to exceed the measured  $NAE_{pro}$  of New Jersey lizards (table 4). If the total energy devoted to the production of eggs by Nebraska yearlings had instead been allocated to growth, the projected wet mass would be very similar to the actual wet mass of yearlings from New Jersey (table 4). This suggests that differences in body size between yearlings from Nebraska and New Jersey are mainly a function of differences



**Table 1:** Estimates of potential activity day length based on microhabitat availability data and a 0% criterion (see "Results")

Site and trimester	1989			1990			Mean daily activity (h)	Mean trimester activity (h)
	Start time	Finish time	Time (h)	Start time	Finish time	Time (h)		
Nebraska:								
1 (61)	0700	1830	11.5	0700	1900	12.0	11.75	717
2 (92)	0600	2030	14.5	0600	2030	14.5	14.5	1,334
3 (61)	0800	1800	10.0	0800	1900	11.0	10.5	641
Season total								2,692
New Jersey:								
1 (61)	0800	1900	11.0	0700	1900	12.0	11.5	702
2 (92)	0630	2030	14.0	0630	2030	14.0	14.0	1,288
3 (61)	1000	1800	8.0	1000	1800	8.0	8.0	488
Season total								2,478

Note: Numbers in parentheses are days.

in proportional allocation of  $NAE_{pro}$  rather than merely the absolute amount of  $NAE_{pro}$ . Alternatively, energy devoted to the production of eggs by yearling Nebraska lizards could have been allocated to storage (e.g., fat bodies) or to a combination of functions other than growth. In either case, it is clear that differences in growth between yearlings from Nebraska and New Jersey resulted in large part from differences in proportional allocation, rather than from differences in total  $NAE_{pro}$ .

There is a surprisingly close association between differences in the estimated length of the activity season length (table 1) and differences in  $NAE_{pro}$ , comparing Nebraska and New Jersey (table 4). On average, New Jersey lizards have approximately 92% as much activity time as Nebraska lizards over the course of a season when the biophysical environment would allow them to maintain their selected body temperature (within the range of observed  $T_b$ 's). With about 92% as much time for activity, New Jersey lizards accumulate approximately 93% of the total  $NAE_{pro}$  that Nebraska lizards accumulate (table 4; estimated  $NAE_{pro}$  total). The Nebraska and New Jersey populations are on opposite ends of the spectrum of variation in life-history characteristics, including hatchling growth rates, age at maturity, average adult body size, and longevity (Jones and Ballinger 1987; Niewiarowski 1994), yet estimated annual activity time and  $NAE_{pro}$  in New Jersey is reduced to only approximately 92% and 93%, respectively, relative to Nebraska.

New Jersey lizards have approximately 76% as much time available for activity during their third trimester (488 vs. 641 h; table 1). Energetic consequences of shorter time available for activity in New Jersey can be interpreted in two ways. Yearling New Jersey lizards collected in this study had a 44% lower  $NAE_{pro}$  than yearling Nebraska lizards (table 4; measured  $NAE_{pro}$ ). A less rigorous comparison of

energy accumulation, based solely on body size of hatchlings at the end of the third trimester suggests a similar deficit in energy accumulated. Average body length (snout vent length, SVL) of Nebraska hatchlings at the end of the third trimester was 44.5 mm compared to 35 mm for New Jersey hatchlings (Niewiarowski and Roosenburg 1993), a difference of 79%. By either comparison, less time available during the third trimester of the activity season is correlated with a profound difference in energetics of lizards from these two populations—particularly hatchlings and yearlings just as they are emerging from hibernation.

Patterns of energy allocation revealed in this study agree qualitatively with a simulation study predicting geographic variation in growth rate, age, and size at maturity of fence lizards as a function of population differences in biophysical environments and the constraints of reproductive seasonality (Adolph and Porter 1996). Clearly, biophysical constraints are correlated with energy allocation and life-history differences. Results presented here indicate that for fence lizards in New Jersey and Nebraska, life-history dif-

**Table 2:** ANOVA comparing wet mass (g) of lizards collected at the beginning and end of the activity season (sample) from both populations

Source	df	Sums of squares	F	P
Sample	1	24,981.340	211.0852	<.0001
Populations	1	394.685	3.3350	.0719
Populations × sample	1	2,508.149	21.193	<.0001
Error	74	8,757.692	...	...
Total	77	36,641.866	...	...

Note: Overall model adjusted  $r^2 = 0.77$ ,  $P < .0001$ .

**Table 3:** ANOVA showing an ANCOVA on abdominal fat-body mass corrected for body size of lizards collected at the beginning and end of the activity season (sample) from both populations

Source	df	Sums of squares	F	P
Covariate	1	.01440	29.28	<.0001
Sample	1	.00259	5.27	.0246
Populations	1	.02169	44.09	<.0001
Covariate × sample	1	.01169	23.78	<.0001
Covariate × populations	1	.00568	11.56	.0011
Sample × populations	1	.01355	27.54	<.0001
Covariate × sample × populations	1	.00748	15.22	.0002
Error	70	.03443	...	...
Total	77	.12709	...	...

Note: Covariate is  $\log(\text{wet mass} - \text{wet fat-body mass})$ . Overall model adjusted  $r^2 = 0.70$ ,  $P < .0001$ .

ferences may be most sensitive to biophysical constraints on energy allocation during the third trimester of a hatchling lizard's life. Net assimilated energy allocated to production of tissue differs only by about 7% over the course of a yearling's activity season. The main difference between New Jersey and Nebraska yearlings is in how that energy is allocated; Nebraska yearlings allocate 60% of  $\text{NAE}_{\text{pro}}$  to reproduction compared to 0% for New Jersey yearlings. However, stronger biophysical constraints on activity in New Jersey are not sufficient to explain differences in proportional allocation patterns. For example, approximately 42% of yearling females in New Jersey have attained minimum reproductive size for the species (Nebraska; 44–45 mm SVL; Ballinger et al. 1981) by the end of May, leaving a full 2 mo in which to provision yolk to follicles and produce a clutch of eggs (P. H. Niewiarowski, unpublished data). Assuming that  $\text{NAE}_{\text{pro}}$  is accumulated linearly, approximately 0.19 kJ/d would be available for the production of a clutch. Over a period of 60 d, an individual would have 11.31 kJ available, which is similar to the minimum kilojoule content of a clutch of eggs for a yearling Nebraska lizard clutch (11.5 kJ; Jones et al. 1987b). What this analysis shows is that, from an energetic perspective, reproduction by New Jersey yearlings appears possible. In other words, the biophysical constraint does not appear to be a sufficient explanation for delayed maturity.

One alternative hypothesis is that although it is bioenergetically possible, there may be a selective disadvantage to reproducing early. In order to test this hypothesis, it would be necessary to compare the fitness of early and delayed maturation phenotypes in the population where

delayed maturity is observed. An experimental approach to testing this hypothesis will have to await a method for altering age at maturity (Niewiarowski et al. 2000). Nevertheless, in lieu of such an experiment, differences in juvenile growth rates and their consequences for other life-history traits among populations of *Sceloporus undulatus* have been described, in part, as reflecting locally selected life-history strategies (Tinkle and Ballinger 1972; Ferguson et al. 1980; Ballinger et al. 1981). However, an adaptationist interpretation has been difficult to evaluate because ecological and evolutionary responses to these environments have not been identified (Ferguson and Brockman 1980; Gillis and Ballinger 1992). Different growth rate responses of *S. undulatus* from Nebraska and New Jersey raised in both localities (Niewiarowski and Roosenburg 1993) and resulting from population-specific differences in allocation of  $\text{NAE}_{\text{pro}}$  to growth and storage (tables 2, 3) reflect evolutionary divergence and, therefore, provide an opportunity to evaluate hypothetical evolutionary mechanisms that could have led to the divergence. Most hypotheses focus on how resources and schedules of mortality affect the relative costs and benefits associated with slow growth and delayed maturity versus rapid growth and early maturity. For example, it has been suggested that rapid juvenile growth leading to early maturity is expected when resources are relatively abundant and extrinsic mortality is relatively high (Tinkle and Ballinger 1972; Ferguson and Brockman 1980; Ballinger et al. 1981; Tinkle and Dunham 1986). Alternatively, slow juvenile growth leading to delayed maturity should be favored when resources are relatively limited and extrinsic mortality is relatively low (Tinkle and Ballinger 1972; Ferguson and Brockman 1980; Ballinger et al. 1981; Tinkle and Dunham 1986). Consider how the populations in Nebraska and New Jersey fit this pattern. In Nebraska, only approximately 10% of hatchling *S. undulatus* survived to the yearling stage (Jones and Ballinger 1987), placing a high premium on rapid growth that makes possible the attainment of minimum reproductive size by 9 mo of age. Furthermore, food is apparently abundant and does not appear to limit hatchling growth rates (Jones et al. 1987a). The combination of high growth rates and early maturity of Nebraska *S. undulatus* fits neatly into the above scheme, but what about *S. undulatus* from New Jersey? Hatchlings from New Jersey have a similarly low probability of surviving their first year (~13%; P. H. Niewiarowski, unpublished data), yet contrary to Nebraska *S. undulatus*, they delay reproduction until 21 mo of age (Niewiarowski 1992). Slow growth and resulting delayed maturity might be dictated by lower resource availability and/or reduced activity time as others have suggested for eastern woodland populations in general (Tinkle and Ballinger 1972; Ferguson et al. 1980; Ballinger et al. 1981). While food does not appear to limit growth rate in New

**Table 4:** Average  $\pm$  1 SE mass and energy equivalents of carcass components of yearlings captured in 1989 and 1990 at the beginning and end of the activity season from Nebraska and New Jersey

	New Jersey		Nebraska	
	Start (27)	End (16)	Start (23)	End (12)
SVL (mm)	36.85 $\pm$ .55	59.46 $\pm$ 1.02	47.06 $\pm$ .91	54.58 $\pm$ 1.07
Wet mass (g)	1.59 $\pm$ .09	5.84 $\pm$ .34	2.31 $\pm$ .10	4.71 $\pm$ .28
Carcass (kJ)	9.72 $\pm$ .53	45.29 $\pm$ 2.98	20.70 $\pm$ 1.19	31.96 $\pm$ 1.73
FB (kJ)	.010 $\pm$ .01	4.780 $\pm$ 1.53	1.16 $\pm$ .27	7.693 $\pm$ .99
Measured NAE <sub>pro</sub> total (kJ)	9.74	50.08	22.32	39.66
%FB of measured NAE <sub>pro</sub> (kJ)	.16	9.56	7.02	18.81
Eggs (kJ)	.00	.00	.00	26.10
Estimated NAE <sub>pro</sub> total (kJ)	9.74	50.08	22.32	65.76
%FB of estimated NAE <sub>pro</sub> (kJ)	.16	9.56	5.24	19.40
Projected wet mass (g)	1.59	5.84	2.31	6.28
Projected %FB	.010	9.560	5.240	39.840

Note: Numbers in parentheses are sample size. Measured NAE<sub>pro</sub> refers to the energy equivalent of the sum of the carcass and fat-body mass actually measured. Estimated NAE<sub>pro</sub> refers to the energy equivalent of the carcass and fat-body (FB) mass plus the energetic value of two average clutches of eggs (Jones and Ballinger 1987). Projected wet mass is the estimated wet mass of collected lizards had the reproductive energy of the clutch of eggs been allocated entirely to lean-body growth. Projected fat-body percentage is based on estimated fat-body mass had the energy of the clutch of eggs been allocated entirely to fat-body storage.

Jersey (Niewiarowski 1995), data presented in this study provide quantitative support that potential activity time may limit growth rate of hatchlings in New Jersey relative to Nebraska (table 1) because, even if they had the genetic potential to take advantage of reduced thermal constraints on activity, thermally suitable microhabitats in New Jersey do constrain activity time (Niewiarowski and Roosenburg 1993).

To summarize, results presented here suggest that the basis of differences in absolute allocation of energy to growth arise from population-specific differences in proportional allocation of NAE<sub>pro</sub> to G, S, and R (Table 4). Population-specific responses to alternative environments are consistent with the hypothesis that these two populations have diverged with respect to the life-history rules (Dunham et al. 1989) that specify age-specific allocation of NAE (Niewiarowski and Roosenburg 1993). I argue that the study of allocation patterns and knowledge of their genetic and environmental basis represent the conceptual framework for understanding variation in growth rate and other life-history traits. Increasing use of this framework in a variety of systems (e.g., Schultze and Conover 1997; McManus and Travis 1998; Travis et al. 1999) should be pivotal in developing the next generation of life-history models.

Finally, even if evolutionary divergence between allocation strategies can be demonstrated definitively, evaluating the importance of the present Nebraska and New Jersey environments in the adaptive evolution of life-history traits is still problematical. In *S. undulatus*, covariation between

life-history traits, such as growth rate and the resource/demographic characteristics of habitats, has been cited as evidence for the importance of local selective environments in the evolution of life-history traits (Tinkle and Ballinger 1972; Ferguson et al. 1980; Ballinger et al. 1981; Gillis and Ballinger 1992). However, even when genetic divergence in life-history traits seems likely (as between Nebraska and New Jersey), an unknown phylogenetic history of the populations in question still confounds adaptationist interpretations (Ballinger 1983; Dunham and Miles 1985; Tinkle and Dunham 1986; Jones and Ballinger 1987; Dunham et al. 1988; Wanntorp et al. 1990; Gillis and Ballinger 1992). In order to understand fully, when using comparative approaches, how environments shape the evolution by natural selection of life-history traits, it will be necessary to incorporate the phylogenetic history of the taxa involved and to expand well beyond a two-population comparison (Garland and Adolph 1994). In the case of *S. undulatus*, a population-level phylogeny and multiple-population comparative analyses (e.g., Garland et al. 1999) would allow us to determine the extent to which present-day population-specific life-history traits, regardless of the habitats they are associated with, can be explained by derived versus ancestral allocation strategies (Wanntorp et al. 1990; Niewiarowski 1994). Nevertheless, studies such as the one described here, as well as experimental manipulation of local phenotypes and environments, will remain essential to testing proposed mechanisms underlying adaptive hypotheses that are suggested by multiple population, phylogenetically based comparative approaches.

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