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LIFE-HISTORY VARIATION IN THE SAGEBRUSH LIZARD: PHENOTYPIC PLASTICITY OR LOCAL ADAPTATION?

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Abstract. We performed a laboratory common-environment study to determine the genetic and environmental sources of variation in growth rates of the sagebrush lizard (*Sceloporus graciosus*). Hatchling lizards were reared from gravid females collected from three study populations along an elevational gradient in southern Utah, USA. Hatchlings were fed ad libidum and were maintained on a 14:10 light:dark cycle, with temperatures at 33°C and 21°C during photophase and scotophase, respectively. Each hatchling was randomly assigned to either a water-supplementation treatment or a control group receiving no supplemental water. Once every five days, the water-supplemented lizards were administered orally a quantity of water equal to 5% of their body mass. Growth was quantified as the total change in body size (length and mass) for 30 d after hatching. Resting metabolic rates of a subset of lizards were measured at hatching and at the end of the study. After adjusting growth for food intake, change in length did not differ between water-supplemented and control lizards, and did not differ among the three populations. Metabolic rates were similar across the study for all treatment groups. Water-supplemented lizards did gain wet mass more rapidly than control lizards; however, the difference in growth between groups was attributed to hydration state, because growth in dry mass did not differ between groups. The effects of water supplementation on growth that were observed by other investigators were likely manifested through changes in thermoregulatory behavior or increased activity.

Key words: altitudinal effect on life history; common-environment study; countergradient variation; geographic variation; growth rates; intraspecific variation; life history; phenotypic plasticity; sagebrush lizard; Sceloporus graciosus; *water availability.*

INTRODUCTION

Variation in life-history traits is common in species that are geographically widespread (Roff 1992, Stearns 1992). This variation is created and maintained by differences in the availability and quality of resources among habitats or by differences in biotic interactions among habitats, and is often considered to be evidence of adaptive strategies for dealing with disparate environments (Reznick 1996, Blanckenhorn 1998, 1999, Travis et al. 1999, Leips et al. 2000, Sultan 2001). Variation in life histories is produced either through the plastic response of a single genotype to environmental conditions (known as ''phenotypic plasticity'') or through local adaptation of genotypes to specific sets of environmental conditions (Via and Lande 1985, Stearns 1989, Conover and Schultz 1995). In either case, the mechanistic links between the environment and the phenotype that is expressed are complex and often difficult to discern. Yet, knowledge of these mechanistic links is essential to understanding how variation in life-history traits is produced (Dunham et al. 1989, Conover and Schultz 1995, Merila et al. 2001). Much progress in understanding the links between environments and life histories has been made through the study of species distributed over steep environmental gradients, such as latitudinal or altitudinal clines.

Because environments change predictably with elevation, elevational gradients provide opportunities to investigate the sources of variation in life-history traits. With increasing elevation, air temperature becomes cooler, relative humidity increases, annual rainfall increases, and the partial pressure of oxygen (pO_2) decreases (Yoshino 1975). Consequently, as elevation increases, the activity of ectotherms may become more limited. Reduced periods for activity can limit the acquisition of energy resulting in reduced rates of growth and reproductive output by limiting opportunities to locate, ingest, and process food (Adolph and Porter 1993, Angilletta 2001*a*). Indeed, empirical studies have demonstrated that vertebrate ectotherms grow faster when provided longer access to infrared radiation (e.g., see review by Avery [1994], Niewiarowski 2001), like that provided by lower elevations.

Populations of the sagebrush lizard (*Sceloporus graciosus*) along an elevational gradient in southwestern Utah (USA) exhibit an unexpected cline in life history

TABLE 1. Comparison of intrinsic growth rates for sage-brush lizards (*Sceloporus graciosus*) along an elevational gradient in southwestern Utah, USA. Lizards from high elevation (GCK) exhibit higher rates of intrinsic growth than lizards from lower elevations (CC and FPK).

Site†	Model‡	R^2	N	A (mm)§	rǁ
CC	LBL	0.999	52	64.97 (0.495)	0.0188 (0.0014)
FPK	LBL	0.999	91	66.21 (0.705)	0.0171 (0.0013)
GCK	LBL	0.999	38	65.57 (0.89)	0.0231 (0.0010)
CC	LBW	0.999	52	64.63 (0.49)	0.0239 (0.0018)
FPK	LBW	0.999	91	65.72 (0.662)	0.0222 (0.0016)
GCK	LBW	0.999	38	65.06 (0.77)	0.0303 (0.0012)

Notes: Using snout–vent length (in millimeters) as input, parameter estimates for both growth models (pooled for years 1996–1999) are calculated for individuals recaptured within a single growing season with a recapture interval of no less than 20 d. The growth parameter and asymptotic body size are reported with 95% ''support plane'' confidence intervals (CI) (as per Dunham 1978) in parentheses. N is the sample size, and R^2 is the coefficient of determination.

† CC = Clear Creek, FPK = Firepit Knoll, GCK = Goose Creek Knoll; all sites are in Zion National Park, Utah, USA.

‡ LBL = logistic-by-length model; LBW = logistic-by-weight model.

§ A = asymptotic body size.

ǁ r = growth parameter.

(Sears 2001). Lizards at the highest elevation grow fastest despite the least amount of time available for activity (see Table 1 for comparisons of intrinsic rates of growth). Yearlings at low elevation are larger in the spring, but those at high elevation grow faster over the summer and fall to reach the same body size by the following spring (Fig. 1). Additionally, lizards at high elevation incur a greater risk of mortality each year, which might be caused by the energy demands of an extended winter hibernation or cold exposure in poorly suited hibernacula. These results are at odds with other theoretical and empirical studies of phenotypic plasticity in ectotherms. For example, Adolph and Porter (1993, 1996) argued that lizards with less opportunity for activity, such as those at high elevations, should have a greater annual production, larger adult body sizes, and lower annual mortality.

The pattern of growth observed in *S. graciosus* is consistent with patterns produced by countergradient variation (reviewed in Conover and Schultz [1995]). Countergradient variation occurs when variation in a trait (e.g., growth rate) is expressed in opposition to variation in an environmental variable (e.g., activity time). Countergradient variation in growth is uncommon in lizards, but it has been observed in many other taxonomic groups (reviewed in Conover and Schultz [1995]). For instance, individuals in northern populations of some species of fish grow faster than individuals in southern populations. Fast growth by northern fish counteracts the shorter growing season at high latitudes, resulting in body sizes of fish in northern and southern populations converging by the end of the growing season (Conover and Present 1990, Imsland et al. 2000, Jonassen et al. 2000). These studies also

confirmed a genetic basis for the latitudinal variation in growth rate, suggesting that there has been local adaptation of life history (Conover 1998). The patterns observed in fish are very similar to the pattern observed in the sagebrush lizard, *S. graciosus*. Lizards that exhibit the fastest growth are those from the highest elevation, where daily and seasonal opportunities for activity are the least.

Although the thermal environment tends to retard growth at high elevations, the increased availability of water at high elevations could speed growth. In south-western Utah, yearly rainfall increases with elevation within local mountain ranges (Daly et al. 1994, Fig.
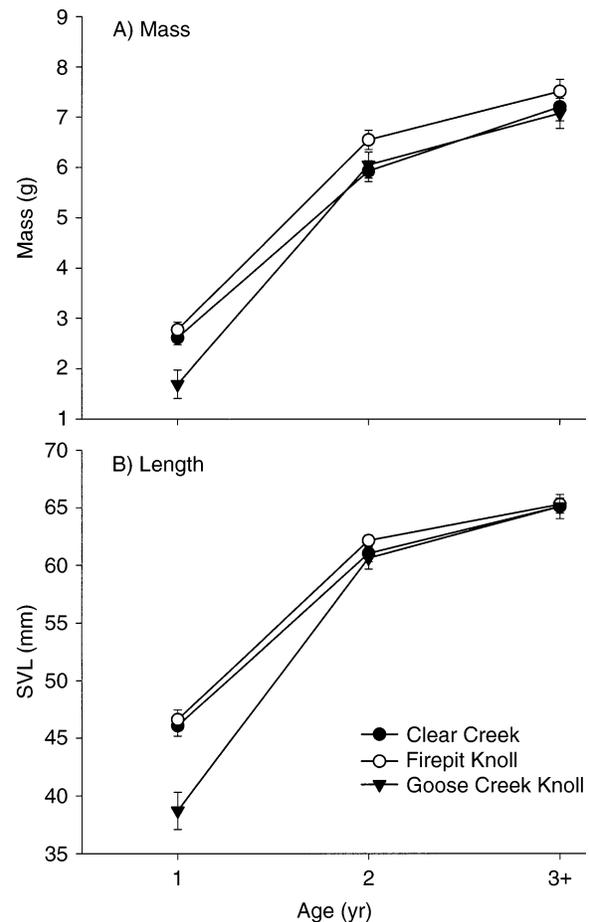

FIG. 1. Body size in sagebrush lizards is smallest for lizards at high elevation during the first year of growth, but body size of lizards at high elevation is similar to that of lizards at low elevation in subsequent age classes. Body sizes in June for different age-classed individuals from each of the three study populations are plotted with regard to (A) mass and (B) length (SVL = snout-to-vent length). Individuals are represented only once for all years of the study; bars on the data points are 95% confidence intervals. Body size differed among populations (mass, MS = 16.46, $F_{2,541}$ = 26.12, $P <$ 0.001; SVL, MS = 419.22, $F_{2,543}$ = 37.92, $P <$ 0.001), and there was a significant interaction for body size with respect to age class and population (mass, MS = 6.12, $F_{4,541}$ = 9.68, $P <$ 0.001; SVL, MS = 360.85, $F_{4,543}$ = 32.64, $P <$ 0.001).
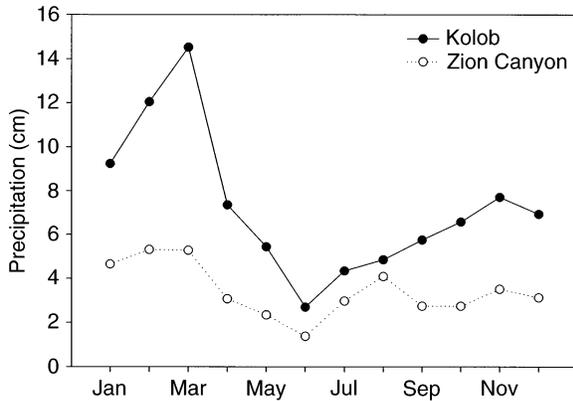
FIG. 2. Precipitation increases with elevation in southwestern Utah (USA). Long-term data from two local weather stations illustrate the precipitation gradient associated with elevation at Zion National Park, Utah. The Zion weather station (NCDC station 429717; data from 1971–2000) is located at an elevation of 1234 m and receives 41.2 cm of precipitation annually, while the Kolob weather station (NCRS station KLBU1; data from 1981–2000) is located at an elevation of 2819 m and receives 88.7 cm of precipitation. If linearity is assumed, precipitation increases ~3 cm per 100 m gain in elevation. This increase would represent a difference of 15 cm per year between the lowest- and highest-elevation sites in this study.

2). Variation in water availability has been associated with growth rate in some species of lizards (Stamps and Tanaka 1981, Jennsen and Andrews 1984). In laboratory experiments, Lorenzon et al. (1999) and Stamps and Tanaka (1981) showed that growth rates of lizards were higher for those with unlimited access to water vs. those with limited access to water. In free-ranging tropical lizards, studies have shown that growth rates, under similar thermal and food conditions, are higher in the wet season vs. the dry season (Stamps and Tanaka 1981, Jennsen and Andrews 1984). Although Jones et al. (1987) failed to show water-induced changes in the growth of *Sceloporus undulatus*, they suggested that supplemental water does increase activity, and that greater activity can in turn promote growth. Furthermore, annual variation in juvenile body size of sagebrush lizards at our Firepit Knoll site was correlated with annual variation in precipitation in a long-term demographic study (Tinkle et al. 1993).

Common-environment experiments are a powerful tool employed to determine the genetic and environmental sources of variation associated with patterns of phenotypic variation observed in natural populations (reviewed in Conover and Schultz 1995, Gotthard and Nylin 1995). Here, we addressed two issues regarding the phenotypic plasticity of growth in sagebrush lizards by conducting a laboratory common-environment experiment. First, we wished to discern whether lizards from high elevation are genetically predisposed to grow faster than lizards from low elevation, or whether they are responding to a greater availability of resources in the environment. Second, we wished to address whether water availability might be driving differences in growth, as populations at high elevations tend to experience more rainfall, and cooler temperatures with higher relative humidity (which would lead to decreased evaporative water loss). To accomplish these ends, we reared hatchling lizards from each of three study populations in a common environment, controlling the consumption of food by all lizards and supplementing a subset of lizards with water. This experiment enabled us to discern whether lizards from high elevation have higher growth efficiencies than lizards from lower elevation, and whether increased consumption of water increases growth efficiency.

METHODS

Study organism

Sagebrush lizards (*Sceloporus graciosus*) were collected from three populations in Zion National Park (Utah, USA). The three study populations—Clear Creek (CC), Firepit Knoll (FPK), and Goose Creek Knoll (GCK)—span the entire elevational range over which sagebrush lizards occur in the park. Clear Creek (1752 m above sea level; Universal Transverse Mercator [North American Datum 1927]: E 333624, N 4122954) is located in a sandy canyon bottom consisting of mixed conifers (pinyon-juniper and Ponderosa pine) and desert scrub with the dominant vegetation being Gambel oak (*Quercus* sp.) and manzanita (*Arctostaphylos* sp.). Firepit Knoll (1961 m; UTM: E 313264, N 4134600, formerly known as Rattlesnake Ridge, see Tinkle [1973] and Tinkle et al. [1993]) is located on a rocky hillside consisting mainly of exposed sandstone. Vegetative cover is primarily manzanita and Gambel oak scrub, with the occasional Ponderosa pine (*Pinus* sp.). Goose Creek Knoll (2255 m; UTM (NAD27): E 321350, N 4138950) is located on an exposed limestone ridge top in a mixed pine–fir forest. Vegetative cover consists of a mix of manzanita, mountain mahogany (*Cercocarpus* sp.), serviceberry (*Amelanchier* sp.), Gambel oak, and live oak (*Quercus* sp.).

Experimental design and measurement of growth

For this study, gravid females were collected from each site and transported to the University of Pennsylvania, Philadelphia, Pennsylvania, USA. Females were placed in 6-L aquaria containing moist sphagnum. Females were held at 28°C and were fed crickets (*Acheta domestica*) ad libitum. Females were allowed to oviposit naturally. Freshly laid eggs were transplanted to sand and incubated at 28°C until hatching. The incubation medium was fine sand, standardized to the same soil moisture (1 g H_2O/100 g sand, yielding a water potential of −200 kPa; Angilletta and Sears 2000). The water content of the incubation medium was maintained gravimetrically during the incubation

period. Control of temperature and soil moisture during incubation was critical because these parameters may affect the growth of individuals after hatching (Qualls and Andrews 1996, Qualls and Shine 1998).

Hatchlings were reared under different hydric conditions and were fed crickets ad libitum. We assigned lizards to a water-supplementation treatment or a control group receiving no supplemental water. A stratified random design was implemented to assure that no single clutch or study population was overrepresented in any given treatment. Once every five days, a quantity of water equal to 5% of a lizard's body mass was given orally (by pipette) to supplemented lizards. The amount of water delivered to each lizard was equivalent to 50% of a free-ranging lizard's mass-specific water influx (determined from a doubly labeled water study of *S. graciosus,* summarized in Nagy [1982]). Body mass was taken before and after pipetting to ensure that the desired amount of water was indeed delivered. Lizards in the control group had a pipette inserted into their mouths but no water was delivered. All lizards were maintained on a 14:10 light:dark cycle at 33°C and 21°C during photophase and scotophase, respectively.

Survival between the water-supplemented group and control group was compared to evaluate whether our manipulation had any acute negative effects on hatchlings. An analysis of the number of successful days in the experiment was performed using the two-sample test (failure time analysis) included in the Survival Analysis module of Statistica for Windows (StatSoft 2000).

We measured snout–vent length (SVL) (to the nearest millimeter) and body mass (to the nearest 0.01 mg) once every five days for the first 30 days post-hatching to assess growth and body condition. Growth was analyzed using an ANCOVA with site and water availability as fixed effects and wet mass of ingested food as a covariate. A body-condition index was calculated by taking the residuals from a regression of log (body mass) on log (SVL). Thus, a positive value represents an animal that is on average heavy for its body length, and a negative value represents an animal that is light for its body length. These residuals were taken for each animal at the beginning of the experiment and after 30 days (at the end of the experiment). Initial residual values were subtracted from final values to evaluate the change in body condition over the course of the experiment (relative to an average individual); a difference of >0 represents an animal whose body condition improved over the course of the experiment, and a difference <0 represents an animal whose body condition deteriorated. An ANCOVA was used to examine the effects of population origin and water supplementation on change in body condition. The mass of food consumed was used as a covariate in the analyses for growth and body condition to factor out the variation in growth that was simply due to variation in the consumption of food. The amount of food consumed by each lizard was determined by counting the number of individual crickets each lizard consumed and multiplying that number by the average mass of subsamples of crickets fed to lizards on each day (crickets were all roughly the same instar so that variation in cricket mass among individuals was minimized).

To determine whether potential differences in wet body mass were caused by differences in hydration or the synthesis of tissue, dry masses were compared at the end of the experiment. Since animals from each study population were randomly assigned to the water-treatment groups, we assumed that the average dry body mass of lizards was the same for all treatment groups (at least for the control group vs. the water-supplemented group). Thus, any differences in dry mass at the end of the study should have reflected differences due to the water treatment that we imposed. Dry masses were determined by freeze-drying individuals for 72 h, and immediately taking their mass to the nearest 0.1 mg. Dry masses were analyzed using ANCOVA with study population and water treatment as independent variables and consumed wet mass as a covariate. Since ANCOVA was used, estimates of growth corrected for food consumption are reported as least-square means.

Measurement of metabolic rates

For each lizard, resting metabolic rate at 33°C was measured just after hatching and at the end of the experiment (day 30) using flow-through respirometry (Model TR3, Sable Systems International, Henderson, Nevada, USA). Details of the configuration and use of our respirometry system for measuring metabolic rates of lizards have been described previously (Angilletta 2001*b*). Initial metabolic rates of lizards were measured after hatching before their first feeding. For measures of metabolic rates at the end of the experiment, animals were fasted for 36 h prior to each measurement to ensure that they were post-absorptive. Due to logistical constraints, we could only remeasure metabolic rates of a random subset of the animals measured at hatching. Each individual was weighed and placed in a 30-mL respirometry chamber within a dark incubator. After placing individuals in chambers, we waited 2 h before measuring metabolic rate to allow individuals to reach thermal equilibrium and to habituate to the chamber. While animals were resting, CO_2 production was measured continuously for 6 min. To minimize the potential influence of time of day on metabolism, all metabolic rates were measured between 1200 and 1600 hours.

The data analysis program DAN (Sable Systems International) 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. Volumes of CO_2 consumption (in milliliters per hour) at standard temperature and pressure were used as estimates of

TABLE 2. Results of ANCOVA for the effects of water supplementation and population origin on various measures of the growth of lizards.

Dependent variable†	Source population			Water supplementation			Source × Water			Error	
	df	MS	F	df	MS	F	df	MS	F	df	MS
Food consumption	2	0.042	0.371	1	0.0003	0.002	2	0.8168	0.717	67	0.114
Change in SVL	2	0.297	0.270	2	0.015	0.020	2	1.238	1.592	66	0.778
Change in wet mass	2	0.001	2.234	1	0.037	8.271**	2	0.009	1.916	66	0.004
Change in condition	2	0.001	0.217	1	0.0190	6.154*	2	0.001	0.230	66	0.003
Dry mass	2	0.001	2.009	1	0.001	2.317	2	0.0003	0.575	57	0.0005
Initial RMR	2	0.0015	0.948	1	0.0005	0.316	2	0.001	0.683	68	0.002
Final RMR	2	0.00009	0.182	1	0.000003	0.055	2	0.00005	0.089	28	0.0005

* $P < 0.05$, ** $P < 0.01$.

† SVL = snout–vent length; Dry mass at end of experiment; RMR = resting metabolic rate. Food consumption was used as a covariate in analyses of growth, whereas log wet mass was used as a covariate in analyses of RMR.

resting metabolic rate. For a post-absorptive, uricotelic carnivore, like *Sceloporus graciosus,* the error associated with estimating energy expenditure from measures of CO_2 production ranges from -1.3% to 0.5% (Gessaman and Nagy 1988). Log-transformed values of resting metabolic rate were compared by ANCOVA, using population origin and water supplementation as independent variables and body mass as a covariate. Since ANCOVA was used, estimates of metabolic rate adjusted for mass are reported as least-square means.

RESULTS

Offspring characteristics

Population of origin contributed very little to variation in egg mass and offspring characteristics. Although hatchlings from larger eggs were both heavier ($P < 0.001$, $r^2 = 0.50$) and longer ($P = 0.01$, $r^2 = 0.25$), egg mass did not vary significantly among populations (MS = 0.002, $F_{2,23} = 0.70$, $P = 0.51$). After adjusting for egg mass, body masses of hatchlings did not differ among populations (MS = 0.003, $F_{2,21} = 1.76$, $P = 0.20$, LSM (least-square mean) = 0.56 g, 0.57 g, and 0.53 g, respectively, for Clear Creek, Firepit Knoll, and Goose Creek Knoll), but snout–vent lengths of hatchlings did (MS = 2.56, $F_{2,21} = 4.44$, $P = 0.02$). Hatchlings from Firepit Knoll (LSM = 29.5 mm) were significantly longer than hatchlings from Goose Creek Knoll (LSM = 28.2 mm), though no differences in length were apparent between hatchlings from Clear Creek (LSM = 28.8 mm) and those from either Goose Creek Knoll or Firepit Knoll (Tukey's HSD test).

Growth and body condition

To determine whether the process of water supplementation was overly stressful, the survival of supplemented lizards was compared to that of control lizards. Of the 90 animals used, 73 (81%) survived the experiment. Survival did not differ significantly between water-supplemented and control lizards (Cox's $F_{92,88} = 1.01$, $P = 0.49$).

None of the four measures of growth differed significantly among populations (Table 2, Fig. 3). Lizards from Clear Creek, Firepit Knoll, and Goose Creek Canyon underwent similar changes in SVL (2.2 mm, 2.4 mm, and 2.3 mm, respectively), wet mass (0.080 g, 0.096 g, and 0.046 g, respectively), and body condition (0.002 vs. 0.002 vs. -0.008, respectively). Dry body mass at the end of the experiment was not significantly affected by water supplementation (0.148 g for the control group vs. 0.138 g for the water-supplemented group). Growth measured in terms of SVL was similar for control and water-supplemented lizards (2.3 mm for the control group and the water-supplemented group). Water supplementation enhanced growth in terms of wet mass by 108% (0.048 g for the control group vs. 0.100 g for the water-supplemented group). Since growth in wet mass differed between groups but growth in SVL did not, water-supplemented lizards improved their body condition more rapidly than control lizards (-0.020 for the control group vs. 0.017 for the water-supplemented group). However, the difference in the increase in wet mass (and condition) between water-supplemented and control lizards was due to hydration state rather than the growth of tissue. This conclusion is supported by the fact that dry body masses of water-supplemented and control lizards did not differ significantly.

Metabolic rates

Resting metabolic rate was not influenced by population of origin or water supplementation. Upon hatching, lizards from all three populations had similar metabolic rates (Table 2). No difference in initial resting metabolic rate (RMR) was found between lizards assigned to the water-supplementation (LSM = 1.2 mL CO_2/h for lizards from all populations) and control groups (LSM = 1.2 mL CO_2/h for lizards from all populations). At the end of 30 d there were still no significant differences in RMR among populations (LSM = 1.2 mL CO_2/h). Furthermore, water supplementation for 30 d had no effect on RMR (Table 1).

DISCUSSION

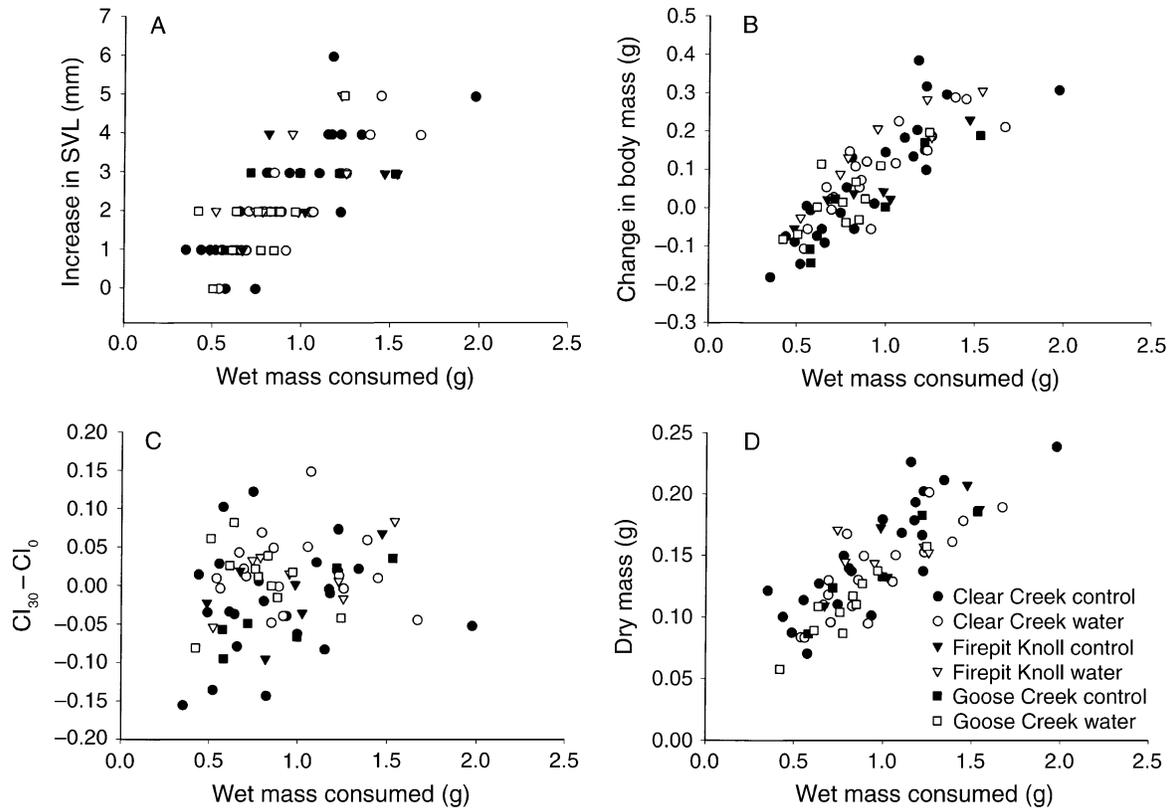Growth rates of free-ranging sagebrush lizards at different elevations are consistent with the pattern of

FIG. 3. Relationships between the consumption of food and (A) change in length, (B) change in body mass, (C) change in condition, and (D) final dry mass. Changes in body size (A and B) are differences between final and initial sizes. Change in body condition (C) is the difference between estimates of condition index estimated at the beginning (CI_0), and end (CI_{30}) of the experiment for the relationship between log snout–vent length (SVL) and log wet mass. A difference in residuals ($CI_{30} - CI_0$) greater than zero reflects an individual that became "fatter" over the course of the experiment, while a negative value represents a "leaner" individual.

growth produced by countergradient variation. However, evidence from our experiment supports the conclusion that elevational variation in growth is due to proximate environmental effects and that individuals from our study populations have not diverged in their capacity for growth. In our study, variation in growth rates among lizards could only be attributed to the amount of food consumed by individuals, and could not be attributed to the availability of water, maternal effects, or effects of the source population. Though our measurements of growth were taken under a fairly strict thermal regime (active temperatures set at 33°C), the temperatures and duration of activity chosen for this experiment are similar to those experienced by lizards in their natural environments (Sears 2001), thereby minimizing the likelihood that our results merely reflect a chance incident that we happened to measure animal performance where reaction norms overlap among populations. Given that these populations from different elevations shared a similar capacity for growth in a common laboratory environment, we must consider the

proximate mechanisms that could account for the phenotypic plasticity in the growth of juveniles.

Maternal effects on offspring do not explain patterns of growth and body size observed in our source populations of *S. graciosus*. Maternal effects on the growth of hatchlings can be mediated through a female's energy investment in eggs (reviewed in Bernardo [1996]). Though offspring from larger eggs might contain a greater quantity of residual yolk, egg size did not vary among populations in our study. Alternatively, even though similarly sized eggs could have proportionately different amounts of yolk, our results do not support this notion because hatchling mass corrected for egg size did not differ among source populations. Thus, the larger body size of emerging juveniles from lower elevations in the spring probably results from a greater duration of growth before winter dormancy. Lizards from Goose Creek Knoll (the highest-elevation site) hatch later than lizards from Clear Creek or Firepit Knoll and have less time available to forage and grow, once they have hatched, until winter dormancy (Sears

2001). Furthermore, hatchlings from Goose Creek Knoll emerge approximately one month later in the spring than populations at lower elevation due to both snow pack and limited thermal opportunity (M. W. Sears, *personal observation*). These differences in the body sizes of yearlings among populations are similar to differences between the body size of hatchlings from the first and second clutches of the year in a single population (Sears 2001).

Given the results of our experiment, the faster growth of free-ranging lizards at high elevation cannot be attributed to inherent differences in growth efficiency among populations (due either to water availability or to population-specific responses to our experimental conditions). Controlling for the consumption of food, growth in both mass and length was similar for all populations, i.e., growth efficiency (biomass gain per amount of food intake) was similar. Faster-growing individuals in our experiment merely consumed more food, and individuals from all three populations had the same propensity to feed. One proximate hypothesis for fast growth in free-ranging lizards, given our experimental results, is that food availability in nature differs among sites. Possibly, hatchlings at Goose Creek Knoll realize higher rates of food intake than hatchlings at Clear Creek or Firepit Knoll do, because temporal fluctuations in the growth rates of lizards frequently correspond to changes in food abundance (Dunham 1978, Wikelski et al. 1997). However, no differences in food abundance have been observed among the three populations (Sears 2001). Furthermore, there is less time available for foraging at high elevation, based on thermal constraints on potential activity time. It could be the case that longer activity times at lower elevations do not favor higher rates of growth, especially if maintenance costs begin to exceed energy intake. Evidence of reduced growth with extended activity times has been demonstrated in the laboratory in *S. graciosus* (Sinervo and Adolph 1994).

Water availability also is known to affect the growth rates of lizards (Stamps and Tanaka 1981, Jennsen and Andrews 1984, Lorenzon et al. 1999). A long-term demographic study of sagebrush lizards at Firepit Knoll revealed that hatchling body size varied with the amount of rainfall (Tinkle et al. 1993). In our study, water intake did not affect growth under conditions of constant temperature. If animals were allowed to thermoregulate, and hydration state affected the preferred body temperature, differences in growth might have been seen. However, it seems that there is no physiological predisposition for an individual to grow faster when it is more hydrated. Lorenzon et al. (1999) did observe that lizards that were provided a greater quantity of water grew faster, but water-supplemented individuals chose higher body temperatures, which might account for their faster growth. Water-stressed individuals chose lower body temperatures and exhibited reduced activity, likely to reduce rates of water loss.

Jones et al. (1987) supplemented free-ranging lizards with water, but did not observe differences in growth, even though water-supplemented lizards were more active than control lizards. Unfortunately, Jones et al.'s experiment was conducted during a period of abundant rainfall, which might have dampened any effect that water supplementation might have had. In this study, water-supplemented lizards maintained higher states of hydration (i.e., greater percentage of body water) than control lizards. If hydrated individuals are more active, water availability might account for the relatively fast growth of sagebrush lizards at high elevation.

Besides the maternal and environmental factors that we examined in the laboratory, several other factors could be acting to produce faster growth at high elevations, including (1) acclimatization of physiology to local environments, (2) behavioral differences in foraging activity, and (3) selection for traits without any corresponding genetic variation. If one or more of these mechanisms are valid, no genetic divergence among populations is necessary to explain elevational variation in growth.

Acclimatization of resting metabolic rate could produce variation in juvenile growth rate among natural populations. Though growth over 30 d did not vary among treatment groups, long-term measures of growth rate would be expected to differ among populations if metabolic rates began to diverge during our experiment. In our present study, individuals from all populations exhibited similar metabolic rates at hatching, and metabolic rates did not diverge over the course of the experiment. The fact that metabolic rates did not differ for hatchlings is consistent with the hypothesis that metabolic rates of free-ranging individuals may later acclimatize to environmental conditions. Exposure to cold is sometimes associated with reduced resting metabolic rate within some species of sceloporine lizards (Tsuji 1988, though compensatory changes in metabolic rate in response to the environment have also been observed). In another study, field-caught lizards from Goose Creek Knoll exhibited lower RMRs than lizards from low elevation (Sears 2001). Individuals at Goose Creek Knoll experience cooler, shorter days, which may induce a reduction in RMR (similar to a concept known as "metabolic scope for survival" in Hochachka and Somero 2002). A lowered RMR coupled with a shorter activity period would reduce energy expenditure (e.g., Angilletta 2001*b*), which could promote faster growth at high elevations. Because we held lizards from all three populations under identical thermal conditions, we would not have detected differences in metabolic rate associated with the thermal environment.

Thermal acclimation may also occur during embryonic development. Although maternal investment does not explain elevational variation in the growth of hatchlings, the incubation environment can affect hatchling body size and growth after hatching (Qualls and Shine

1998, Andrews et al. 2000). Though the incubation environment was the same for all populations in this study, incubation environments probably vary among natural populations. Lizards from Goose Creek Knoll experiences soil temperatures that are ~3°C lower at comparable depths than at Clear Creek (Sears 2001). Also, embryos at Goose Creek Knoll may experience more soil moisture as Goose Creek Knoll receives more rainfall. Incubation temperature and water potential are known to affect embryonic development and hatching phenotypes (reviewed in Deeming and Ferguson 1991, Packard 1991), though these effects are varied. For instance, lower incubation temperatures lengthen the incubation period, decrease hatching success, and produce smaller, slower growing hatchlings in *Sceloporus virgatus* (Qualls and Andrews 1999). In another congener, *S. undulatus*, lower incubation temperatures lengthen the incubation, but do not affect body size at hatching or growth after hatching (Andrews et al. 2000, Angilletta et al. 2000). It would be useful to know the effect of incubation temperature on the growth rates of hatchlings of *S. graciosus*. Despite the evidence that nest temperatures may influence growth after hatching, it is not likely that variation in nest temperatures cause the faster growth of lizards at high elevations because colder incubation environments do not usually result in faster growth after hatching (e.g., see Qualls and Shine 1996, Qualls and Andrews 1999).

Heterogeneity of environmental temperatures could also produce variation in growth of individuals among populations by limiting the duration of foraging. Though the thermal environment is known to limit activity, few studies have examined how operative temperatures (sensu Bakken 1992) affect foraging behavior (but see Ayers and Shine [1997] and Bozinovic and Vasquez [1999] for examples). Sinervo and Adolph (1994) observed that sagebrush lizards grew faster when exposed for longer time periods to thermal environments favorable for activity. For most terrestrial ectotherms, operative environmental temperatures are distributed temporally and spatially; an individual can be active but not have uninhibited access to its prey (Tracy and Christian 1986). The influence of environmental heterogeneity of operative temperatures on activity is especially important for small-bodied organisms, which have low thermal inertia. Therefore, large fluctuations in operative environmental temperatures will make some portions of the habitat unavailable. Although lizards at low elevation can be active at their preferred body temperature for a longer duration, much of their habitat exceeds their critical thermal maximum during midday, prohibiting foraging opportunities. At higher elevations, the thermal environment is less restrictive at midday (M. W. Sears, *personal observation*). Thus, lizards at high elevation might have greater success at foraging even when the abundance of prey is the same at all elevations.

Additionally, the relative risk of predation might be an important source of variation in growth rates of lizards. Predators can alter the growth of their prey by reducing the foraging effort of individuals (Lima and Dill 1990, Lima 1998). Although predator-mediated behavior has been studied intensively in birds, mammals, fish, and invertebrates, few studies are documented in reptiles (but see Martin and Lopez 1999, Cooper 2000). Empirical evidence supports the notion that individuals will forage less often when foraging increases the risk of being eaten (Relyea and Werner 1999, Anholt et al. 2000, Thiemann and Wassersug 2000). Furthermore, theoretical models predict that animals should alter their foraging behavior in the presence of predators to minimize the risk of mortality associated with a certain rate of growth (e.g., Werner and Anholt 1993). Reptilian systems offer an excellent opportunity to study the effects of predation risk on foraging and growth. Predators of reptiles and other large ectotherms are rare at high elevation because of lower environmental temperatures. At our high-elevation site, only one predatory skink (*Eumeces skiltonianus*) has been observed in five years of field studies; however, several predatory snakes (*Crotalus viridis* and *Masticophus taeniatus*) and lizards (*Crotaphytus insularis*) were sighted frequently at our mid- and low-elevation sites. Thus, if sagebrush lizards respond to predators as do other organisms, lizards at low elevations would be expected to forage less often than lizards at high elevation. Even if the abundance of food is similar at all elevations, higher rates of feeding (and growth) might be realized at high elevations. Experiments that modify a lizard's perception of predation risk might lead to novel insights about the causes of life-history variation.

Finally, neither genetic divergence nor phenotypic plasticity is necessary to explain altitudinal variation in juvenile growth rate. Though phenotypic selection may favor faster juvenile growth, growth rates may not be heritable. For example, suppose that fast-growing individuals enjoy greater survival at higher elevations. Individuals that grow slower might not forage to the degree necessary to acquire the resources needed to survive the longer overwinter period at high elevations. Consequently, only the faster growing, larger-sized individuals (from a cohort) would remain in the spring. At lower elevations, there might be sufficient time to grow before winter, and survival would be associated with growth rate. Given this scenario, the average growth rate for the population at high elevation would be higher than that for the population at low elevation. Importantly, if juvenile growth rates are not heritable, juvenile growth rates in the populations would not evolve over time (Falconer 1989). Therefore, apparent differences in the capacity for growth among populations can be maintained without genetic differentiation. Future demographic analyses concentrating on hatchling body size and juvenile growth should reveal if this mechanism is plausible.

Conclusions

The lack of genetic differentiation among populations with respect to growth capacity, found in this study, is consistent with life-history theory that predicts variation in life-history traits produced through environmental variation (Adolph and Porter 1993, 1996). For instance, increased opportunity for foraging (mediated by the thermal environment) should result in more energy that can be used for growth. Thus, ectotherms that experience longer activity seasons may be expected to exhibit higher rates of growth and reproductive output over an environmental gradient that produces variation in the amount of time available for activity. Geographic variation in the body size of sagebrush lizards indicates that longer activity seasons result in faster growth and larger adult body size (Tinkle et al. 1993). Furthermore, laboratory studies have shown that increased thermal opportunity (for foraging) produces faster growth in sagebrush lizards (Sinervo and Adolph 1989, 1994). Surprisingly, however, populations of sagebrush lizards that are located over an elevational gradient in southwestern Utah exhibit a pattern of growth in opposition to the geographic pattern—lizards at high elevation, with less time available for activity, grow faster than lizards from lower elevations. Because the elevational pattern of growth is not caused by adaptation to local environments (i.e., divergent responses of individuals from different populations to local environments), differences in growth must be caused by either environmental variation or physiological acclimatization to the environment. Furthermore, while population-specific differences in growth were not observed in our study, plasticity of growth to different thermal and hydric conditions may itself be an adaptive response to the range of conditions that this species has historically encountered.

Our study indicates that environmental variation caused by elevational changes may not be similar, in many aspects, to larger-scale geographic variation. At high elevations, though there is less time available for activity, the thermal availability of microhabitats may allow an animal to use their habitat more effectively than animals at lower elevation. Furthermore, low thermal opportunity at high elevation is not necessarily the same as an equal amount of thermal opportunity found at higher latitudes at lower elevation because day length (in terms of light) and pO_2 will be different between these areas of comparable thermal opportunity. These additional differences caused by elevation may become increasingly important when elevation begins to limit physiological processes (e.g., oxygen limitation at high elevation). Our study demonstrates that life histories, though environmentally driven, may not be predictable from simple environmental gradients. An understanding of life-history variation among populations will require both a thorough characterization of the environmental variation among populations and

a set of physiological mechanisms that translates environmental variation into life-history phenotypes for a given organism. Further understanding of the evolution of life histories will require further experimentation on growth under different controlled combinations of thermal and hydric conditions, or by reciprocally transplanting individuals among populations with apparent differences in life histories.

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