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Geographic variation in the life history of the sagebrush lizard: the role of thermal constraints on activity

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Abstract Thermal constraints on the time available for activity have been proposed as a proximate mechanism to explain variation in suites of life history traits. The longer that an ectotherm can maintain activity, the more time it has to forage and the greater chance that it will encounter a predator and be eaten. Thus, the thermal environment may produce a trade off between growth and survival when variation in the environment favors increased activity. I used mark-recapture data from a demographic study of three natural populations of the sagebrush lizard (*Sceloporus graciosus*) and estimates of thermal opportunity for each population to evaluate whether variation in the thermal environment can explain patterns of growth and survival that occur over an elevational gradient. Lizards from the highest elevation population exhibited higher individual growth rates than those of lizards from lower elevation, while mortality rates increased with elevation for these populations. The covariation of fast growth and high mortality with increased thermal opportunity is the opposite trend expected if the thermal environment alone is to explain patterns of life history in these lizards. Additional factors including thermal heterogeneity in the distribution of microhabitats of lizards, adaptation to local environmental conditions, and a potential trade-off between resource acquisition and predation risk need to be addressed to obtain a satisfactory explanation of the causative mechanisms producing life history variation.

Keywords Geographic variation · Body size · *Sceloporus* · Temperature · Activity

Introduction

Despite the many instances of geographic variation in the life histories of ectotherms which have been documented, particularly with respect to growth and body size (e.g., Arnett and Gotelli 1999; Billerbeck et al. 2000; Trussell 2000; Ashton 2001, 2002; Vila-Gispert and Moreno-Amich 2002; Morrison and Hero 2003), no general conclusions have been drawn that can explain when a certain gradient in growth or body size should be expected. In environments with high rates of juvenile mortality, classic models of life history (that utilize life tables from known populations, e.g. Stearns and Crandall 1981) predict that faster rates of growth should evolve to maximize survival to adulthood, and such a strategy often leads to relatively small adult body size (Stearns 2000). Thus, an adaptive explanation for geographic variation in growth would predict that juvenile mortality and rates of growth would be positively correlated among populations (Sears and Angilletta, in review). Alternatively, variation in environmental resources among populations may produce similar patterns of growth and body size without invoking local adaptation. A recurrent theme in many proposed proximate explanations for geographic patterns of body size is the influence of environmental temperatures (Adolph and Porter 1993; Berrigan and Charnov 1994; Atkinson 1994, 1995; vanderHave and deJong 1996; Atkinson and Sibly 1997).

Environmental temperatures are important because they influence many aspects of physiology and behavior of individuals (reviewed in Congdon 1989; Huey 1991) that may lead to specific geographic patterns in growth and body size. For instance, it has been proposed that warm climates should lead to higher levels of rates of mortality and productivity for ectotherms (Adolph and Porter 1993) because warm climates, in general, allow for potentially longer periods of daily and seasonal activity than in cooler climates. Prey encounter rates and food ingestion rates are limited by the time available for

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activity during which an ectotherm may forage (Grant and Dunham 1988; Van Damme et al. 1991). Other physiological processes, such as respiration and digestion, are sensitive to temperature and often exhibit a thermal optimum over which net assimilated energy is maximized (Waldschmidt et al. 1987; Zimmerman and Tracy 1989). Because temperatures that maximize net assimilated energy are often at or near body temperatures exhibited during activity, daily energy assimilation (and thus potential growth) will be increased the longer that an individual can maintain a body temperature necessary for activity (Adolph and Porter 1993; Niewiarowski 2001; Angilletta 2001). Consequently, it is not a surprise that ectotherms choose a narrow range of body temperatures during activity (Avery 1982). Interestingly, by choosing temperatures that are beneficial for activity and the assimilation of energy, ectotherms may also decrease their survivorship by increasing the risk of predation (Huey and Slatkin 1976; Pitt 1999) because the longer that an animal is active (and conspicuous in its environment), the greater are its chances of being eaten (Otto 1993; Heinen 1994; Skelly 1994; Anholt and Werner 1995; Martel and Dill 1995). Consequently, individuals will often decrease levels of activity in the presence of predators to minimize their risk of mortality (McCollum et al. 1998; Relyea and Werner 1999; Anholt et al. 2000; Eklov and Werner 2000; Thiemann and Wassersug 2000). Furthermore, environments amenable to longer periods of activity may also inherently produce higher rates of mortality, all else being equal. For example, mortality of *Uta stansburiana* increased with the available time for daily activity within an activity season (Wilson 1991). Studies have also shown that populations of lizards (e.g., *Lacerta vivipara* and *Sceloporus merriami*) from lower elevations, where activity seasons are longer, exhibit higher mortality than populations from higher elevations (Sorci et al. 1996; AE Dunham, unpublished data). Thus, species that comprise geographically widespread populations will likely exhibit among-population variation in growth and survival due to differences in the thermal environment that influence the duration of activity (Adolph and Porter 1993).

Geographic variation in the sagebrush lizard

The pattern of geographic variation in the body size of sagebrush lizards suggests that thermal constraints on activity may influence body size among populations. In natural populations, longer seasonal activity is associated with a relatively large maximal adult body size (Fig. 1). A longer duration of activity likely translates into increased individual growth because lizards have more time (opportunity) to forage. For example, sagebrush lizards from Mt. Diablo, California, which experience approximately 55% longer activity seasons than do sagebrush lizards from Kolob Mesa, Utah, grow to a larger asymptotic body size (Ruth 1977; Tinkle et al.

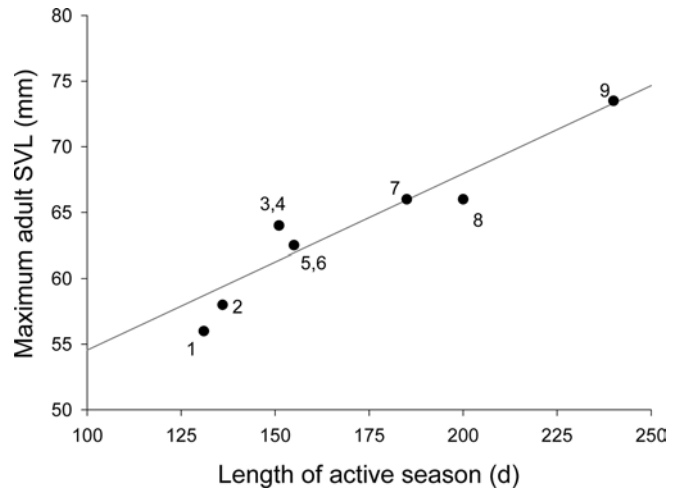


Fig. 1 Maximum body size (reported as snout to vent length *SVL*) of adult sagebrush lizards increases with the length of the activity season in days (mean squares = 179.5, $F_{1,6} = 51.6$, $P < 0.001$, $r^2 = 0.87$). The individual locations are as follows: 1 Yellowstone National Park, Wyo., 2 Butte Co., Calif., 3 Nevada and Placer Co., Calif., 4 Napa Co., Calif., 5 Kolob Mesa, Calif., 6 Salt Lake Co., Utah, 7 Utah Co., Utah, 8 Los Angeles Co., Calif., 9 Contra Costa Co., Calif.. Sources for the original data are Mueller and Moore (1969), Tinkle et al. (1993), Ruth (1977), Goldberg (1975), Burkholder and Tanner (1974), Jameson (1974), Marcellini (1966), and Stebbins and Robinson (1946).

1993). Increased growth in lizards from Mt. Diablo is accomplished by growing faster during the first year of life than yearlings from Kolob Mesa. Despite the differences in absolute growth, the proportion of the total energy budget allocated to growth is similar for the two populations, suggesting that thermal opportunity for activity may limit the acquisition of food. Thus, barring local adaptation, differences in growth in free-ranging lizards between these populations may be explained by differences in biophysical constraints on foraging activity, differences in availability of food, or through thermal constraints on physiological processes that produce variation in net energy assimilation (Grant and Dunham 1988, 1990; Congdon 1989; Dunham et al. 1989).

Laboratory studies have provided additional evidence that the thermal environment is an important influence on body size in sagebrush lizards (Sinervo and Adolph 1989, 1994). Growth of sagebrush lizards is positively correlated with the amount of time over which body temperatures suitable for activity can be maintained while under an unrestricted diet. Increases in thermal opportunity for activity from 6 to 12 h per day produced nearly a twofold increase in mass-specific growth rates. In addition, lizards that experienced a 50% reduction in food availability suffered a decrease in growth rate equivalent to a 50% reduction in thermal opportunity. While these results suggest that food availability and thermal opportunity are similar in their effects on growth, it is important to note that growth rates decreased when thermal opportunity was increased from 12 to 15 h per day. This result suggests that sagebrush lizards are limited in their capacity to process

additional food items that could be ingested with an additional 3 h of activity, or that energetic expenditure begins to outweigh the increases in energy intake that are gained with increased thermal opportunity. Nonetheless, data from the above-mentioned field work and laboratory experiments show that understanding how sagebrush lizards interact with their thermal environment is key to understanding geographic patterns of growth in this species.

Here, I examine whether small-scale geographic patterns in life history variation of sagebrush lizards occurring over a local elevational gradient can be explained by variation in thermal opportunity for activity, as suggested by large-scale geographic patterns and laboratory studies. Three populations of sagebrush lizards were studied over a local elevational gradient where extreme climatic variation should be less dramatic than climatic variation between populations that are more distant from each other, i.e. temperature should decrease and rainfall should increase with increases in elevation. Furthermore, these populations exhibit the same capacity for growth in a common environment, despite observed differences in growth in nature, suggesting that such patterns might be explained by variation in environmental resources among these populations (Sears and Angilletta 2003). Because the duration of daily and seasonal activity (mediated by the thermal environment) should decrease with increasing elevation, mortality and growth would both be expected to decrease with increasing elevation. I used mark-recapture data to determine rates of individual growth and mortality for these three populations. Operative temperatures of lizards were estimated by a mathematical model to estimate the potential duration of annual and daily activity. I discuss the results in the context of the temporal and spatial availability of thermal opportunity for activity as a determinant of growth, and further discuss alternative explanations (both proximate and evolutionary) for the patterns of growth observed in this system, which argue for including behavioral responses to perceived predation in addition to bioenergetic responses to thermal conditions. Such integrative conceptual models have not been widely considered in the current formulation of life history theory (reviewed in Stearns 2000).

Materials and methods

Study organism

Given its natural history and geographic distribution, the sagebrush lizard (*Sceloporus graciosus*) is a model organism for the study of life history variation in ectotherms. The sagebrush lizard is a small (5–10 g as an adult) insectivorous lizard that is relatively long-lived compared to other lizards of similar size (Miles and Dunham 1992). Sagebrush lizards are geographically widespread across the western United States ranging from the coast of Washington, south to parts of Baja

California, and east to the Great Plains states (Stebbins 1985). Sagebrush lizards are typically a montane species that experience a highly temperate climate, often with prolonged winters that reduce the length of sagebrush lizards' activity season compared to other lizards. Sagebrush lizards also range over a broad altitudinal gradient, from sea level at the northern extent of their range to over 3,000 m above sea level at the southern extent of their range. Over their geographic range, sagebrush lizards are found in a variety of habitats including sagebrush, manzanita-scrub oak, sand dune, and pine-fir communities. Sagebrush lizards will also utilize different features of their habitat to actively thermoregulate to consistent body temperatures across an altitudinal range (Adolph 1990). Thus, the broad range of habitats and wide geographic distribution make sagebrush lizards an excellent species for the study of life history variation, especially with respect to the thermal environment.

Populations of sagebrush lizards (*S. graciosus*) were monitored at three sites in Zion National Park (ZNP), Utah, during 1996–1999. The three sites—Clear Creek Canyon (CCC), Firepit Knoll (FPK), and Goose Creek Knoll (GCK)—span the entire elevational range over which sagebrush lizards occur in the park. Although, these populations are located proximally to one another, there is likely little, if any, genetic flow among populations given the absolute distance among the study areas (GCK is 20.16 and 9.18 km from CCC and FPK, respectively; and FPK is 23.45 km from CCC) and the discontinuity of habitat between the study areas. The CCC site (1.07 ha; 1,752 m above sea level; UTM: 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 gambeli*) and manzanita (*Arctostaphylos uva-ursi*). The FPK site (0.82 ha; 1,961 m; UTM: E 313264, N 4134600) is located on a rocky SW-facing hillside consisting mainly of exposed sandstone. Vegetative cover is primarily manzanita and Gambel oak scrub, with the occasional Ponderosa pine (*Pinus ponderosa*). The population at FPK was the subject of a previous, intensive demographic study (referred to as Rattlesnake Ridge in Tinkle 1973; Tinkle et al. 1993). The GCK site (0.57 ha; 2,255 m; E 321350, N 4138950) is located on an exposed limestone ridge top along the edge of 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.*). (Distances are straight line distances.)

Body size and growth trajectory analysis

Data from a mark-recapture study were used to examine body size and individual growth trajectories. Lizards from each of the three study sites were censused annually from 1997 to 1999. Within each annual census, monthly surveys were taken (typically from May to August) until no new lizards were captured during that month. Upon initial

capture, lizards were permanently identified using a unique toe clip for subsequent identification. Body size was taken at each capture: snout–vent length (SVL) was measured to the nearest millimeter with a clear plastic ruler, and mass was measured to the nearest 0.1 g using a Pesola spring scale. Lizards were followed from their initial capture until their presence could no longer be detected at the site (either due to emigration or death). To minimize the possibility that the disappearance of an individual was not due to mortality but emigration, a 50-m buffer around each site was searched during censusing periods. Because body size measurements among years (and ages) on the same individual are not independent of one another, a single, randomly chosen measurement was used for individuals with multiple measurements among years. Body size data were analyzed with analysis of variance (ANOVA) with year, site, and age as fixed effects. All post-hoc comparisons were made using Tukey's honest significant difference test (for unequal n). All comparisons of body size were performed using Statistica for Windows (StatSoft 1996).

For analysis of growth trajectories, SVL data were used instead of mass data because they are less subject to variation in nutritional or reproductive state (Dunham and Gibbons 1990). To minimize the influence of measurement error on growth, intervals of less than 14 days were excluded from the analysis. Additionally, if a single individual had more than one growth interval measured within a year, only one randomly selected growth interval was entered into the growth model. Using the approach described by Dunham (1978a) and Schoener and Schoener (1978), I estimated the free parameters (asymptotic body size and characteristic growth parameter) of the interval forms of the logistic-by-length, logistic-by-weight, and Von Bertalanffy growth models from recapture growth data for lizards at each of the sites. Models were fitted using a Marquardt non-linear least-squares regression procedure (Dunham 1978b). Free parameter estimates were compared among sites by calculating a t -statistic (2-sided test) using the mean, jackknifed standard deviation, and sample size for each estimate.

Survival analysis

Mark-recapture data were used to compare survival rates among the populations. The age of last appearance for each lizard was recorded when a lizard was absent from three consecutive surveys. These data, where lizards were presumed absent, were entered into the analysis as uncensored data (see Cox and Oakes 1984 for a discussion of data censoring). The ages of lizards that had not disappeared by the end of the study period were used in the analysis, but were entered as censored data. In both cases, only lizards of known age were entered into the analysis. Differences in survival times among the three study populations were analyzed using the survival analysis package of Statistica for Windows (StatSoft 1996). The multiple sample test used in the Statistica survival package is a

generalization of Gehan's generalized Wilcoxon, Peto and Peto's generalized Wilcoxon, and the log-rank test (Gehan 1965; Peto and Peto 1972). A score was assigned to each survival time using Mantel's procedure (Mantel 1967), and a chi-squared value was calculated using the score sums for each site. A P -value of 0.05 was considered statistically significant. Furthermore, all pair-wise comparisons among sites were made using Cox's F -test. A Bonferroni-adjusted P -value of 0.016 was used to test for statistical significance.

Thermal opportunity

The duration of potential daily and seasonal activity was estimated for each population using the model by Adolph and Porter (1993). Adolph and Porter's model incorporates microclimate data, an organism's biophysical characteristics, and an organism's behavior to predict body temperatures obtainable by that organism on an hourly basis for an average day of each month of the year. Given a range of body temperatures, the model predicts the potential activity time for each day, and these can be summed to determine seasonal or annual activity. For this study, lizards were considered active if (1) their estimated T_b ranged from 29°C to 37°C, and (2), because these lizards burrow, the ground surface temperature must have reached at least 20°C, the minimum temperature at which lizards from these populations emerge (Sears, unpublished data). Thermal opportunity was calculated as the sum of daily activity times for the entire year. Parameter values used in determining activity times were identical to those used in Table 1 of Adolph and Porter (1993), with the exception of temperature and humidity data supplied from local weather stations. Monthly averages of available weather data from November 1997 to March 2002 (the extent for which long-term air temperature were available) were used for the analysis of thermal opportunity from two local weather stations. The Lava Point RAWS weather station (37.39 W, 113.04 N, 7,851 ft, LPRU1 RAWS) was used for GCK and the ZNP East Gate weather station (37.25 W, 112.86 N, 5,670 ft, ZNP Snownet) was used for CCC. The ZNP Snownet and LPRU1 RAWS weather stations were located within 1 km of the CCC and GCK sites, respectively, and air temperatures and relative humidities collected from these weather stations were used directly as model input. Air temperatures for FPK were estimated from the ZNP Snownet weather station by correcting air temperatures for elevation using the dry air adiabatic cooling rate of 9.9°C km⁻¹.

Results

Thermal opportunity

The estimated time available for activity decreased from the low to the high elevation study sites. For each site,

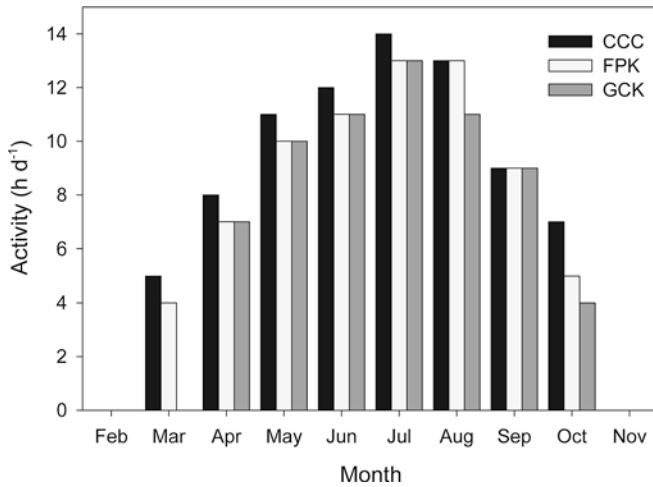


Fig. 2 Average daily potential activity times (estimated by the model of Adolph and Porter 1993) for each of the study sites are shown for each month of the year during which lizards may be active. Total seasonal activity times are 2,420, 2,205, and 1,988 h year⁻¹ for CCC, FPK, and GCK, respectively

average daily activity times for each month are reported in Fig. 2. Potential thermal opportunity for activity was estimated to be 2,420 h year⁻¹ for CCC, 2,205 h year⁻¹ for FPK, and 1,988 h year⁻¹ for GCK. The difference in potential total activity times between CCC and GCK is equivalent to thirty-six 12-h activity days (assuming that activity was possible over every hour of the day during daylight hours).

Growth trajectories

Growth of lizards from the high elevation population was faster than growth of lizards from the low and middle elevation populations. Parameter estimates derived from the Von Bertalanffy growth model were used for pair-wise comparisons among sites because the Von Bertalanffy growth model gave the best fit to the data overall (parameter estimates of all models are reported in Table 1), though both the logistic-by-length and

Table 1 Summary of the parameter estimation of von Bertalanffy (*VB*), logistic-by-weight (*LBW*), and logistic-by-length (*LBL*) growth models (see Dunham 1978a, for the mathematical formulation of the growth models used here). The growth parameter (*r*) and asymptotic body size (*A*) are reported with 95% support plane confidence intervals (*CI*; as per Dunham 1978a; *N* sample size, *R*² coefficient of determination)

Site	Model	<i>R</i> ²	<i>N</i>	<i>A</i>	<i>CI</i>	<i>r</i>	<i>CI</i>
CCC	VB	0.999	52	65.47	0.535	0.0141	0.0012
FPK	VB	0.999	91	66.91	0.773	0.0126	0.0013
GCK	VB	0.999	38	66.31	1.127	0.0156	0.0011
CCC	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	0.890	0.0231	0.0010
CCC	LBW	0.999	52	64.63	0.490	0.0239	0.0018
FPK	LBW	0.999	91	65.72	0.662	0.0222	0.0016
GCK	LBW	0.999	38	65.06	0.770	0.0303	0.0012

logistic-by-weight models performed nearly equally as well. Both asymptotic body sizes (CCC versus FPK: $P < 0.001$; CCC versus GCK: $P < 0.001$; FPK versus GCK: $P < 0.001$) and the characteristic growth parameter (CCC versus FPK: $P < 0.001$; CCC versus GCK: $P < 0.001$; FPK versus GCK: $P < 0.001$) varied significantly among sites.

Body size comparisons

Body size (SVL and mass) differed significantly among populations over the duration of this study (see Tables 2 and 3 for ANOVA table and descriptive statistics, respectively; Fig. 3). With regard to SVL, GCK lizards were smaller than CCC and FPK lizards ($P < 0.001$ in both cases), while CCC and FPK lizards were similar in size. SVL of first year GCK lizards were smaller than CCC and FPK lizards ($P < 0.001$ in both cases), with CCC and FPK first year lizards similar in size. SVL of second-year lizards varied only between the GCK and FPK populations, with FPK lizards being larger ($P = 0.033$). All third year plus lizards were similar in size among sites. With regards to mass FPK lizards were larger than both CCC ($P < 0.001$) and GCK ($P < 0.001$), and CCC lizards were larger than GCK lizards ($P < 0.001$). Mass of first year GCK lizards was less than CCC ($P < 0.001$) and FPK lizards ($P < 0.001$), with CCC and FPK first year lizards similar in size. Mass of second year FPK lizards was greater than both CCC ($P = 0.016$) and GCK ($P < 0.001$) second year lizards. Second year lizards from CCC and GCK were similar in size. All third year masses were similar among the sites.

Body size varied depending on the year (Table 2, Fig. 3). With regard to SVL, lizards were larger in 1997 than they were in 1998 ($P < 0.001$) and 1999 ($P < 0.001$), and 1998 lizards were larger than 1999 lizards ($P < 0.001$). Differences in size can be ascribed to variation

Table 2 ANOVA summaries for body size comparisons among sites, age classes, and years (SVL snout-vent length, MS mean squares)

Dependent variable	Effect	<i>df</i>	MS	<i>F</i>	<i>P</i> -level
Mass	Year	2	8.23	13.07	< 0.001
	Site	2	16.46	26.12	< 0.001
	Age	2	956.75	1518.51	< 0.001
	Year × site	4	4.53	7.19	< 0.001
	Year × age	4	3.61	5.73	< 0.001
	Site × age	4	6.12	9.68	< 0.001
	Year × site × age	8	0.32	0.51	0.85
	Error	541	0.63		
SVL	Year	2	212.59	19.23	< 0.001
	Site	2	419.22	37.92	< 0.001
	Age	2	19220.88	1738.76	< 0.001
	Year × site	4	61.3	4.51	< 0.001
	Year × age	4	230.07	20.81	< 0.001
	Site × age	4	360.85	32.64	< 0.001
	Year × site × age	8	7.35	0.665	0.72
	Error	543	11.05		

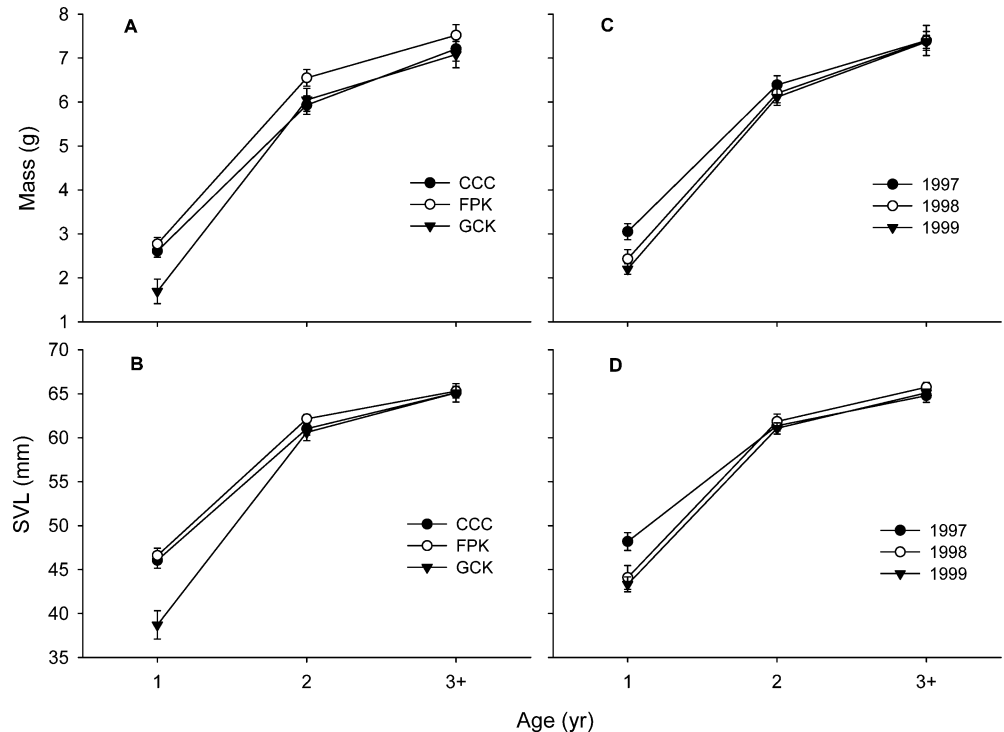
Table 3 Lengths (mm) and masses (g) used in the ANOVA for body size. The sample size, mean, and 95% confidence interval are reported for each grouping. Note that each individual is only reported for one age over its entire lifetime, not all three age classes

Site	Age	1997			1998			1999		
		N	SVL	CI	N	SVL	CI	N	SVL	CI
Length										
CCC	1	28	50.20	1.23	15	45.60	2.09	53	44.00	1.01
CCC	2	18	60.22	1.26	12	62.50	0.85	16	60.81	1.15
CCC	3+	10	64.10	1.41	10	66.20	0.96	18	65.08	0.67
FPK	1	31	49.74	1.11	39	47.91	1.33	50	43.64	1.16
FPK	2	29	61.52	0.73	21	63.19	0.61	14	61.93	1.13
FPK	3+	21	64.67	1.08	19	66.42	0.93	21	64.93	0.82
GCK	1	21	43.05	2.40	21	35.57	1.13	6	34.08	1.80
GCK	2	27	61.70	1.33	27	59.59	1.86	15	60.53	1.43
GCK	3+	3	67.67	3.27	15	65.20	1.60	10	64.20	1.16
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Mass										
CCC	1	28	3.29	0.18	15	2.59	0.35	53	2.25	0.15
CCC	2	18	5.92	0.36	12	5.90	0.50	16	5.98	0.28
CCC	3+	10	7.11	0.90	10	7.22	0.39	18	7.25	0.27
FPK	1	31	3.35	0.23	39	2.96	0.25	50	2.27	0.18
FPK	2	29	6.44	0.31	21	6.82	0.31	14	6.39	0.33
FPK	3+	21	7.33	0.48	19	7.92	0.45	21	7.35	0.28
GCK	1	21	2.32	0.52	21	1.25	0.10	6	1.04	0.18
GCK	2	27	6.60	0.47	26	5.57	0.32	15	5.93	0.45
GCK	3+	3	7.87	1.31	15	6.90	0.41	9	7.10	0.37

in first year body size. SVLs of first year lizards were larger in 1997 than in 1998 ($p < 0.001$) and 1999 ($P < 0.001$), and SVLs larger in 1998 than 1999 ($P < 0.001$). SVL of other age classes did not vary among years. With regard to mass, lizards were heavier in 1997 than they were in 1998 ($P < 0.001$) and 1999 ($P < 0.001$), and 1998

lizards were heavier than 1999 lizards ($P = 0.035$). Differences in mass can be ascribed to variation in first year body size (Fig. 4). Masses of first year lizards were greater in 1997 than in 1998 ($P < 0.001$) and 1999 ($P < 0.001$), and masses were greater in 1998 than 1999 ($P < 0.001$). Masses of other age classes did not vary

Fig. 3 Body sizes for different age classes plotted for individuals during the month of June. Body size patterns with respect to population of origin (a, b; pooled across years) and year of study (c, d; pooled across sites)



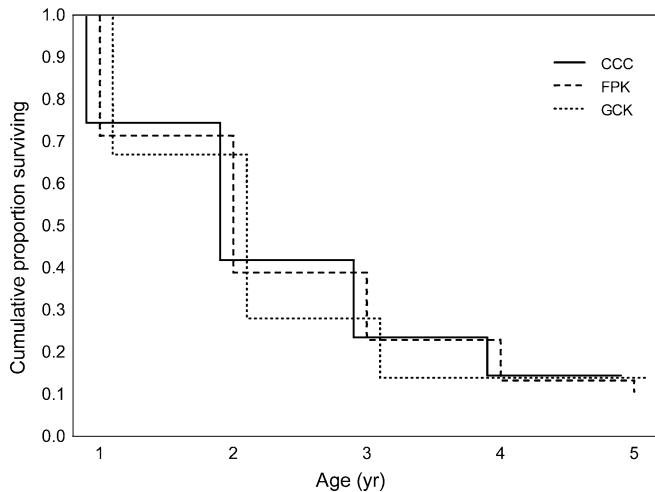


Fig. 4 A Kaplan-Meier plot of the cumulative proportion of animals surviving to age (x) for each site (CCC, FPK, and GCK). Lines corresponding to each site are offset for clarity

among years. These differences in body size may be attributable to 1998-1999 encompassing an El Niño event with cooler and wetter temperatures (see [Discussion](#)).

Survival

There is a trend for differences in survival among the sites ($X^2 = 5.95$, $df = 2$, $P = 0.051$) with survival decreasing with increasing elevation. Survival curves are illustrated in a Kaplan-Meier plot of the cumulative survival frequencies for each of the sites (Fig. 4). Furthermore, pair-wise comparisons among sites show that CCC and FPK do not differ in survival rates (Cox's $F_{256, 414} = 1.16$, $P = 0.089$), but both CCC and FPK exhibit significantly higher survivorship than GCK (CCC versus GCK: Cox's $F_{256, 254} = 1.67$, $P < 0.001$; FPK versus GCK: Cox's $F_{414, 254} = 1.44$, $P < 0.001$).

Discussion

The patterns of growth and survival exhibited among populations of sagebrush lizards at ZNP differ from that predicted if thermal opportunity for activity were the exclusive factor producing among-population variation. Lizards with less thermal opportunity for activity, such as those at high elevations or northern latitudes, should have reduced annual production, smaller adult body sizes, and lower annual mortality (Adolph and Porter 1993, 1996). Counter to such an argument, the sagebrush lizard population at high elevation exhibits faster growth than do the populations at lower elevations, despite having cooler environmental temperatures and shorter seasonal activity. Yearlings at low and mid elevation are larger in spring, but those at high elevation grow faster over the summer and fall to reach the same body size by the following spring as lizards from lower

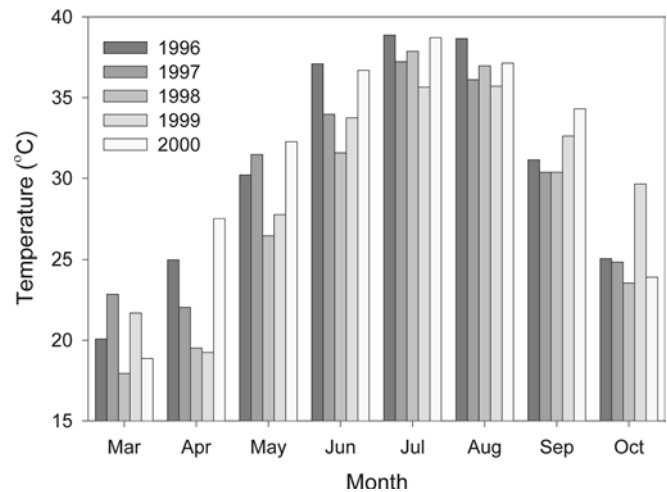


Fig. 5 The average maximum air temperature for each month of the lizard activity season for the years 1996–2000. Due to incomplete and unavailable data, temperatures were taken from the Zion National Park weather station located at the visitor center (approximately 1,200 m above sea level) instead of from the weather stations used in the analysis of thermal opportunity

elevations. Also, contrary to predictions with respect to thermal opportunity, lizards from high elevation incur a greater risk of mortality each year. Interestingly, among year variation in thermal opportunity may explain patterns of growth within a population. While these observations may seem counterintuitive, I will outline in the following discussion the reasons why such an outcome is likely in this specific system, and in general.

Patterns of variation in growth and survival

Why doesn't growth increase with increased thermal opportunity for activity? Growth rates will be affected most immediately by the amount of food available for growth and access to that food by individuals (Dunham 1978a; Tracy 1999). Unfortunately, the relationship between the abundance of food in the environment and that available to individuals is difficult to discern at best. For an ectotherm, foraging areas and areas thermally suitable for activity must coincide for the maximal potential utilization of food resources (Tracy and Christian 1986). Furthermore, intraspecific interactions (e.g., territoriality or competitive exclusion) may limit an individual's access to available food. For instance, during an 11-year demographic study, the growth rates of juveniles at FPK decreased as the densities of adults increased (Tinkle et al 1993). While population densities may influence growth within populations, intraspecific competition for food does not appear to explain the patterns of growth or survival among populations because densities at GCK were higher than densities at the other sites for years when growth trajectories were estimated (Fig. 5; Sears 2001). Furthermore, preliminary data suggest that the abundance of arthropods is similar among sites, and that trends in the abundance of

arthropods do not correspond with growth [Kruskal-Wallis ANOVA ($P = 0.092$); insect densities were 54.1 (15.1), 87.3(22.4), 68.1 (20.1) insects $\text{h}^{-1} \text{m}^{-2}$ (CI) for CCC, FPK, and GCK, respectively; Sears 2001]. Given the potential complexity in translating food abundance in the environment to food intake by lizards, it is not surprising to find no obvious relationships between food abundance and growth. Results for a congeneric species (*S. merriami*) showed that while food availability among sites increases with elevation, lizards at intermediate elevation exhibit the fastest rates of growth (Dunham et al. 1989; Grant and Dunham 1990). Additionally, Tracy (1999) reports that amount of time available to forage may be more important than the absolute food abundance in the environment in explaining growth patterns in chuckwalla (*Sauromalus obesus*). Such data suggest that realized growth is a complex interaction between food availability and foraging opportunity, and possibly differentiation among populations in physiological rates (Congdon 1989).

Why don't among-population survival rates covary with differences in thermal opportunity? Either predation rates are higher at GCK or mortality from extended overwintering periods at GCK outweighs other sources of mortality incurred during the active season. Predation risk is not a likely explanation for increased mortality at GCK because, as with many cooler environments, reptilian predators of lizards (snakes and skinks) are nearly absent from GCK; I have never observed a predation event. In contrast, FPK and CCC support moderate numbers of snakes (*Masticophis taeniatus* and *Crotalus viridis*) and predatory lizards (*Eumeces skiltonianus* and *Crotaphytus insularis*), and I often observed multiple predation events each year. While predation may not explain higher mortality at high elevation, overwintering mortality may. At GCK, lizards may experience up to an additional 2 months of winter inactivity. Due to the additional energy requirements necessary for prolonged hibernation, or possibly due to unpredictable weather imposing a severe penalty for early emergence, higher mortality at GCK is not a reasonable possibility. Increased severity and length of winters have been shown to decrease the survival rates of individuals (Johnson and Evans 1991; Hurst and Conover 1998; Frederiksen and Bregnballe 2001). Furthermore, body size and condition affect overwinter survival in a variety of ectotherms (Civantos and Forsman 2000; Fullerton et al. 2000; Smith 2002)—larger animals tend to have higher overwinter survivorship. Because hatchlings from GCK have less time to forage before the onset of hibernation, and therefore are likely to be smaller (or leaner) while overwintering, overwinter mortality is a strong candidate for explaining the higher annual mortality rate at GCK.

Trade-offs between growth and survival

The longer an ectotherm can maintain activity, the more time it has to forage and the greater chance that it will

encounter a predator and be eaten. Thus, the thermal environment may produce a trade-off between growth and survival when variation in the environment favors increased activity. Adolph and Porter (1993) presented a theoretical consideration of such a trade-off produced by variation in thermal opportunity. Their model assumes that (1) life history variation arises via the environment (i.e. no genetic differentiation among populations is necessary), (2) activity time is correlated with resource acquisition, and (3) mortality risk increases with activity. Since thermal opportunity determines, in part, when an ectotherm may be active, their model predicts that both mortality and production (somatic and reproductive) should increase with increased thermal opportunity, and thus mortality should increase with production. Adolph and Porter support their model with empirical data from the eastern fence lizard (*Sceloporus undulatus*), with growth and reproductive output higher and survival lower for populations that have relatively high amounts of thermal opportunity. Niewiarowski (2001) has further demonstrated that growth in juvenile *S. undulatus* is influenced by thermal constraints on time available for activity.

Natural populations of sagebrush lizards do not show the same response to the thermal environment as their congeners. Though the results of this study are not consistent with the direct predictions of Adolph and Porter, they may be explained by a theory that further incorporates behavioral decisions about foraging time being mediated by predation risk. Adolph and Porter's model assumes that increased rates of energy intake are positively correlated with increased mortality, but the model does not incorporate the possibility that individuals may reduce their foraging intensity with increased risks of predation. In fact, increased effort to acquire resources may increase the probability of mortality by predation (McNamara and Houston 1987), and there is much evidence that this trade-off between predation risk and resource acquisition are mediated by individual behavior (reviewed in Lima and Dill 1990; Lima 1998). Using the criterion that animals should minimize the ratio of mortality to growth rate, Werner and Anholt (1993) predicted that individual behavior should vary depending upon resource level and the relationship between activity and mortality. Preliminary data suggests that resource abundance in the ZNP system is similar across all sites. Although realized annual mortality is higher at GCK, the actual (hourly or daily) risk of predation is likely higher at lower elevations given that the abundance of lizard predators increases with decreasing elevation (Sears, personal observation). Under this scenario, Werner and Anholt's model would suggest that lizards from the lower elevation sites should decrease time spent foraging or increase the intensity of foraging during activity to mediate the risk of mortality. Lizards from high elevation should also increase time spent foraging if increases in mortality are unrelated to activity (which is likely if higher annual mortality at high elevation is due to overwinter stress from an extended

period of hibernation or death caused by exposure to extreme cold conditions). In fact, predator-induced behavioral shifts in foraging intensity have been shown to decrease growth (Lardner 2000; Thiemann and Wassursug 2000; Van Buskirk and Yurewicz 1998; Lewis 2001). So it is important to note that, if food availability and predation risk were similar across all sites in this study, Adolph and Porter's model would make the same predictions as that of Werner and Anholt.

Interestingly, when comparing body size among years but within site, years that would likely have had reduced activity rates due to cool cloudy days show reduced body size. During the El Niño event of 1998–1999, daily maximum temperatures were cooler in the spring and early summer, when lizards typically grow the most (Fig. 6). To know whether this pattern of growth is a more general phenomenon or not, long term observations will need to be further documented. Regardless, reduced growth during cooler years is consistent with growth rates being limited by thermal constraints (Adolph and Porter 1993; Niewiarowski 2001). Thermal constraints on growth likely have more influence within a population than among populations because predation pressures among years within each study site are likely to be more similar than predation pressures among study sites regardless of year. The results of this study argue for the incorporation of other ecological factors into a model such as Adolph and Porter's, such as relaxing the implicit assumption that predation risk and time spent (or intensity of) foraging are independent.

Spatial aspects of the thermal environment

Another facet of an organism's thermal environment to consider is the spatial distribution of environmental temperatures. While the temporal distribution of operative temperatures in an animal's environment sets

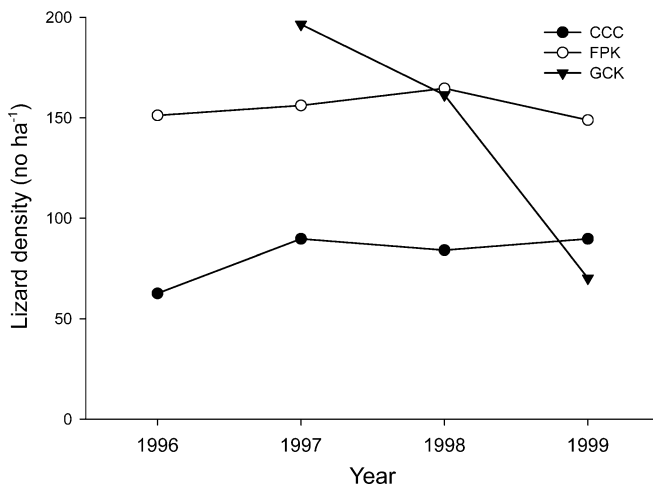


Fig. 6 Lizard density of known individuals on each of the study sites (CCC, FPK, and GCK). Data for GCK were not collected in 1996 due to a wildfire

bounds on the duration of daily and seasonal activity, the spatial distribution of operative temperatures at any given time will constrain where an individual can be active. Thus, the behavioral decisions of individuals are constrained because the time spent thermoregulating among microhabitat patches may take away from other activities such as foraging, predator avoidance, and mate acquisition (Huey and Slatkin 1976; Dunham et al 1989; Huey 1991). Further constraints are also placed on activity if specific microhabitats are used exclusively for particular behaviors such as foraging or thermoregulation (Adolph 1990; Blouin-Demers and Weatherhead 2001).

Because sagebrush lizards modify their use of microhabitat to actively thermoregulate within a narrow set of body temperatures (Adolph 1990), the interaction of habitat configuration and environmental temperatures may allow lizards at GCK to have more unrestricted access to foraging sites than do lizards at lower elevations, where environmental temperatures are warmer. The composition of microhabitats at each study location is quite different. GCK is comprised of regularly spaced shrubs on a largely shale substrate. Distances between shrubs are generally pretty small (< 5 m), and consequently, lizards can move freely across the habitat at most times of the day. At FPK, vegetation is largely clumped, with much of the habitat being composed of large expanses of slick rock with little thermal refugia on the surface. At midday, the exposed areas of slick rock are too warm for lizard activity. At CCC, vegetation is not as clumped as at FPK, but the substrate between vegetation tends to be sand, which heats to nearly 70°C at midday, and lizard activity is even more limited than at FPK. Because environmental temperatures are also less at higher elevations, lizards from GCK might realize faster growth because they may have less restricted access to habitats over which to forage across all times of the day. Lizards at the two lower elevation sites must not only deal with warmer overall temperatures, but also larger (and thermally more extreme) distances between patches of vegetation where activity can be maintained for most times of day. Ongoing studies of the influence of the spatial distribution of operative temperatures on activity and microhabitat use will lend insight into the observed patterns of growth for these populations.

Adaptive growth

While among-population patterns of growth in this system may be consistent with adaptive explanations (Case 1978; Arendt 1997; Kozłowski and Teriokhin 1999), patterns of growth are not likely caused by local adaptation. Increased growth rates would be favored either to compensate for a short growing season, where there is a minimum size necessary for reproduction, or to minimize mortality where larger size is linked to higher overwinter survival. Lizards from GCK are inactive for

up to 2 months longer than lizards from lower elevation, yet all males were reproductively mature during their second summer and all females produced at least one clutch during their second summer for the duration of this study (Sears, unpublished data). If lizards must reach a minimum size for reproduction during their first year of growth, one might expect that lizards at GCK have evolved increased growth rates to compensate for a short growing season (e.g., Conover and Present 1990; Ayres and Scriber 1994). To the contrary, evidence from a common-environment experiment supports the conclusion that elevational variation in growth is due to proximate environmental effects. Sagebrush lizards from all three sites were reared from eggs under similar thermal conditions with varied consumption of food and water (Sears and Angilletta 2003). Differences 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 source population. Therefore, differences in growth under conditions in the field are due to variation in some environmental resource (e.g. availability of thermal habitats for foraging) or through acclimatization of physiological rates to the different thermal regimes experienced at each of the sites (Congdon 1989).

Conclusions

Though tempting to pursue, simple generalizable explanations for the intraspecific patterns of geographic variation in life histories are not likely to be found, especially if we consider the numerous trade-offs that result from the interactions of individuals with their environment. Given the thermal dependency of physiology and behavior, many ecologists have concentrated on thermal aspects of the environment to explain the life history of individuals. Though thermal constraints on the duration of activity influence the growth and survival of individuals for geographically widespread species, other ecological factors must also be considered in theoretical frameworks before a robust understanding of environmental influences on life history can be reached. Temporal and spatial aspects of the thermal environment will largely determine the limits to the duration and types of activities an animal may engage in, but other influences on the behavior of animals will contribute to when an animal chooses to be active. Of particular interest for future investigation is the potential trade-off between resource acquisition and predation risk. Experimental manipulation of the density or perception of predators in an environment and/or reciprocal transplantation of individuals from contrasting environments may lend much insight into the relative importance of predators and the thermal environment in determining the life histories of animals.

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