Elevational Covariation in Environmental Constraints and Life Histories of the Desert Lizard Sceloporus Merriami

Bruce W. Grant, Arthur E. Dunham

Ecology, Volume 71, Issue 5 (Oct., 1990), 1765-1776.

Your use of the JSTOR database indicates your acceptance of JSTOR's Terms and Conditions of Use. A copy of JSTOR's Terms and Conditions of Use is available at http://www.jstor.org/about/terms.html, by contacting JSTOR at jstor-info@umich.edu, or by calling JSTOR at (888)388-3574, (734)998-9101 or (FAX) (734)998-9113. No part of a JSTOR transmission may be copied, downloaded, stored, further transmitted, transferred, distributed, altered, or otherwise used, in any form or by any means, except: (1) one stored electronic and one paper copy of any article solely for your personal, non-commercial use, or (2) with prior written permission of JSTOR and the publisher of the article or other text.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

Ecology is published by The Ecological Society of America. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at http://www.jstor.org/journals/esa.html.

Ecology
©1990 The Ecological Society of America

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2001 JSTOR

http://www.jstor.org/
Tue Aug 14 12:05:31 2001

Ecology, 71(5), 1990, pp. 1765–1776

ELEVATIONAL COVARIATION IN ENVIRONMENTAL CONSTRAINTS AND LIFE HISTORIES OF THE DESERT LIZARD *SCELOPORUS MERRIAMI*[1]

BRUCE W. GRANT[2]
Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706 USA

ARTHUR E. DUNHAM
Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104 USA

Abstract. We examine environmental constraints on life history characters among three elevationally distinct populations of the desert lizard *Sceloporus merriami* in west Texas. We show how environmental gradients in temperature and food abundance interact to constrain body temperatures, daily activity times, growth rates, and age-specific body size. We suggest that these differences resulted in opposite responses from males and females with respect to their size and age at first reproduction.

The highest elevation site, Maple Canyon (1609 m), has more rainfall, higher food availability, and cooler temperatures compared with the lower elevation sites, Grapevine (1036 m) and Boquillas (560 m). Lizards were active throughout the day at Maple Canyon, but were restricted to midday inactivity at the lower sites. Body temperatures (T_b) were higher during inactivity and late-afternoon activity at the lower sites. We suggest that low food availability, fewer hours to forage, and higher T_b constrained the energy budgets of lizards at Boquillas. Consequently, these lizards had low activity rates and low daily growth rates. Paradoxically, lizards at Maple Canyon, the most food-rich site, also exhibited low daily growth rates. This may have resulted from high daily activity expenditure (longer activity period) and lower food processing rate (low inactive T_b). Grapevine lizards had the highest individual activity and growth rates.

On a seasonal basis, the pattern of activity time was reversed, and Maple Canyon lizards had a shorter annual active season by ≈ 1 mo compared with Grapevine and 2 mo compared with Boquillas. Despite low growth rates at Boquillas, a 2-mo longer activity season proximally resulted in the largest yearlings by May–June. Maple Canyon yearlings grew at a similar rate, but over a shorter time period and were the smallest. At Grapevine, high summer growth rates resulted in large yearlings by late summer and the largest adults, whereas low summer growth rates at Boquillas and Maple Canyon led to smaller adults.

The resulting difference in body size between yearling and older age classes was great at Maple Canyon and at Grapevine, which forced yearling males to delay reproduction until they had grown to a size to compete successfully for breeding territories. However, Boquillas yearlings and age >1 yr lizards were much more similar in size, and many yearlings were able to acquire breeding territories. This suggests that male age of first reproduction was lowest at the low elevation site.

In contrast, more yearling females reproduced earlier at the highest elevation site than at other sites. At Grapevine and Boquillas, females similar in size to breeding females at Maple Canyon did not breed in May–June and instead grew and were reproductively active in July–August. We hypothesize that the brief growing season at Maple Canyon may have constrained females to breed early to allow sufficient time for themselves, as well as for their offspring, to amass winter stores. Also, this would increase the likelihood that their offspring were large enough to breed as yearlings.

Results suggest an interaction between resource levels and biophysical constraints that may greatly influence differences among populations in important life history characteristics. Although these responses are hypothesized to be proximally induced by environmental constraints, the resulting life history differences in age-specific resource allocation to growth, storage, and reproduction may significantly affect fitness.

Key words: activity; age at maturity; biophysical constraint; body size; body temperature; desert; elevational gradient; environmental constraint; growth rate; growth season; life history; lizard; reproduction; Sceloporus merriami; *thermal biology.*

---

[1] Manuscript received 13 April 1989; revised 19 September 1989; accepted 7 October 1989.

[2] Present address: Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29801 USA.

INTRODUCTION

Correlated variation in life history characters and environmental factors, such as resource abundance or length of the growing season, has been documented in numerous reptilian systems (e.g., Tinkle 1972*a, b,* Tinkle and Ballinger 1972, Derickson 1974, 1976*a, b,* Dunham 1978, 1981, Ballinger 1979, Ballinger and Congdon 1980). Patterns of covariation in life histories and environmental gradients have been referred to as "proximal" in origin or "environmentally induced" (Dunham 1978, Ballinger 1983). But this does not necessitate that such variation is entirely nongenetic and thereby irrelevant to selection on life history phenotypes. Environment–genotype interactions exist and can lead to adaptive plasticity in variable and unpredictable environments (Resnick 1985, Stearns 1986, Lynch et al. 1988, Newman 1988). Although comparative data cannot reveal genetic mechanisms leading to such an interaction, in some cases life history phenotypic responses (sensu Dunham et al. 1989) to specific environmental constraints are likely to be adaptive (Williams 1966, Tinkle 1972*a, b*).

For example, in an extensive study of life history variation in *Sceloporus merriami* in the Grapevine Hills, Dunham (1978, 1981) found that during wet years more arthropod prey were available, more were consumed, individual growth rates were higher, reproducing females were larger in size, prehibernation lipid levels were greater, and females exhibited greater size-specific fecundity than for the same population during dry years.

D. W. Tinkle showed in *Uta* that northern populations were active over a shorter growing season than were southern conspecifics (Tinkle 1967, 1969*a, b,* 1972*a*), and postbrumation lipids were critical to vitellogenesis for the first clutch within the short season populations (Hahn and Tinkle 1965). Offspring from this clutch emerged early in the summer, and had sufficient time to grow to a minimum size for maturity (if male) and to amass minimum lipid stores for vitellogenesis (if female) by the next spring. In contrast, offspring from the later clutches did not attain minimum mature size until much later. This was interpreted as an adaptive shift in resource allocation (from storage to reproduction) in response to a proximate environmental constraint (a short growth season). To suggest that the timing of lipid mobilization exhibited by short season lizards is purely "environmentally induced" misses the point that as a result of this response a female cannot only produce an additional clutch per year, but may also guarantee the production of "grandchildren" within 1 yr. There are few clearer instances of adaptive responses by life history phenotypes to environmentally imposed constraints.

This paper shows how the resource and biophysical environments constrain daily and seasonal activity, age-specific growth and body size, and size and age of first reproduction among three populations of the desert lizard *Sceloporus merriami* (Iguanidae) along an elevational gradient in Big Bend National Park, Texas. Character data we present illustrate the coupling of operative environments (sensu Mason and Langenheim 1957, Spomer 1973) and life history phenotypes (sensu Congdon 1989, Dunham et al. 1989). Many life history characters of *S. merriami* showed reversed trends, inversions, and/or site-by-sex interactions among localities. These patterns cannot be accounted for by current life history theory, which was formulated to explain correlations between single character and environmental gradient pairs (Wilbur et al. 1974, Stearns 1976, Dunham et al. 1989). We hypothesize that a combination of operative gradients in resource abundance, and daily and seasonal environmental temperature, may explain many of the observed differences in life history phenotypic responses among these populations.

MATERIALS AND METHODS

Site descriptions.—Study populations occur at three ecologically distinct localities in Big Bend National Park, Texas, along an elevational gradient (Maple Canyon: 1609 m, Grapevine Hills: 1036 m, and Boquillas Canyon: 560 m). Investigations of life history variation have been ongoing since 1981 at Boquillas and Maple Canyon, and since 1974 at Grapevine. These studies have monitored long-term variation in population sizes, age-specific survivorships, growth rates, reproductive tactics, fecundities, home range dynamics, social structure, thermal biology, and other demographic characters (Dunham 1978, 1980, 1981, 1982, 1983, Congdon et al. 1982, Huey and Dunham 1987, Ruby and Dunham 1987, Grant 1988, Grant and Dunham 1988, Dunham et al. 1989).

The study localities represent a wide range of environmental types (Table 1). Boquillas is near the lower elevation limit for *S. merriami* and is hotter, drier, least vegetated, and least food rich. Maple Canyon is near the upper elevation limit and is much cooler, receives about twice the annual and summer precipitation, is relatively thickly vegetated, and has the most food. Grapevine is intermediate in these characteristics.

Active season length was estimated as the number of days with an average air temperature ≥18°C. This value was selected based on observations at Boquillas in fall 1985 and spring 1986 (B. W. Grant and S. R. Waldschmidt, *personal observations*), and observations at Grapevine reported in Dunham (1981).

Body size and growth data.—Lizards on each study site were captured by noosing, and individual mass (±0.05 g), snout–vent length (≡SVL, ±0.5 mm), and tail length (±0.5 mm, including any regeneration) were measured. For the first capture, each lizard was assigned a unique toe-clip and a small paint mark was applied to its dorsum. After these measurements were taken, each lizard was released at the exact point of

TABLE 1. Among-site differences.*

	Maple Canyon	Grapevine Hills	Boquillas Canyon
Elevation (m)	1609	1036	560
Annual rainfall (cm)			
Mean ± 2 SE	43.6 ± 4.5	33.7 ± 3.8	24.1 ± 2.1
No. data years	28	27	28
May–August rainfall (cm)			
Mean ± 2 SE	26.5 ± 2.9	18.6 ± 2.0	13.5 ± 2.0
No. data years	24	25	25
July average $\langle T_a \rangle$ (°C)	23.5	27.1	31.0
July deep crevice temp. (°C)	24.4	30.3	31.5
Vegetation cover (%)	32.8	23.2	15.1
Food abundance (items per trap hour)	0.290	0.137	0.086

* Climate data were obtained from United States Weather Bureau stations in the Chisos Basin (1640 m, 3.4 km southwest of Maple Canyon), Panther Junction (1140 m, 9.3 km south-southeast of Grapevine), and Rio Grande Village (562 m, 3.3 km southwest of Boquillas). Deep crevice temperatures are 24-h averages of thermocouple readings taken ≥ 1.5 m into crevices on lizard home ranges. Vegetation cover was the fraction of sample points beneath vegetation at 1-m intervals along line transects. Food availability estimates used 8-cm (3-inch) tape squares coated with Tanglefoot sticky resin trap (Ruby and Dunham 1987).

capture. Age assignments were made using standard methods (Tinkle 1972*a*, Dunham 1981).

Individual growth rates during summer activity were calculated as the change in SVL, or mass, divided by the number of days between successive captures (minimum of 10 d). These linearizations are adequate bases for comparison in this case because the intercapture interval was much less than the lifetime of a lizard, thus growth rates are approximately linear.

Reproductive data.—Reproductive condition for females was inferred at the time of each capture by palpation (Tinkle 1967). Females covered with mud had recently oviposited (Dunham 1981). The presence of follicles, oviductal eggs, or mud was sufficient to score a female as reproductively active. Frequencies of reproductive activity were calculated for yearling and age >1 yr females for May–June and July–August, and analyzed using a general log-linear model (procedure CATMOD, SAS 1982).

Social status and reproductive activity for males were determined by field observations of individual behavior during natural encounters with other lizards and by spatial proximity with females (Ruby and Dunham 1987). During the summer, many adult males were highly territorial and aggressively displaced other males, whenever detected, from areas occupied by females. Males who were winners of territorial encounters or males whose home ranges did not overlap other males and overlapped the home ranges of one or more adult females were assigned socially dominant status. Consistent losers of territorial encounters, isolated males, and males who did not appear to have permanent home ranges were assigned socially subordinate status (a more detailed description appears in Ruby and Dunham 1987). Due to spatial exclusion by dominants, subordinate males had very limited opportunity to court and inseminate resident females. Although many subordinates were sexually mature (Dunham 1981), their first opportunity to reproduce probably did not occur until they were socially dominant (Ruby and Dunham 1987). In most cases, dominant males were physically larger than subordinates (see *Results: Male size and age of first reproduction*); however, body size was not a criterion for social status assignment. Observations of social behavior were much more intensive at Grapevine and Boquillas, and our confidence in social status assignment is highest at these sites. At Maple Canyon, home range overlap with at least one adult female was sufficient to be scored as a dominant.

Body temperatures exhibited and thermal microclimates selected.—Body temperatures (T_b) were recorded by noosing lizards and inserting the bulb of a fast-reading thermometer into the individual's cloaca within 10 s of capture. The operative environmental temperatures (T_e, Bakken and Gates 1975) of thermal microclimates selected by lizards were recorded by locating a perching lizard and placing a painted, hollow-body, copper model of *S. merriami* in the location and orientation of the lizard when it was first seen. These models accurately estimate microclimate temperatures for these lizards (Grant 1988).

Lizard activity.—Rates of lizard movements, foraging, social displays, and the number of 5-min periods during which none of the above occurred were estimated for active male lizards during continuous 30-min observations using methods in Grant and Dunham (1988). Observations occurred during the morning activity period on sunny dates in the summer of 1984. A MANOVA was used to assess differences in activity rates among sites because the estimated rates of specific behaviors were correlated. Each 30-min observation contributed one datum to the MANOVA.

Thermal microclimate availability and daily activity time.—Time and space constraints on lizard activity were estimated by the relative availability of thermal microclimates using an array of randomly placed and

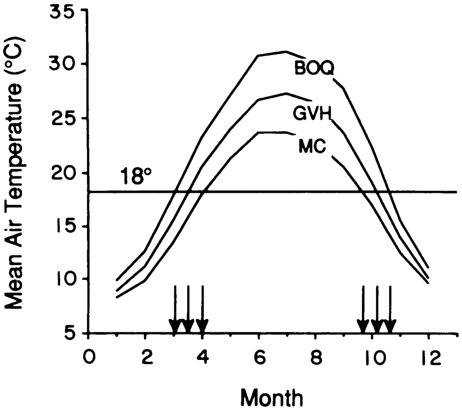

FIG. 1. Monthly average daily air temperatures among sites estimated at nearby National Park Service weather stations (BOQ = Boquillas Canyon, GVH = Grapevine Hills, MC = Maple Canyon; see Table 1). The line at 18°C represents the estimated lower cutoff for seasonal activity. Arrows point to the beginning or end of active season for each site. *X*-axis tick marks are positioned at the 15th of each month.

oriented painted copper models of *S. merriami* (Grant 1988). Upper and lower body temperatures for activity were chosen to bracket 95% of all body temperature recordings during the summer for cloudless weather (see *Results: Thermal microclimate availability and daily activity time*). Activity was defined to be possible at a particular time of day if at least 10% of the available microclimates (copper lizards scanned) exhibited a T_e within this T_b interval. This cutoff value is conservative, based upon field observations of lizard emergence and retreat times (Ruby and Dunham 1987, Grant 1988, Grant and Dunham 1988).

RESULTS

Active season length. — Monthly estimates of average daily air temperature among sites appear in Fig. 1. Using a value of 18°C as the lower average air temperature cutoff for seasonal activity, lizard activity seasons were 232 d at Boquillas, 203 d at Grapevine, and 173 d at Maple Canyon. Changing the 18° cutoff by 1°–2° changes the total season length for each site, but does not change the relative difference in season length among sites. We estimate that lizards at Boquillas were active for ≈2 mo longer per year than were lizards at Maple Canyon. Grapevine active season length was almost exactly intermediate.

Activity body temperatures and microclimate temperatures. — Average body temperatures and operative environmental temperatures of microclimates used by lizards (copper models placed where lizards were seen perching) appear in Fig. 2. The averages among sites in the morning differed at most by 1.8°. However, in the afternoon, T_b and perch T_e averages at the lower two sites were almost 5° higher than at Maple Canyon. According to a two-way ANOVA, the effects of site and time block of day, morning vs. afternoon, on body temperatures interact ($F_{2,1080} = 11.66$, $P < .001$). A similar interaction occurs for the perch environmental temperature data ($F_{2,1053} = 9.58$, $P < .001$). Note in Fig. 2 that for each site and time block, T_b and perch T_e averages were fairly similar, indicating that the temperatures of these lizards reflected thermal microclimate use.

Thermal microclimate availability and daily activity time. — Body temperatures of 26.9° and 37.8° enclose 95% of 1170 T_b measurements on active lizards for all sites on sunny cloudless dates during the summers of 1982–1986. These upper and lower body temperatures are a measure of the range of acceptable T_b exhibited by *S. merriami* among these populations in Big Bend. When a large fraction of the available microclimates was within the interval 26.9°–37.8° lizard activity was relatively unconstrained.

Total daily activity time was much lower at the lower elevation sites (Fig. 3A, B). At Maple Canyon, lizards were active throughout the day (13.2 h), whereas lizards at Grapevine and Boquillas were inactive at midday (7.3 h at Grapevine, and 6.4 and 5.0 h for the east and west sides at Boquillas).

Lizard activity. — Average rates of specific behaviors relating to feeding and social biology differed among sites (Table 2). Lizards at Grapevine moved at the highest average rate and had the highest display rate. Although food was more than twice as plentiful at Maple Canyon as at Grapevine (Table 1), feeding strike rates were about the same at these sites. These rates tended to exceed the rate at Boquillas ($P = .067$), where much less food was available (Table 1). The numbers of 5-min blocks per 30 min during which no movement or behavior occurred did not differ among sites, although there was a trend for lizards at Grapevine to have spent less time immobile.

Body size. — Average body lengths (SVL) for yearling and age >1 yr males and females for May–June and

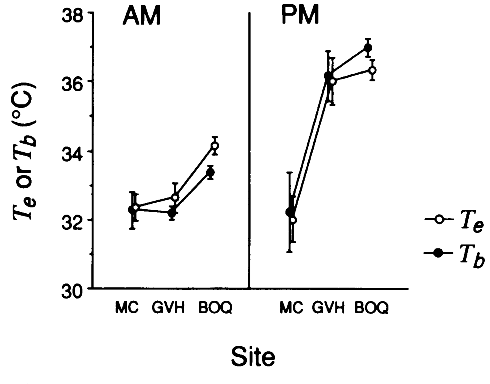

FIG. 2. Body temperatures (T_b, ●) and microclimate temperatures where lizards were seen perching (T_e, ○), means ± 2 SE, for active lizards on cloudless dates during the summers of 1982–1986 at Maple Canyon (MC), Grapevine Hills (GVH), and Boquillas (BOQ). Symbols at left are averages for the morning (AM) between sunrise and 1400. Symbols at right are averages for afternoon (PM) after 1400.

July–August are presented in Fig. 4. In May–June, yearlings were largest at Boquillas and smallest at Maple Canyon (MANOVA on $\log_e$-transformed SVL and mass, Table 3). However, later in the summer (July–August), yearlings were similar in size at Grapevine and Boquillas, and smallest at Maple Canyon.

The pattern of body size variation for age >1 yr lizards differs from the pattern for yearlings. Both sexes of Grapevine age >1 yr lizards were larger than same-sexed lizards at Boquillas. Maple Canyon males were slightly smaller than Boquillas males, but females were the same size at these sites (Fig. 4, Table 3).

Individual growth rate.—The pattern of growth during the summer among sites and sexes is complex, and heterogeneous slopes (growth rate vs. initial size) precluded covariance analyses. Instead, we calculated average growth rates in SVL and mass for 5 mm length classes and 1 g mass classes, respectively (Fig. 5). In every trio of connected points in Fig. 5 (same sex and size class, $n = 14$), the growth rate for Grapevine ranked highest. This has a 3^{-14} chance of occurring at random and is significant (binomial test, $P < .001$). The rate for Boquillas ranked second 9/14 times and for Maple Canyon 5/14 times, neither of which differs from 0.5 (binomial test, $P > .05$).

Male size and age of first reproduction.—The average size of socially dominant male lizards at Grapevine in May–June was 54.4 ± 0.54 mm SVL ($\bar{X} \pm 2$ SE, $n = 127$), and <1% of yearling males had attained this size by this time. However, at Boquillas many more yearlings had attained the average size of socially dominant males at Boquillas, 52.4 ± 0.92 mm SVL ($n = 55$), in May–June than had attained 54.4 mm SVL at Grapevine ($\chi^2 = 10.804$, $P < .01$, $n = 517$). Grapevine male yearlings who were known to have obtained a territory and become socially dominant (see *Materials and methods: Reproductive data*) averaged 50.5 ± 0.95 mm SVL ($n = 34$) in May–June, and ≈38% of all male yearlings were this size or greater. However, at Boquillas a much higher number (≈58%) of yearlings had attained the average size of known socially dominant yearlings, 49.7 ± 1.30 mm SVL ($n = 24$), than were ≥50.5 mm SVL at Grapevine ($\chi^2 = 18.831$, $P < .01$, $n = 517$).

Data at Maple Canyon suggest that the size- and age-specific attainment of social dominance is more similar to the pattern at Grapevine than to the pattern at Boquillas. The average size of known dominants was 49.7 ± 0.78 mm SVL ($n = 113$) and only ≈2% of the males had attained this size by their yearling summer (the comparable estimate was 1% at Grapevine). Maple Canyon male yearlings who were socially dominant averaged 44.4 ± 1.17 mm SVL ($n = 35$) in May–June, and ≈37% of all yearlings were this size or greater. The numbers of yearlings larger and smaller than 44.4 mm SVL at Maple Canyon did not differ from the comparable numbers at Grapevine who were larger and smaller than 50.5 mm SVL ($\chi^2 = 0.01$, $P > .05$, $n = 327$). However, these numbers at Maple Canyon differed from the comparable numbers of yearlings at Boquillas ($\chi^2 = 11.03$, $P < .01$, $n = 380$), which is similar to the relation between Grapevine and Boquillas. Thus, at Boquillas more male yearlings were large enough to become social dominants, which is a prerequisite to breeding (Ruby and Dunham 1987), than were large enough to attain dominance at Maple Canyon and Grapevine.

Female size and age of first reproduction.—Size frequency histograms by site for all yearling females and for the fraction that was reproductively active in May–June appear in Fig. 6. Note that only relatively large yearling females were breeding within each site. However, a high fraction of smaller yearling females (43–47 mm SVL) at Grapevine and Boquillas were not reproductively active, despite the fact that same-sized yearling females were breeding at Maple Canyon ($\chi^2 = 22.73$, df = 2, $P < .001$, $n = 256$).

Frequency estimates of reproductive activity by age and season are summarized in Fig. 7 (only yearlings with SVL ≥43 mm in May–June, and SVL ≥42 mm in July–August were included since these were the minimal sizes observed to breed). According to a log-linear analysis (CATMOD procedure, SAS 1982), the effects of site and season interact ($\chi^2 = 30.82$, df = 2, $P < .001$), and the effects of site and age interact ($\chi^2 = 8.78$, df = 2, $P < .05$). To disentangle these interactions, we performed separate analyses for each age and site (Table 4). In May–June, a higher fraction of yearling females was reproductively active at Maple Canyon than at Boquillas and Grapevine. However, in July–August, the ranking was reversed with the most yearlings breeding at Grapevine and the least at Maple Canyon (significant site × season interaction for yearlings, and significant season effects at both sites, Table 4). The fraction of reproductively active age >1 yr females at Maple Canyon exhibited a similar decline as did yearlings during the summer. At Grapevine, many age >1 yr females were reproductive in both halves of the summer. Among halves of the summer, the fractions of breeding Boquillas yearling and age >1 yr females were relatively low and constant and only the effect of age was significant at Boquillas (Table 4, Fig. 7). These data suggest that many yearling females delayed reproduction at Grapevine and Boquillas, especially for smaller yearlings in May–June.

DISCUSSION

Our data demonstrate that environmental constraints vary among elevationally distinct populations of the lizard *Sceloporus merriami* in Big Bend, Texas. These constraints stem from decreased rainfall and food availability and from increased environmental temperature with decreased elevation (Fig. 8) and are "operative" on life history phenotypes (Mason and Langenheim 1957, Spomer 1973). Paradoxically, few life history differences among populations were correlated

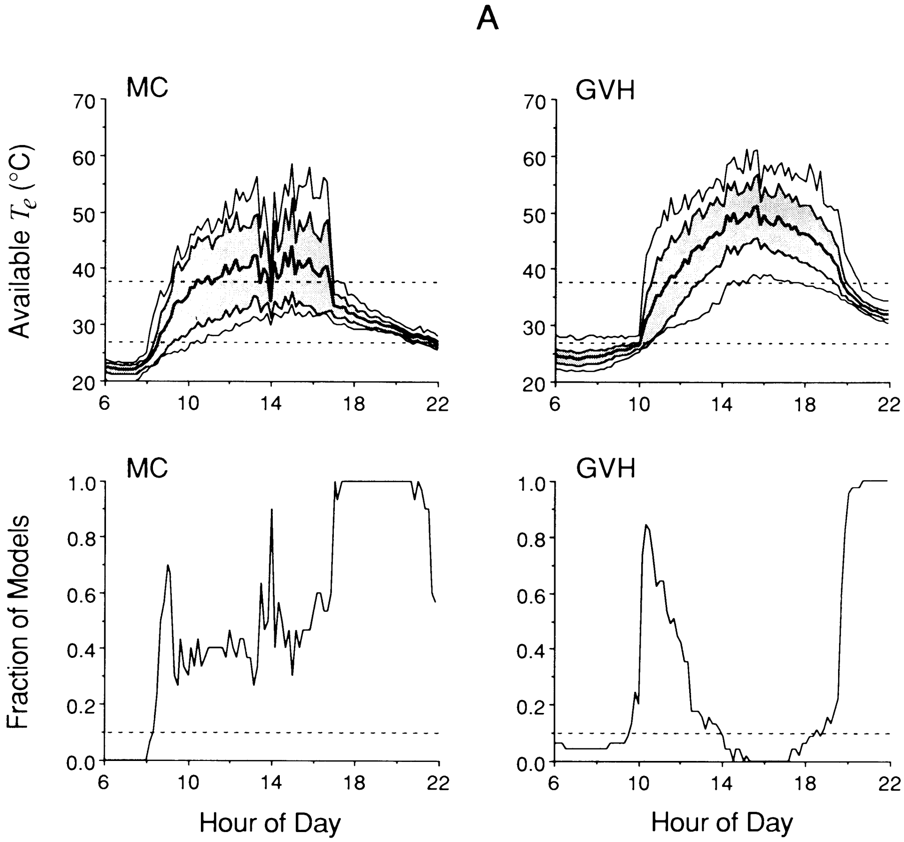

FIG. 3. Top row A and B. The distribution of environmental temperatures (T_e) available on *S. merriami* home ranges for typical sunny and dry days for Maple Canyon (MC) and Grapevine (GVH) in A, and for the west (BOQ-W) and east (BOQ-E) sides of the Boquillas site in B. The upper and lower curves represent the range of available T_e, the middle curve is the average available T_e and the shaded region encloses ±1 SD. Dashed lines at 26.9° and 37.8°C bracket 95% of all T_b data. Bottom row A and B. The fraction of environmental temperatures (T_e) within the interval 26.9°–37.8° for the same sampling dates plotted above. High fractions indicate that lizard activity was unconstrained by T_e availability. Dashed lines at 0.1 represent the minimum frequency of favorable thermal microclimates for activity. Since these lizards were not active at night, 2130 was the latest time for activity for all sites.

with these operative gradients (Fig. 9). Although Grapevine is intermediate in environmental characters, it is often at an extreme with respect to life history phenotypic responses. We first hypothesize how several of the simpler correlations between life history characters and single gradients are mechanistically generated (T_b, daily and seasonal activity times), and then invoke combinations of operative gradients (Fig. 8) to explain several of the principal inverted and transposed phenotypic responses in Fig. 9, such as activity rates, daily growth rate, age-specific body size, and size and age of first reproduction.

Body temperatures for active lizards in the morning were very similar among sites. However, during afternoon activity, body temperatures at the lower elevation sites were higher than at Maple Canyon. This difference is driven by differences in the distributions of environmental temperatures (T_e). At the lower elevation sites, higher T_e forced lizards to be active at higher T_b in late afternoon or remain inactive (DeWitt 1967, Grant 1988). Similarly, 6°–7°C lower inactivity T_b at Maple Canyon relative to the other sites is driven by lower crevice T_e. Inactive lizards had no option but to be cooler at Maple Canyon.

Although lizards at the lower elevation sites exhibited a higher T_b and extended daily activity in the afternoon, the daily total time for activity declined dramatically with elevation. The cooler thermal environment at Maple Canyon allowed lizards to remain active at a T_b of 32° all day (≈13 h) during which lizards moved about, fed, and engaged in social interactions for 4–6 h at midday when animals at other populations were inactive to avoid lethal environmental temperatures. This decline in summer daily activity time with elevation was ultimately caused by higher T_e. Similarly, higher environmental temperatures during the fall and spring allowed a longer active season by ≈1 mo at Grapevine and 2 mo at Boquillas relative to Maple Canyon. In sum, among-site variation in body temperatures and in daily and seasonal activity time were

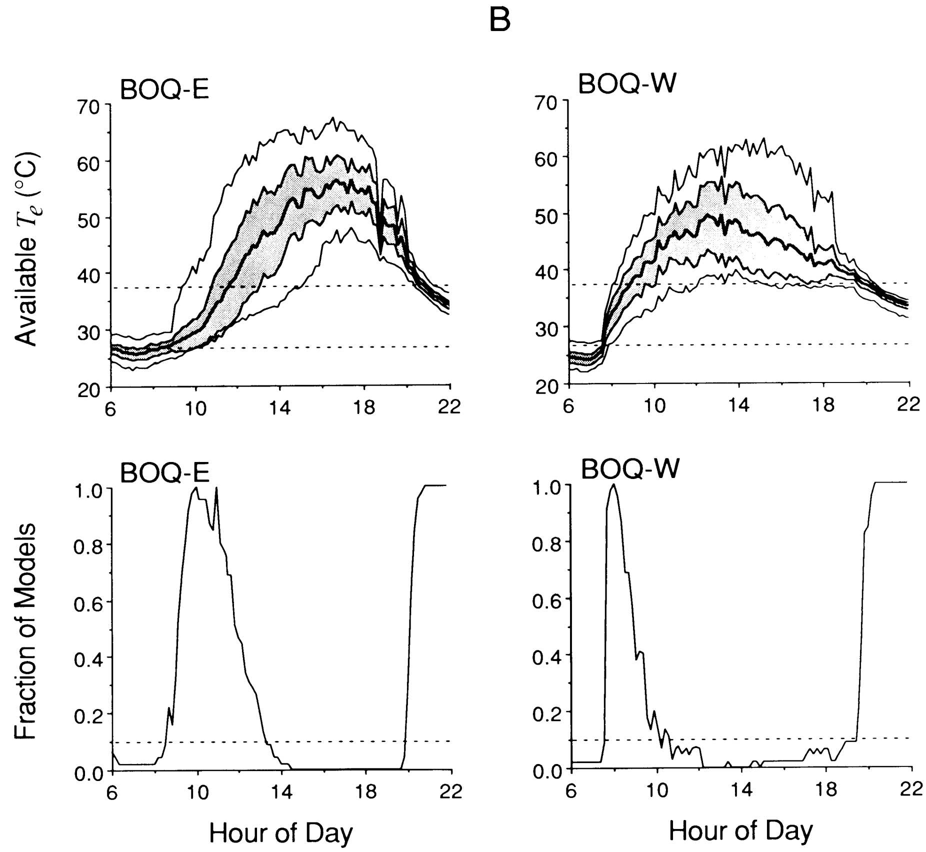

FIG. 3. Continued.

positively correlated and mechanistically linked to variation in environmental temperature availability, but these do not correlate with life historical allocation of time and resource to activity (rates of movements, feeding, and displays, or home range size, Fig. 9).

Similarly, individual growth rates among sites do not correlate with either environmental temperature or food availability. Despite the highest food availability and greatest time available for feeding, Maple Canyon lizards of all sizes exhibited growth rates more like those at Boquillas, and Grapevine lizards had the highest daily growth rates. At Boquillas, low food avail-

TABLE 2. Rates of behaviors from 30-min observations.* Data are means ± 2 SE.

Measure	Maple Canyon (n = 76)	Grapevine (n = 98)	Boquillas (n = 103)
Discrete moves	13.91 ± 3.05	16.23 ± 2.92	11.77 ± 1.99
Total distance	5.28 ± 1.26	7.71 ± 1.57	5.07 ± 1.04
Feeding strikes	3.29 ± 1.18	3.03 ± 1.14	1.82 ± 0.54
Displays	4.30 ± 1.49	7.51 ± 1.80	5.00 ± 1.21
5 min immobile	1.94 ± 0.33	1.61 ± 0.33	1.98 ± 0.32

MANOVA for comparing behavioral data by sites

Univariate tests	$F_{2,274}$	P
Discrete moves	3,126	.045*
Total distance	5.186	.006**
Feeding strikes	2.727	.067
Displays	4.825	.009**
5 min immobile	1.609	.202
Multivariate test	$F_{10,540}$ = 2.194	P = .017*

* All rates have units of number per 30 min except total distance which has units of metres per 30 min. The term "5 min immobile" refers to the number of complete 5-min periods per 30-min observation during which no movement or behavior occurred. (* $P < .05$, ** $P < .01$.)

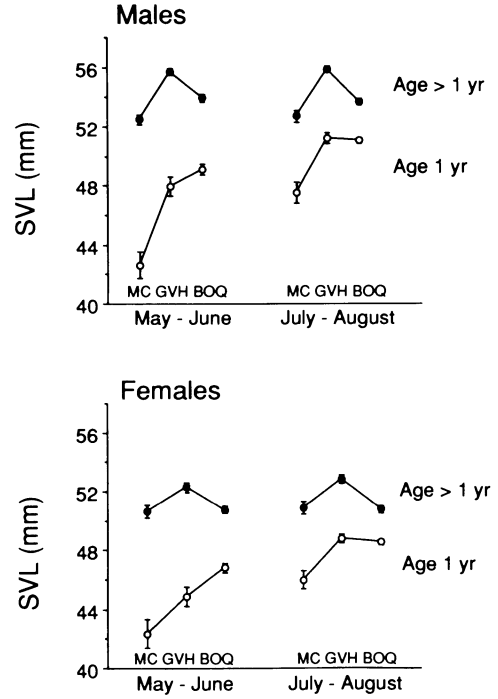

FIG. 4. Average snout–vent lengths (SVL) for yearling and age >1 males and females for May–June and July–August. Each trio of connected points represents the average (±2 SE) for Maple Canyon (MC), Grapevine Hills (GVH), and Boquillas (BOQ), for each age group and month interval.

ability and higher T_b could have led to low ingestion rates and higher metabolic expenditure, respectively, either of which could limit growth rate.

Several hypotheses can explain why high food availability and consumption at Maple Canyon did not result in higher growth rates. First, low nighttime T_b (crevice T_e = 24.4°, Table 1) may have adversely affected their digestion. Data from another insectivorous iguanid, *Uta stansburiana* (Waldschmidt et al. 1986), indicate that food required 3–6 d to pass through the gut at 24°, depending on the feeding regime. Similar data were found by these authors in *Sceloporous undulatus* (S. R. Waldschmidt, *personal communication*). If this occurs in *S. merriami*, then it is conceivable that Maple Canyon lizards were unable to process all of the food they ate and may have had a lower total amount of assimilated resource to allocate to growth. This is a form of resource limitation. However, rather than being ingestion limited (hypothesized for Boquillas), Maple Canyon lizards may have been limited by their capacity to process ingested food (see Congdon 1989).

TABLE 3. MANOVAs for $\log_e$(SVL) and $\log_e$(mass) by season, age, and sex.*

Sex	Wilks' lambda	SVL contrast	Mass contrast
	May–June yearlings		
♂	$F_{4,1212}$ = 46.27	B > G > M†	B > G > M
♀	$F_{4,1310}$ = 26.55	B > G > M	B > G > M
	May–June age > 1		
♂	$F_{4,968}$ = 75.72	G > B > M	G > B > M
♀	$F_{4,632}$ = 20.27	G > B = M	G > B > M
	July–August yearlings		
♂	$F_{4,1211}$ = 31.20	G = B > M	G = B > M
♀	$F_{4,1222}$ = 31.96	G = B > M	G > B > M
	July–August age > 1		
♂	$F_{4,1044}$ = 84.35	G > B > M	G > B > M
♀	$F_{4,608}$ = 31.32	G > B = M	G > B = M

* Significant two-, three-, and four-way interactions necessitated separate MANOVAs to test differences among sites for each level of sex, age, and season (each trio of connected points in Fig. 4). For all eight tests above $P < .001$.

† B = Boquillas site, G = Grapevine Hills site, and M = Maple Canyon site.

Second, low growth rates at Maple Canyon may have resulted from higher daily energy expenditure on activity, since these lizards were active for ≈13 h/d (Fig. 3A, B). Simple calculations based on the energetics model in Bennett and Dawson (1976) corroborate this speculation (see Grant 1988); however, the effects of depressed individual movement rates and home range size at Maple Canyon relative to Grapevine (Table 2) could counteract the effect of a longer period of daily

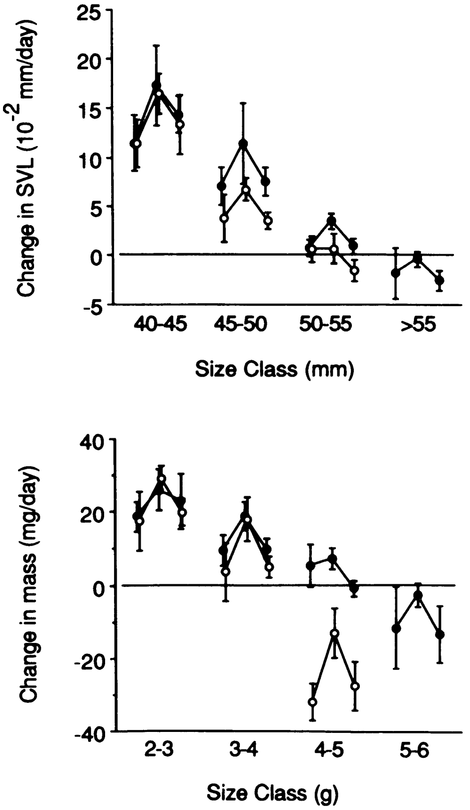

FIG. 5. Change in SVL for 5 mm length classes (above), and change in mass for 1 g mass classes (below). As in Fig. 4 each trio of connected points represents the average (±2 SE) from Maple Canyon, Grapevine Hills, and Boquillas from left to right, for each sex and size class. Averages are plotted only if ≥4 measurements occurred for all three sites for each sex and class.

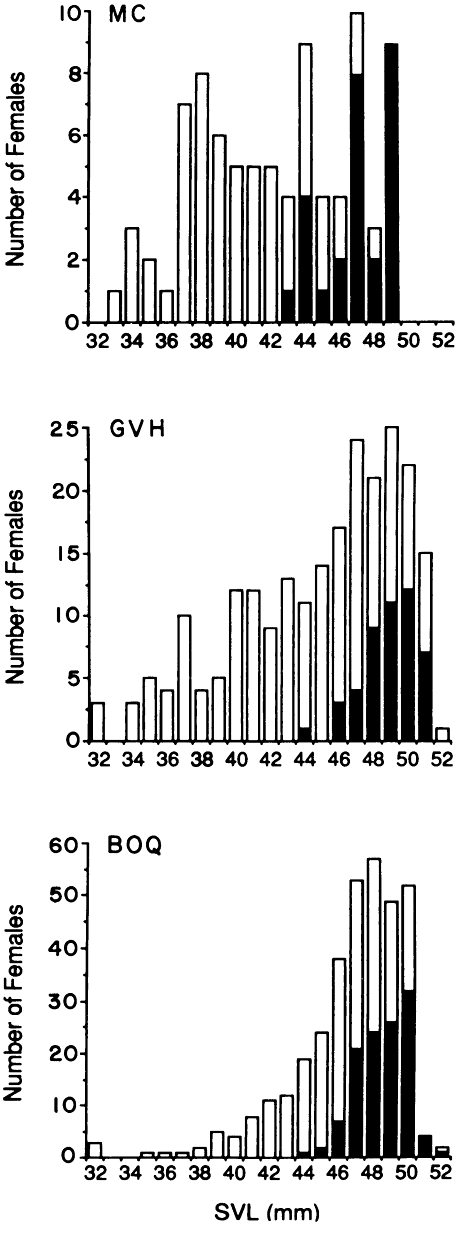

FIG. 6. Frequency histograms of SVL for yearling females for May–June at the three sites. The shaded portions indicate the sizes of females that were reproductively active (enlarged follicles, oviductal eggs, or recently oviposited) when captured, for Maple Canyon (MC), Grapevine Hills (GVH), and Boquillas (BOQ).

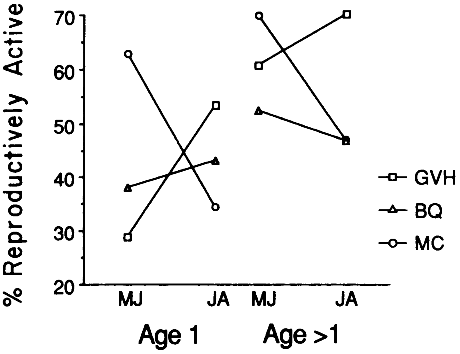

FIG. 7. Frequency estimates of female reproductive activity (enlarged follicles, oviductal eggs, or recently oviposited when captured) among sites, month intervals, and age classes. At right are fractions for all age >1 females, and at left are fractions for yearling females with SVL ≥ 43 mm in May–June (MJ), and SVL ≥ 42 in July–August (JA), which were the minimum observed sizes for female reproductive activity. MC = Maple Canyon, GVH = Grapevine Hills, BOQ = Boquillas.

activity time to an unknown extent (a site-specific estimate of the energy cost of activity is needed).

It is possible that character similarities between Maple Canyon and Boquillas (Fig. 9) reflect hidden similarities in resource allocation (production vs. activity) due to the common problem of a smaller total assimilated resource near the elevational extremes of this species. We suggest that Boquillas lizards had low ingestion rates and high inactive expenditure, whereas Maple Canyon lizards had low processing rates and high activity expenditure. These are alternate mechanisms for resource limitation.

Since body size is the proximate result of daily growth rate times the number of days growing, among-site variation in adult body size is driven to a large extent by daily processes influencing growth rate, and monthly processes influencing growth season length (seasonal temperature variation). The long growing season at Boquillas may have compensated for low daily growth rates to produce the largest yearlings in May–June. Maple Canyon yearlings grew slowly, over the shortest season, and were the smallest. Grapevine yearlings in May–June were intermediate in size, but by July–August, high growth rates resulted in yearlings as large as Boquillas yearlings. Maple Canyon yearlings grew slowly and did not catch up. By May–June of the following summer, Grapevine age >1 yr lizards were the largest. Boquillas age >1 yr males were intermediate in size, and females were the same size as Maple Canyon female age >1 yr lizards. This pattern of age-specific body size does not separately correlate with either the amount of food available or the length of the growing season, and we suggest that the interaction of these two simple environmental gradients drives this pattern.

Ballinger and Congdon (1981) suggested that in environments characterized by shorter growing seasons, selection should favor a prolonged period of juvenile growth and delayed reproduction. Male *S. merriami* in Big Bend conform to this prediction. At Boquillas, where yearlings were large (long hatchling growing season) and adults were small (low food availability and low growth rates), many yearlings were relatively large enough to successfully compete with age >1 yr lizards for access to females, which is necessary for breeding (Ruby and Dunham 1987). In contrast, at Grapevine

TABLE 4. ANOVA on frequency counts of female reproductive activity by age class and by site.*

Effects of site and season by age

Source	Yearling females			Age >1 females		
	df	χ^2	P	df	χ^2	P
Site	2	2.23	NS	2	12.95	<.001
Season	1	0.02	NS	1	2.00	NS
Site × season	2	24.60	<.001	2	8.85	<.05

Effects of age and season by site

Source	Maple Canyon			Grapevine Hills			Boquillas		
	df	χ^2	P	df	χ^2	P	df	χ^2	P
Season	1	14.01	<.001	1	18.25	<.001	1	0.00	NS
Age	1	2.16	NS	1	35.47	<.001	1	6.03	<.015
Season × age	1	0.14	NS	1	3.33	NS	1	2.01	NS

* Only yearlings with SVL ≥43 mm in May–June, and SVL ≥42 mm in July–August were included in these analyses, since these are the minimum sizes observed to be reproductive. Analyses are from the general log-linear ANOVA by the CATMOD procedure (SAS 1982).

and Maple Canyon, older lizards were relatively much larger than yearlings (on average by 7–10 mm SVL), few yearlings became socially dominant, and most yearlings spent their first summer as social subordinates and/or in marginal areas. Smaller males did not engage in prolonged territorial encounters, and instead they fed and grew at high rates (at least at Grapevine, Fig. 5), and by the beginning of their 2nd yr they were much larger, and could socially dominate, the upcoming cohort of yearlings.

Although males were sexually mature if they were larger than ≈43 mm SVL (A. E. Dunham 1981, *unpublished manuscript*), we suggest that the size and age of first reproduction for males differed greatly among sites, and were driven by environmental factors influencing body size ratios among successive cohorts. When larger males were locally common, smaller yearlings were constrained to delay reproduction until they had attained a larger relative size. This does not mean that the social behavioral response of yearling males was a passive effect of proximate environmental differences. Instead we view the set of behaviors associated with a social status, and the concomitant age of first reproduction, as a potentially adaptive response by yearling males to their social/demographic environment (Dunham et al. 1989). The fitness consequences of this response are obvious.

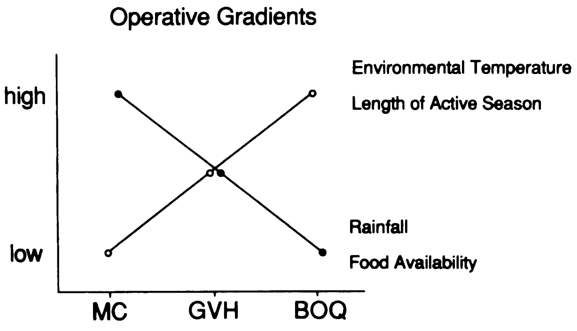

FIG. 8. Summary schematic of environmental gradients (in rainfall, food availability, environmental temperature, and active season length) that differ among sites and operate on the life history phenotypes of individuals.

The onset of reproduction for females was very different from that of males. Although females that reproduced in early summer of their 1st yr were relatively large for their age class (probably from earlier clutches of the previous summer), their absolute sizes differed among sites. Fewer weeks of fall and spring growth at Maple Canyon produced different size-frequency distributions for juvenile females compared with the other sites (Fig. 6). Nonetheless, females at Grapevine and Boquillas that were as large as breeding females at Maple Canyon delayed reproduction and instead grew to a larger body size (Figs. 5 and 6). In fact, many more Grapevine yearlings bred in late summer than in early summer, which is consistent with the result in Dunham (1981) that the average body size of females producing clutch I was greater than for females producing clutch II. Small females at Grapevine had high daily growth rates, and by the second half of the summer, at the time of breeding, they had attained the body size of Boquillas yearling females.

Several hypotheses can account for earlier reproduction by Maple Canyon females (yearlings and age >1 yr). For example, the shorter postreproductive season at Maple Canyon may have forced females to breed early to allow sufficient time to amass lipid stores for winter brumation (Tinkle 1969*a*). Additionally, lower soil temperatures (Table 1) may have prolonged egg development time, necessitating an earlier date of oviposition and fewer late-summer clutches (Ballinger and Congdon 1981). Finally, the shorter hatchling growing season at Maple Canyon may have placed a high premium on breeding early in the summer to allow hatchlings longer time to deposit stores for brumation (increased juvenile survivorship) and/or attain a size large enough to breed during the following spring (increased

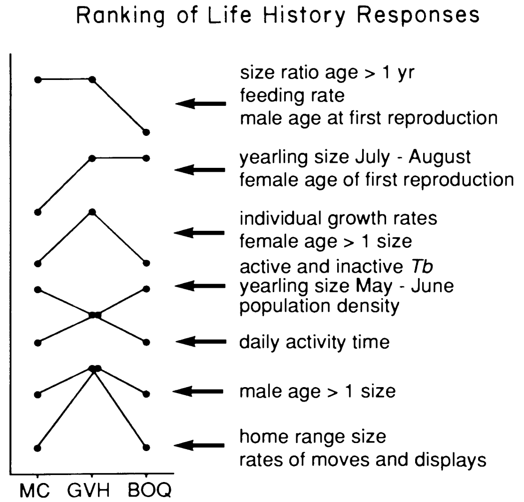

FIG. 9. Summary schematic of rankings of life history characters among sites. Horizontal lines indicate ties. MC = Maple Canyon, GVH = Grapevine Hills, BOQ = Boquillas. Variation in the shapes of these gradients represents an unknown contribution of genetic and nongenetic responses of life history phenotypes to the gradients in Fig. 8 (see *Discussion*). Population densities and home range size estimates are from Ruby and Dunham (1987).

reproductive rate) (Hahn and Tinkle 1965, Tinkle 1969*a*, Ballinger 1979). Breeding at a smaller body size potentially affects population replacement rate, since clutch size increases with body size in *S. merriami* (A. E. Dunham 1981, *unpublished manuscript*). Lower population densities at Maple Canyon could be the result of smaller females only breeding in the first half of the summer, all else being equal.

In sum, male *S. merriami* conform to the predicted delayed reproduction at higher elevation by Ballinger and Congdon (1981); however, females exhibited the opposite pattern. We suggest that these delays were the indirect result of environmental gradients (Fig. 8) operating on individual growth rate, growth season length, and body size ratios among successive cohorts.

Our results suggest that major life history differences in this system are influenced by variation in environmental constraints on time and energy budgets. The net effect of these environmental differences is hypothesized to cause differences in the total amount of resource available, as well as in the pattern of resource allocation to growth, maintenance, storage, and reproduction in a life history (Congdon 1989, Dunham et al. 1989). But this does not mean that life history differences we report are purely phenotypic, environmentally induced, and nongenetic. This is an extremely oversimplified view of the interaction of organisms and their environments to which we do not subscribe. An unknown component of the life history variation reported may be due to ecotypic variation among resource and time allocation phenotypes (Congdon 1989, Dunham et al. 1989). This component can be estimated by controlled field and laboratory experiments and should be interpreted in the context of the available data on unmanipulated life history variations.

We view these environmental differences as potential sources of selection for life history characteristics including daily growth rate, the temperature dependence of physiological performance (locomotion and resource processing capacity), and the intensities of activities such as movements, foraging, and social interactions (Dunham et al. 1989). All of these potentially affect home range size, social biology, age-specific survivorship and fecundity, population density and regulation. The pattern of covariation in environmental constraints and phenotypic responses in body size, growth, and reproduction in this system may be typical of the pattern in many intra- or interspecific comparisons along elevational or latitudinal gradients. This argues for increasing the intensity and resolution of such studies in the elucidation of life history variation in response to environmental variation as a prerequisite to modeling the evolution of life histories.

ACKNOWLEDGMENTS

No significance should be attached to the order of authorship. This paper has benefitted from the illuminating comments of R. Ballinger, S. Beaupre, B. French, P. Niewiarowski, K. Overall, W. Porter, and W. Roosenberg. Major contributors during conceptual stages include J. Bernardo, L. Clark, W. Porter, and S. Waldschmidt. Warren Porter graciously loaned environmental monitoring equipment. A generation of field ecologists and students contributed to this study including J. Bernardo, R. Cary, J. Howland, R. Newman, P. Niewiarowski, K. Overall, R. Roche, D. Ruby, and S. Waldschmidt. K. Overall helped greatly with logistics during the long field season. The National Park Service in Big Bend provided critical facilities. This project was funded by grants from Sigma Xi, the Theodore Roosevelt Memorial Fund, and the Shell Foundation to B. W. Grant, and by NSF DEB 81-04690, National Geographic Society 2877-84, University of Pennsylvania Research Grants 3-70575 and 3-71071 to A. E. Dunham, and by U.S. Department of Energy grant DE-FG02-88ER60633 to Dr. Warren P. Porter.

LITERATURE CITED

Bakken, G. S., and D. M. Gates. 1975. Heat transfer analysis of animals: some implications for field ecology, physiology, and evolution. Perspectives of biophysical ecology. D. M. Gates and R. B. Schmerl, editors. Ecological Studies **12**: 255–290.

Ballinger, R. E. 1979. Intraspecific variation in demography and life history of the lizard, *Sceloporus jarrovi*, along an altitudinal gradient in southeastern Arizona. Ecology **60**: 901–909.

———. 1983. Life-history variations. Pages 241–260 *in* R. B. Huey, E. R. Pianka, and T. W. Schoener, editors. Lizard ecology: studies of a model organism. Harvard University Press, Cambridge, Massachusetts, USA.

Ballinger, R. E., and J. D. Congdon. 1980. Food resource limitation of body growth rates in *Sceloporus scalaris* (Sauria, Iguanidae). Copeia 1980:921–923.

Ballinger, R. E., and J. D. Congdon. 1981. Population ecology and life history strategy of a montane lizard (*Sceloporus scalaris*) in southeastern Arizona. Journal of Natural History **15**:213–222.

Bennett, A. F., and W. R. Dawson. 1976. Metabolism. Pages

127–224 *in* C. Gans and W. R. Dawson, editors. Biology of the Reptilia. Volume 5. Academic Press, New York, New York, USA.

Congdon, J. D. 1989. Proximate and evolutionary constraints on energy relations of reptiles. Physiological Zoology **62**:356–373.

Congdon, J. D., A. E. Dunham, and D. W. Tinkle. 1982. Energy budgets and life histories of reptiles. Pages 233–271 *in* C. Gans and F. H. Pough, editors. Biology of the Reptilia. Volume 13. Academic Press, New York, New York, USA.

Derickson, W. K. 1974. Lipid deposition and utilization in the sagebrush lizard *Sceloporus graciosus*: its significance for reproduction and maintenance. Comparative Biochemistry and Physiology **47A**:267–272.

———. 1976*a*. Ecological and physiological aspects of reproductive strategies in two lizards. Ecology **57**:445–458.

———. 1976*b*. Lipid storage and utilization in reptiles. American Zoologist **16**:711–723.

DeWitt, C. B. 1967. Precision of thermoregulation and its relation to environmental factors in the desert iguana, *Dipsosaurus dorsalis*. Physiological Zoology **40**:49–66.

Dunham, A. E. 1978. Food availability as a proximate factor influencing individual growth rates in the iguanid lizard *Sceloporus merriami*. Ecology **59**:770–778.

———. 1980. An experimental study of interspecific competition between the iguanid lizards *Sceloporus merriami* and *Urosaurus ornatus*. Ecological Monographs **50**:309–330.

———. 1981. Populations in a fluctuating environment: the comparative population ecology of *Sceloporus merriami* and *Urosaurus ornatus*. Miscellaneous Publications, University of Michigan Museum of Zoology **158**:1–62.

———. 1982. Demographic and life history variation among populations of the iguanid lizard *Urosaurus ornatus*: implications for the study of life-history phenomena in lizards. Herpetologica **38**:208–221.

———. 1983. Realized niche overlap, resource abundance, and intensity of interspecific competition. Pages 261–280 *in* R. B. Huey, E. R. Pianka, and T. W. Schoener, editors. Lizard ecology: studies of a model organism. Harvard University Press, Cambridge, Massachusetts, USA.

Dunham, A. E., B. W. Grant, and K. L. Overall. 1989. Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. Physiological Zoology **62**:335–355.

Grant, B. W. 1988. The thermal biophysical ecology of the desert lizard *Sceloporus merriami* (Iguanidae): implications for the study of life history evolution. Dissertation. University of Pennsylvania, Philadelphia, Pennsylvania, USA.

Grant, B. W., and A. E. Dunham. 1988. Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. Ecology **69**:167–176.

Hahn, W. E., and D. W. Tinkle. 1965. Fatbody cycling and experimental evidence for its adaptive significance to ovarian follicular development in the lizard, *Uta stansburiana*. Journal of Experimental Zoology **158**:79–86.

Huey, R. B., and A. E. Dunham. 1987. Repeatability of locomotor performance in natural populations of the lizard *Sceloporus merriami*. Evolution **41**:1116–1120.

Lynch, C. B., D. S. Sulzbach, and M. S. Connolly. 1988. Quantitative genetic analysis of temperature regulation in *Mus domesticus*. IV. Pleiotropy and genotype-by-environment interactions. American Naturalist **132**:521–537.

Mason, H. L., and J. H. Langenheim. 1957. Language analysis and the concept environment. Ecology **38**:325–340.

Newman, R. A. 1988. Adaptive plasticity in development of *Scaphiopus couchii* tadpoles in desert ponds. Evolution **42**:774–783.

Resnick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos **44**:257–267.

Ruby, D. E., and A. E. Dunham. 1987. Variation in home range size along an elevational gradient in the iguanid lizard *Sceloporus merriami*. Oecologia (Berlin) **71**:473–480.

SAS. 1982. SAS user's guide. SAS Institute, Cary, North Carolina, USA.

Spomer, G. G. 1973. The concepts of "interaction" and "operational environment" in environmental analyses. Ecology **54**:200–204.

Stearns, S. C. 1976. Life history tactics: a review of the ideas. Quarterly Review of Biology **51**:3–47.

———. 1986. Evolution of phenotypic plasticity in life history traits: prediction of reaction norms for age and size of maturity. Evolution **40**:893–913.

Tinkle, D. W. 1967. The life and demography of the side-blotched lizard, *Uta stansburiana*. Miscellaneous Publications, University of Michigan Museum of Zoology Number **132**.

———. 1969*a*. Evolutionary implications of comparative population studies in the lizard *Uta stansburiana*. Pages 133–160 *in* Proceedings of an International Conference on Systematic Biology. National Academy of Sciences Publication Number **1692**.

———. 1969*b*. The concept of reproductive effort and its relation to the evolution of life histories of lizards. American Naturalist **103**:501–516.

———. 1972*a*. The dynamics of a Utah population of *Sceloporus undulatus*. Herpetologica **28**:351–359.

———. 1972*b*. The role of environment in the evolution of life history differences within and between lizard species. Pages 77–100 *in* R. T. Allen and F. C. James, editors. A Symposium on Ecosystematics. University of Arkansas Museum Occasional Paper Number **4**.

Tinkle, D. W., and R. E. Ballinger. 1972. *Sceloporus undulatus*: a study of the interspecific comparative demography of a lizard. Ecology **53**:570–584.

Waldschmidt, S. R., S. M. Jones, and W. P. Porter. 1986. The effect of body temperature and feeding regime on activity, passage time, and digestive coefficient in the lizard *Uta stansburiana*. Physiological Zoology **59**:376–383.

Wilbur, H. M., D. W. Tinkle, and J. P. Collins. 1974. Environmental certainty, trophic level, and resource availability in life history evolution. American Naturalist **108**:805–817.

Williams, G. C. 1966. Adaptation and natural selection: a critique of some current evolutionary thought. Princeton University Press, Princeton, New Jersey, USA.