Resting metabolic expenditure as a potential source of variation in growth rates of the sagebrush lizard

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Abstract

Along an elevational gradient on SW Utah, sagebrush lizards (*Sceloporus graciosus*) exhibit an unexpected pattern of growth. Lizards from a high elevation population grow faster than lizards from two populations at lower elevations despite shorter daily and seasonal activity. Results from a common environment study of growth suggest that the differences in growth are not due to adaptation to local environmental conditions. In this study, I test the hypothesis that higher growth rates in lizards from high elevation may be attributable to reduced resting metabolic expenditure compared to that of lizards from populations at two lower elevations. Resting metabolic rates were measured for individuals from each of the study populations across different times of day and over a broad range of temperatures. Under the same laboratory conditions, field-caught lizards from the high elevation population exhibited lower metabolic rates when compared to lizards from lower elevations. Daily resting metabolic expenditures were calculated using the observed metabolic rates coupled with estimates of daily activity. Daily resting metabolic expenditure was 50% greater for individuals from the two lower elevation populations, which could result in 12.5% more energy that could be potentially allocated to growth for lizards from high elevation. Such energetic savings may be able to explain differences in the patterns of growth observed in nature.
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1. Introduction

Descriptions of intraspecific variation in body size among the squamate reptiles reveal a pattern that is in striking contrast to other vertebrate species. Within a species, birds, mammals, amphibians, and turtles generally exhibit larger body size in cooler environments (Freckleton et al., 2003; Meiri and Dayan, 2003; Morrison and Hero, 2003; Ashton, 2002a,b); whereas, snakes and lizards tend to be larger in warmer environments within a species (Ashton and Feldman, 2003). A simple, non-adaptationist explanation for squamates being larger in warmer environments could be that resource acquisition is somehow tied to the thermal environment (Adolph and Porter, 1993). For example, because squamate reptiles tend to be active behavioral thermoregulators, often within a narrow range of body temperatures, warmer environments should generally allow squamates to be active over longer periods of time (although extreme environments that become too warm might become limiting as well if an animal must spend the majority of the day in refugia). In food limited situations, longer periods of activity would allow an animal more opportunity to forage, and thus have a higher potential for growth, all else being equal. Indeed, evidence for a positive correlation between the size of energy budgets and the length of activity have been observed (Niewiarowski, 2001; Angilletta, 2001a; Tinkle et al., 1993). Where increased growth is not associated with longer daily and seasonal activity in ectotherms (such as amphibians and turtles), geographic patterns of mortality may select for faster growth in cooler climates (if high mortality occurs in cooler climates) thereby producing a Bergmann size cline (Sears and Angilletta, in press).

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Consistent with a reverse Bergmann size cline, the geographic pattern of body size in the sagebrush lizard (*Sceloporus graciosus*) appears to be constrained by the duration of daily and seasonal activity rather than by adaptation to the local environment (Sears and Angilletta, in press). Over a large geographic scale, free-ranging individuals from populations with longer periods of seasonal activity exhibit larger maximal adult body sizes (Sears, in press). For example, sagebrush lizards from Mt. Rose, CA have approximately a 60% longer activity season than do those from Kolob Mesa, UT (Tinkle et al., 1993). Interestingly, the corresponding annual energy budgets of sagebrush lizards from Mt. Rose, CA are approximately 60% larger than those of lizards from Kolob Mesa, UT. The proportion of the energy budget that is allocated to growth is similar for both populations, resulting in larger body size for lizards from Mt. Rose. Furthermore, within a population, the growth of individuals from Kolob Mesa is density dependent (Tinkle et al., 1993): the body size of juvenile lizards is negatively correlated with the density of adults in a given area. Two studies have failed to show divergence in the capacity for growth among populations of sagebrush lizards (Sears and Angilletta, 2003; Sinervo and Adolph, 1994). Thus, growth would appear to be simply the result of the duration of time that a lizard is allowed to forage and the amount of food that it subsequently ingests.

Interestingly, sagebrush lizards from populations occurring along an elevational gradient in SW UT exhibit a paradoxical pattern of growth (Sears, in press; Sears and Angilletta, in press). Despite shorter daily and seasonal activity periods (driven by the availability of suitable temperatures for activity), free-ranging lizards from high elevation grow faster than lizards from lower elevations, but reach the same adult body size. Lizards from the population at high elevation grow faster despite having more than 400 h less time available for activity (and potential foraging) over the course of a season as compared to lizards from the population at the lowest elevation. When reared in the laboratory, controlling for thermal conditions, day lengths, and food ingestion, individuals grew at similar rates regardless of their population of origin (Sears and Angilletta, 2003). This result would suggest that food might be less available at lower elevations (although preliminary data suggest no trends in arthropod abundance that would correlate with growth in the field; Sears, 2001), that foraging intensity is lower at lower elevations, or that grow processes are more efficient for lizards at high elevation.

Animals can grow faster either by eating more and/or by using assimilated energy from food more efficiently (Wieser, 1994). If food availability is not different among the three populations of lizards, and if lizards consume the same amount of food regardless of their population of origin, another potential explanation for divergent growth is that energy expenditure is lower for lizards at high elevations, resulting in more energetic resources remaining that could be allocated to growth (Wieser, 1991, 1994;

Koehn, 1991). Furthermore, because lizards at high elevation may consume fewer resources than those at lower elevations (because they have less time to forage given the shorter duration of potential activity compared to that at lower elevations), decreased expenditure may be an especially likely means to more efficient, faster growth. One way to reduce energetic costs would be to reduce metabolic expenditure so that more energy can be made available for growth (Wieser, 1991, 1994). In fact, tradeoffs between metabolic rates (or expenditure) and growth have been documented in other reptiles (Steyermark, 2002; Angilletta, 2001b), and many examples in other taxa show reductions in metabolic expenditure associated with fast growth (Koehn, 1991; Hawkins and Day, 1996; Bayne, 2000). Such reductions in metabolic expenditure could result either from reductions in the amount of activity or through reductions in metabolic rate (associated, for instance, with decreases in protein turnover rates; Hawkins and Day, 1996; Bayne, 2000). Thus, fast growth is not always associated with high metabolic costs, but often the contrary. In this study, I estimate the daily and resting metabolic expenditures (RME) of individuals from each of three study populations (by coupling resting metabolic rates with estimates of annual and daily activity) to evaluate whether reductions in metabolic expenditure contribute to the patterns of growth observed for lizards along an elevational gradient in SW UT.

2. Materials and methods

2.1. Study animals

Sagebrush lizards (*S. graciosus*) were collected during June 1998 from three study populations in Zion National Park, UT. From low elevation to high elevation, the study populations are Clear Creek Canyon (CCC) at 1752 m above sea level, Firepit Knoll (FPK) at 1961 m above sea level, and Goose Creek Knoll (GCK) at 2255 m above sea level. The locations of these sites are sufficiently far enough from each other that gene flow likely does not occur among populations (at least at any appreciable rate). GCK is 20.16 km and 9.18 km from CCC and FPK, respectively; and FPK is 23.45 km from CCC. Further descriptions of the field sites may be found in Sears (in press) and Sears and Angilletta (2003).

Fifty-eight lizards (20 each from CCC and GCK, and 18 from FPK) were captured from sites adjacent to the three study populations and transported to the University of Pennsylvania for metabolic trials. Individuals ranged in size from relatively small juveniles (<1 year old) to full sized adults (>3 years old). Body sizes of lizards used in the experiment are shown in Table 1. Each individual lizard was housed in a 38 l aquarium with access to heat and light on a 12L:12D cycle, which approximates light and thermal availability experienced under natural conditions. Lizards

Table 1
Body mass (in grams), sex, and number of individuals from each study population used in metabolic trials

Study population	Sex	N	$\bar{x}$	Range
CCC	Female	10	4.92	2.66–5.40
CCC	Male	10	5.73	3.69–7.42
FPK	Female	9	4.56	2.68–6.23
FPK	Male	10	5.07	2.37–6.85
GCK	Female	11	3.83	1.57–5.58
GCK	Male	8	4.41	2.45–5.75
Total		58	4.67	1.57–7.42

were offered crickets (*Acheta domestica*) ad libitum daily, except during metabolic trials (see below). Water was provided daily by both misting the aquaria with a spray bottle and in a water dish. Animals that did not maintain body mass (i.e., body mass fell below 20% of initial body mass at the onset of the study) were removed from the metabolic trials. Females used in the experiment were nongravid.

2.2. Measurement of metabolic rates

Carbon dioxide production was measured using flow-through respirometry (Model TR3, Sable Systems, Henderson, NV) to estimate resting metabolic rates (RMR). All lizards were acclimatized to laboratory conditions for 3 days before the onset of metabolic trials. Prior to measurement, lizards were fasted for 36 h to ensure that they were digestively post-absorptive. The mass of each individual was measured to the nearest 0.01 g. Before metabolic trials, lizards were placed in 30 ml respirometry chambers, and allowed to acclimate to the trial temperature for 2 h before measurement. The metabolic rate of each animal was measured continuously for 6 min once during each time of day. The flow rate of metabolic measurements was 50 ml min^{-1}. The respirometry procedure is described in detail in Angilletta et al. (2000).

Metabolic rates of sagebrush lizards were measured in a repeated-measures design with respect to temperature and time of day. For each individual, carbon dioxide production was measured at five different temperatures (either 21 °C, 25 °C, 29 °C, 33 °C, or 37 °C), repeatedly over the course of a day. At each temperature, measurements were taken once during each of five times of day (1200–1600, 1600–2000, 2000–2400, 0000–0400, and 0400–0800). Temperature treatments were randomized across different days to minimize the chance that metabolic rates might respond systematically to the order of temperatures that the animals experienced (the order of temperatures to which lizards were exposed were the same for all individuals in this study). To mimic light conditions that the lizards experience in their natural environment, metabolic rates were measured during photophase for the 1200–1600 and 1600–2000 periods during scotophase for the other sampling periods.

Resting metabolic rates were determined by converting rates of carbon dioxide production to rates of energy expenditure. The data analysis program DAN (Sable Systems) was used to calculate rates of CO_2 production from each recording. Because the chambers were too small to permit activity and lizards appeared to rest while inside, the entire 6 min of each recording was averaged to obtain a metabolic rate. To ensure that RMR was accurately represented, metabolic traces were examined for "spikes" that could be attributed to activity. No such spikes were found and thus their removal was not necessary. CO_2 production was used for energy estimates due to the small size of sagebrush lizards (i.e., O_2 consumption by *S. graciosus* is close to the detection limits for flow-through measurement of O_2). For a fasted uricotelic carnivore (e.g., an insectivorous lizard), the error of measuring energy metabolism using CO_2 ranges from -1.3% to 0.5% (see Table 4 of Gessaman and Nagy, 1988). Thus, if animals are post-absorptive, measures of energy metabolism using CO_2 production are just as accurate as those obtained using O_2 consumption. For conversion of volumes of CO_2 to energy (in Joules), a respiratory quotient (RQ) of 0.72 was assumed (because the animals in this study were fasted). Volumetric rate of CO_2 production (ml h^{-1}) at standard temperature and pressure (STP) were calculated and converted to energy use (J h^{-1}) assuming 27.33 kJ (l CO_2)$^{-1}$ (Gessaman and Nagy, 1988).

Analysis of metabolic rates was performed using a repeated measures design (sensu Potvin et al., 1990). A type III sums of squares analysis of covariance (ANCOVA) with repeated-measures was used to test the between-subject effect of study population on metabolic rate. Body mass, averaged for each individual over the course of the experiment, was used as the covariate. The within-subject effects of time of day (TOD) and temperature on metabolic rate were tested with a multivariate analysis of covariance (MANCOVA), in which repeated measures are treated as dependent variables. All data were log-transformed for statistical analyses. 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). Data were examined for violations of the assumption that slopes of relationships between body mass and metabolic rate were homogeneous among groups prior to analysis (Sokal and Rohlf, 1981). All post hoc pairwise comparisons of temperature and TOD were made using Tukey's Honest Significant Difference test. All statistical analyses were performed using Statistica for Windows (StatSoft, 1996).

2.3. Evaluation of resting metabolic expenditure

Daily resting metabolic expenditure was calculated for lizards from each study population using the resting metabolic rates measured above. For calculations of metabolic expenditure, times of day (during either scotophase or photophase) were combined to simplify the

analysis, and also because animal activity in the field occasionally occurs before and after the times that photophase metabolism was measured. Resting metabolic expenditure during activity was calculated from metabolic rates measured during photophase at 33 °C. A body temperature of 33 °C was used because it is the closest temperature (over which metabolic rates were measured during this study) to the mean field body temperatures of individuals from the study populations (Sears, unpublished data), and this temperature has been used to calculate energy budgets in other populations in this species (Congdon et al., 1982). Resting metabolic expenditure during inactivity was calculated from metabolic rates measured during scotophase at 21 °C, which is close to the 20 °C used in other studies to estimate nighttime energetic expenditure in this species (Congdon et al., 1982; Congdon and Tinkle, 1982). For comparison within this study, and with Congdon et al. and Congdon and Tinkle, RME is calculated for a 5-g lizard.

3. Results

3.1. Resting metabolic rates

Resting metabolic rates varied among study populations (Table 2a, Fig. 1a). Metabolic rates of GCK lizards were significantly lower than metabolic rates of lizards from CCC or FPK (Tukey's test), whereas metabolic rates between CCC and FPK were not significantly different. Though metabolic rates differed among study populations, metabolic rates increased similarly across all temperatures (Table 2b, Fig. 1b), and reached a plateau: metabolic rates were not significantly different from each other between 33 °C and 37 °C (Tukey's test).

Metabolic rates also showed diel variation (Table 2b). The pattern of variation was similar across all study

Table 2
Summary of results for a repeated-measures ANCOVA for log energy expenditure (in Joules) with log mass as a covariate

(a) Between-subject tests

Source	df	MS	F	p
Intercept	1	752.007	3876.69	<0.001
Study population (1)	2	1.396	7.083	0.002
Error	55	0.197		

(b) Within-subjects tests (using Wilk's λ)

Source	df effect	df error	F	p
Temperature (2)	4	52	261.846	<0.001
Time of day (3)	4	52	76.421	<0.001
1*2	8	104	1.262	0.272
1*3	8	104	1.368	0.219
2*3	16	40	5.660	<0.001
1*2*3	32	80	1.310	0.166

Study population is the between-subject variable and temperature and time of day are within-subject variables.
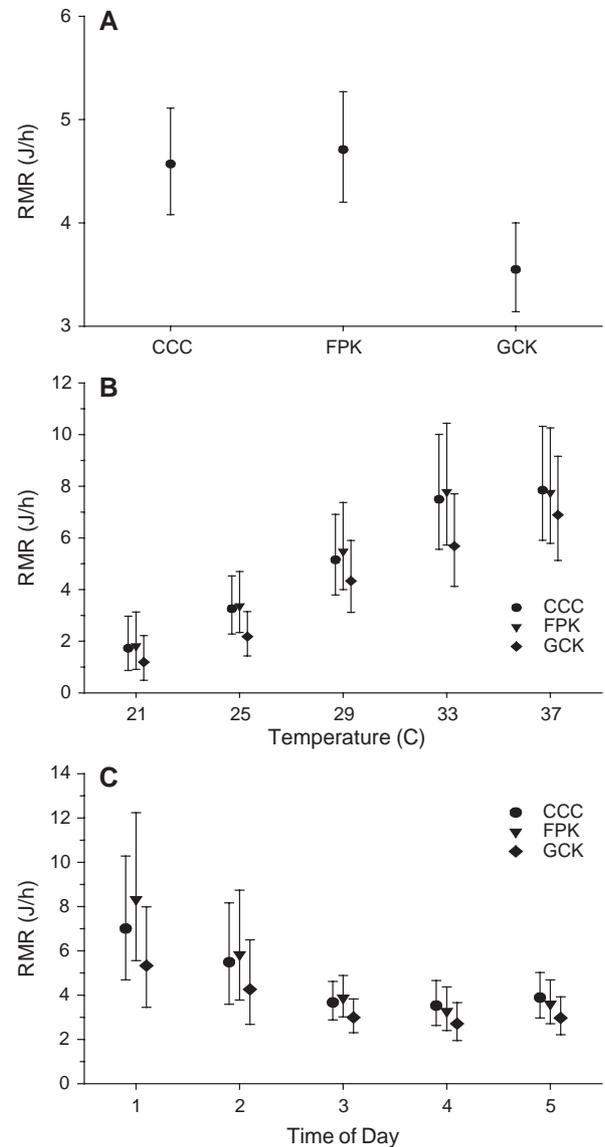
Fig. 1. Lizards from GCK exhibited lower RMR than did lizards from CCC or FPK. RMR is plotted with respect to (A) study population, (B) body temperature, and (C) time of day that metabolic rates were measured. In each graph, least square means (LSM) are plotted along with 95% confidence intervals, and all plotted values have been untransformed (from log values) from the analysis. For viewing clarity, the plotted values of metabolism for each population are offset at each temperature and time of day.

populations (Fig. 1c). Resting metabolic rates were higher during photophase (1200–1600, 1600–2000) and fell during scotophase (2000–2400, 0000–0400, and 0400–0800). Within photophase, metabolic rates decreased significantly between 1200–1600 and 1600–2000 (Tukey's test). Within scotophase, metabolic rates during 0000–0400 were lower than both 2000–2400 and 0400–0800 (Tukey's test), while the later two time periods did not differ from each other (Tukey's test). This diel cycle in metabolic rate dampened with decreasing temperature, such that at higher temperatures the diel cycle was more dramatic than at lower temperatures.
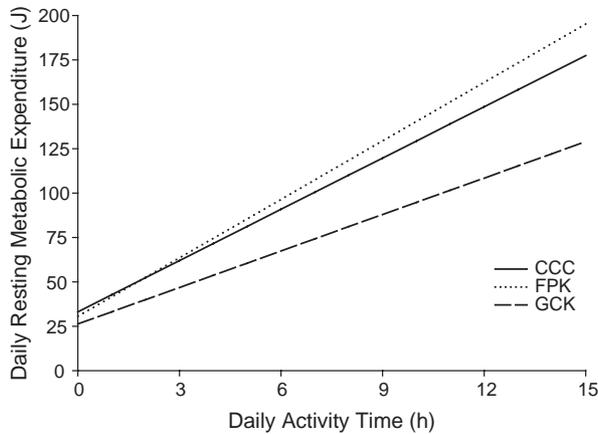
Fig. 2. Average daily resting metabolic expenditure of a 5-g *S. graciosus* is shown for each of the three study populations for activity periods of up to 15 h. As the duration of activity increases, lizards from CCC and FPK incur higher energetic costs than do lizards from GCK.

3.2. Resting metabolic expenditure

Individuals from GCK exhibit reduced resting metabolic expenditure as day length increases, compared to lizards from CCC and FPK. The relative effect of daily activity period on resting metabolic expenditure for a 5-g lizard is shown in Fig. 2. Estimates of activity period for a typical July day are 14 h for CCC, 13 h each for FPK and GCK (from Sears, in press). The resulting RME for a typical July day, calculated by adding RMEs for active and inactive periods are 158.2 J, 162.3 J, and 108.4 J, respectively for individuals from CCC, FPK, and GCK.

4. Discussion

While there is much literature documenting the variation in growth and body size among populations of animals, few studies have examined the physiological mechanisms that might give rise to such patterns among populations (Garland and Adolph, 1991). Variation in environmental factors that affect the rates of food acquisition, energy assimilation, and energetic expenditure can potentially affect the growth rates of ectotherms (Wieser, 1991; Congdon, 1989). In sagebrush lizards, variation in resting metabolic expenditure provides a potential physiological mechanism to produce the patterns of fast growth at high elevation that is observed in nature. Individuals from the high elevation population (GCK) may benefit from increased energetic savings through reduced resting metabolic rates compared to lizards from two lower elevation populations (CCC and FPK); and the difference in energy expenditure is accentuated the longer that lizards are active (Fig. 2). For a 5-g lizard on a typical July day, RME is 50% greater for individuals at either of the two lower elevation sites compared to lizards from GCK. Thus, if lizards from each of these study populations have similarly-sized energy budgets (i.e., they take in similar amounts of

energy on a daily basis), lizards from high elevation would have more energy to allocate to production (and activity) after resting metabolic costs have been paid. If lizards are not terribly limited by food in their environment, consume what they need, and become relatively inactive over the course of a day, such a scenario is fairly plausible.

How much more could a lizard from GCK grow compared to lizards from lower elevations? Congdon and Tinkle (1982) measured field metabolic rates using doubly-labeled water in a population of *S. graciosus* near the mid-elevation study site, and determined that a 5-g lizard has an available energy budget of approximately 400 J day^{-1} during July. Assuming 400 J dday^{-1} would be an average value for lizards from each of the populations studied here, which is fairly realistic given the slight variation in daily activity time among the populations for the month of July, the size of the production budget can be estimated for individuals from each of the study populations by subtracting RME from the total energy budget. This would result in remaining budgets of 241.8 J day^{-1}, 237.7 J day^{-1}, and 291.6 J day^{-1} for CCC, FPK, and GCK lizards, respectively, that could be allocated to production and activity. Basically, lizards from GCK could allocate approximately 12.5% more of their total energy budget toward production as compared to lizards from CCC or FPK. Assuming that the metabolic savings of GCK lizards represent additional energy that is solely used for growth, potential differences in growth can be calculated (Table 3). Thus, a lizard from GCK could potentially produce about 0.02 g more wet mass on an average day of activity than could a lizard from CCC and FPK, or about 0.6 g in a month if the energy budget of a growing lizard over this size range does not change very drastically.

Interestingly, the divergence in metabolic rates among populations of sagebrush lizards may not be genetically based, but instead, due to acclimation to local climatic conditions during growth and development. During a

Table 3
Potential differences in growth for a 5-g lizard are calculated using the following average energetic and material conversions from a body compositional analysis of *Sceloporus* lizards from Vitt (1978): % ash=14.1, %water mass=74.5, kJ (g ash free dry mass)$^{-1}$=22.9

Population	Production (J)	Dry mass (g)	Total potential body mass (g)	Potential growth advantage for GCC
CCC	241.8	0.011	0.093	0.01908
FPK	237.7	0.010	0.091	0.02065
GCK	291.6	0.013	0.112	

From these values, the following equation converts energy in J to g total body mass (TBM): TBM=dry mass+ash mass+water mass, where dry mass=g/(22.9*kg)*x*J/1000, wet mass=0.745*TBM, ash mass=0.141*TBM. Assuming that the energy used for activity is taken equally from the total potential body mass of individuals from all populations, the potential advantage for daily growth for lizards from GCK over the other two populations is simply the difference in the total potential body masses.

common environment study of the growth of individuals from the populations studied here, resting metabolic rates were measured at hatching and at 30 days after hatching. Regardless of the population of origin, resting metabolic rates of hatchlings at 33 °C were not different (Sears and Angilletta, 2003). Thus, the divergence in resting metabolic rates observed in this study might be due to variation in the thermal environment (in terms of variation in daily and seasonal activity) experienced in nature along this elevational gradient. Ectotherms can alter their metabolic rates seasonally in response to variation in their thermal environment (Christian et al., 1999; Tsuji, 1988a,b), with the direction of this response depending on whether an animal is active or dormant during the winter. Those individuals that are active over winter often raise their metabolic rates (metabolic compensation), while individuals that hibernate over winter often decrease their metabolic rates (inverse acclimation). The inverse acclimation strategy is thought to be a means to reduce energetic expenditure during times of negative energy balance, such as that caused by extended periods of inactivity (Christian et al., 1999; Gregory, 1982). Because lizards from GCK spend 1–2 months longer in winter hibernation than do lizards from either CCC or FPK, it might be expected that the metabolic rates of GCK lizards are reduced compared to lizards from lower elevations. Divergence in metabolic rates among populations might arise because lizards from GCK reduce metabolic rates to minimize overwinter energetic expenditure or because lizards from CCC and FPK emerge earlier in the spring than do lizards from GCK and elevate their metabolic rates to support activity in the cool spring temperatures. Further experiments are required to examine the effect of changing thermal conditions on the metabolic profiles of sagebrush lizards, either through altering the thermal environment in the laboratory or by monitoring the metabolic profiles of animals reciprocally-transplanted between thermally distinct environments.

In conclusion, this study illustrates how variation in proximate physiological mechanisms, such as RME, can potentially influence life history traits such as growth. Interestingly, such physiological adjustments might simply be plastic responses to variable environmental conditions, and can be used to mitigate environmental stress without the need for genetic change between generations (Travis et al., 1999). Thus, evolution may have produced plasticity in the RME in response to thermal conditions experienced by sagebrush lizards as an adaptive trait itself to deal with variable environments experienced over short geographic distances, such as those encountered over steep elevational gradients. Further studies in this system will investigate whether intrinsic (genetic) differences among individuals account for the observed differences in metabolic rates or whether individual variation can be environmentally-induced. Furthermore, field-based energetic budgets need to be constructed for growing individuals to support whether the potential energetic savings through reductions in RME are realized and whether these energetic savings can explain the patterns of growth observed in nature.

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