Growth Plasticity and Thermal Opportunity in Sceloporus Lizards

Barry Sinervo, Stephen C. Adolph

GROWTH PLASTICITY AND THERMAL OPPORTUNITY IN *SCELOPORUS* LIZARDS[1]

BARRY SINERVO[2] AND STEPHEN C. ADOLPH[3]
Department of Zoology, University of Washington, Seattle, Washington 98195 USA

Abstract. We studied the relationship between daily activity time and growth rate in hatchling sagebrush lizards (*Sceloporus graciosus*), a mainly montane species, and western fence lizards (*Sceloporus occidentalis*), which inhabit a broader range of thermal environments. The study involved two populations of each species along an altitudinal gradient in southern California and one population of *S. occidentalis* from Oregon. In the field daily activity time varied seasonally: activity periods were short during spring and fall and longer during the summer. Activity patterns also varied geographically: in montane and high-latitude environments, hatchlings experienced reduced opportunity for growth both daily and seasonally, because fewer, shorter days are available before the end of the activity season.

We conducted laboratory experiments to measure the effect of the thermal environment on hatchling growth rates. Laboratory-incubated hatchlings had access to radiant energy for part of each day and were kept at 15°C (too low for activity) the rest of the day. The four experimental treatments (6, 9, 12 and 15 h of radiant energy per day) approximated the range of thermal environments encountered by hatchlings in the wild. Food and water were provided ad libitum. Mass-specific growth rates were plastic and generally increased with potential activity time in hatchlings from all populations. However, the form of this relationship varied among populations: growth rates of California *S. occidentalis* ("growth opportunists") increased roughly linearly with potential activity time, whereas growth rates of Oregon *S. occidentalis* and California *S. graciosus* ("short-day specialists") showed curvilinear responses to potential activity time. Interspecific and large-scale intraspecific differences in the form of the norm of reaction paralleled the differences in thermal environments encountered by hatchlings in nature. Populations of *S. occidentalis* at low elevation in California routinely experience short and long days of activity (e.g., 6–13 h/d) and the norm of reaction for growth rate increases linearly over this range. In contrast, populations of *S. graciosus* rarely experience days with >9 h of activity and the norm of reaction for growth rate plateaus above 9 h/d. Similarly, northern populations of *S. occidentalis* from Oregon rarely experience days with >9 h of activity and the norm of reaction for growth rate also plateaus above 9 h/d. On a large scale, therefore, growth responses appear to be appropriate to the thermal environments to which hatchlings are most commonly exposed. However, conspecific populations from different altitudes in California did not differ in growth response, although hatchlings experience different thermal environments in nature. We observed substantial among-family variation in growth rates of *S. occidentalis,* which may indicate genetic variation, a prerequisite for evolution by natural selection. Moreover, significant family × treatment interaction effects on growth rate that reflect underlying genotype × environment interactions indicate a genetic basis to the observed intraspecific and interspecific differentiation in the norm of reaction. Additional experiments demonstrated that (1) reducing food availability by 50% reduced growth rates by 50% in both species, and (2) growth rates did not differ between hatchlings whose eggs were incubated at 24° vs. 27°C.

Key words: activity time; genotype × environment interaction; geographical variation; growth rate; life history; lizard; norm of reaction; phenotypic plasticity; Sceloporus; *temperature; thermal opportunity; thermal physiology.*

INTRODUCTION

Many organismal traits are phenotypically plastic: they exhibit a norm of reaction across different environments, rather than expressing the same phenotype (Schmalhausen 1949, Stearns 1989, Travis 1994). In some cases, a reaction norm clearly represents an adaptive response to environmental change; examples include predator-induced morphological and chemical defenses (Harvell 1986, Dodson 1989) and diet-induced morphological changes resulting in crypsis (Greene 1989). Smith-Gill (1983) named this type of phenotypic plasticity "developmental conversion," in

which environmental cues (e.g., photoperiod, presence of predators) are used to predict the onset of environmental change and evoke an adaptive response in the trait. However, phenotypic plasticity of many physiological and life history traits represents "phenotypic modulation" (Smith-Gill 1983), in which traits passively respond to environmental variables such as temperature, salinity, and food abundance. Phenotypic modulation is inevitable for many traits (e.g., growth rate), simply because of chemical and physical effects on underlying biochemical and developmental processes (Smith-Gill 1983, Stearns 1989). Thus, evaluating the adaptive significance of phenotypic modulation in a given trait is problematic (Stearns and Koella 1986, Stearns 1989, Adolph and Porter 1993, Travis 1994). In particular, we lack a physiologically based theory that would predict the shape of a particular reaction norm, beyond simple qualitative expectations (e.g., growth rate should increase with food abundance and with temperature).

In the absence of appropriate null models based on physiology, comparative studies provide an alternative for evaluating the ecological and evolutionary significance of phenotypic modulation. In some cases, one can predict qualitative differences in reaction norms between populations found in different environments, assuming that the shape of a reaction norm can respond to natural selection. These predictions can then be tested by conducting common garden experiments (Clausen et al. 1940, 1948) in the laboratory or in the field. In several frog species, for example, reaction norms for tadpole growth and differentiation rates differ among populations (Berven et al. 1979, Berven and Gill 1983). These differences are predictable from the water temperatures experienced by tadpoles in each population: montane tadpoles grow faster than do lowland tadpoles in cold water, whereas lowland tadpoles grow relatively faster in warmer water. Similarly, Conover and Present (1990) found genetically based latitudinal differences in the thermal sensitivity of growth rates in the fish *Menidia menidia*. Both of these studies suggest that natural selection for higher growth rates has altered the shape of the reaction norm of growth as a function of temperature.

Growth rates are probably the most widely studied phenotypically plastic traits. In reptiles, growth rates are affected by a number of environmental factors, particularly food availability and thermal environments (Stamps 1977, Dunham 1978, Ballinger and Congdon 1980, Andrews 1982, Ballinger 1983, Avery 1984, Sinervo and Adolph 1989, Williamson et al. 1989, Sinervo 1990a, Niewiarowski and Roosenburg 1993). Many lizards thermoregulate, which tends to minimize seasonal and geographic differences in body temperatures (T_b's) of active lizards (Cowles and Bogert 1944, Avery 1982). Nevertheless, temperature constrains the amount of time a lizard can be active at high T_b: potential activity time varies among different thermal environments and varies seasonally within the same environment (Porter et al. 1973, Porter and Tracy 1983, Jones et al. 1987, Grant and Dunham 1988, Tsuji 1988a, Niewiarowski and Roosenburg 1993). Average daily T_b, and average daily rates of physiological processes (such as growth) that depend on T_b (Huey 1982), are likely to vary among different thermal environments, even in species that thermoregulate carefully. The amount of time spent at different T_b's is known to affect growth rates in lizards and snakes (Avery 1984, Sinervo and Adolph 1989, Sinervo 1990a; C. R. Peterson, *personal communication*). Thus, thermal environments may be an important proximate source of variation in growth rates of wild lizards and consequently may play a role in the evolution of growth responses. Growth is a key link between lizard thermal physiology and ecology (Huey and Stevenson 1979, Dunham et al. 1989).

Here we report growth rates of hatchling lizards in a laboratory experiment that mimics natural variation in thermal environments as inferred by activity patterns of lizards in the wild. We studied the western fence lizard (*Sceloporus occidentalis*, three populations) and the sagebrush lizard (*S. graciosus*, two populations), using laboratory-reared offspring of wild-caught gravid females. These species have wide latitudinal and elevational ranges in the western United States (Stebbins 1985). Because our study populations occur at different elevations and/or latitudes, they experience thermal environments that differ, both daily and seasonally, in the amount of time available for activity at high T_b (i.e., thermal opportunity).

This study has three general aims. First, we present data on seasonal activity patterns of lizards in the wild, combined with data on reproductive phenology, to provide an ecological context for the laboratory study. Second, we describe how growth rates of laboratory-reared hatchlings vary as a function of thermal opportunity and compare the responses of different families, populations, and species. Third, we discuss the ecological and evolutionary significance of growth responses in the context of the thermal regimes experienced by hatchlings in natural populations.

METHODS

Study organisms and sites

S. graciosus and *S. occidentalis* are found in a variety of open and arid habitats in the western United States (Stebbins 1985). Both species have broad altitudinal ranges, and although *S. graciosus* is usually found at higher elevations, the two species often are syntopic (Rose 1976, Adolph 1990a). Adult *S. occidentalis* (10–20 g) are larger than adult *S. graciosus* (4–10 g), but otherwise the two species are morphologically similar. Like other *Sceloporus* lizards (Cowles and Bogert 1944, Bogert 1949, Brattstrom 1965, Mayhew 1968, Beuchat 1986, Grant 1990), they usually maintain a consistent,

narrow range of relatively high T_b (33°–36°C) while active by using a variety of behavioral mechanisms to thermoregulate, including varying activity times, exposure to solar radiation, and microhabitat use (Adolph 1990a). Adult *S. occidentalis* and *S. graciosus* are virtually identical in several aspects of their thermal physiology, including field T_b, critical thermal limits, and the thermal sensitivity of sprint locomotion (Adolph 1987).

We studied populations along an altitudinal gradient in the San Gabriel Mountains of southern California and a single population of *S. occidentalis* from central Oregon. On the north slope of the San Gabriels, *S. occidentalis* occurs from 1200 m (in the desert at the foot of the mountains) to 2300 m, whereas *S. graciosus* ranges from 1600 to 2800 m. We chose three sites along this gradient: (1) low elevation (1300 m), 8 km east of Valyermo, Los Angeles County, 34°27′ N, 117°45′ W (*S. occidentalis*); (2) intermediate elevation (2200 m), 2 km north of Wrightwood, San Bernardino County, 34°23′ N, 117°40′ W (both species); and (3) high elevation (2600 m), between Dawson Saddle and Throop Peak, Los Angeles County 34°22′ N, 117°48′ W (*S. graciosus*). The Oregon population of *S. occidentalis* is 10 km west of Terrebonne, Deschutes County (750 m elevation, 44°30′ N, 121°30′ W). Further information on the ecology and life histories of these populations is given in Adolph (1987, 1990a, b), Sinervo (1990a, b), Sinervo et al. (1991) and Sinervo and Losos (1991).

Quantifying activity time in the wild

S. occidentalis and *S. graciosus* are active when the thermal environment permits them to attain their preferred range of body temperatures (McGinnis 1970, Guyer and Linder 1985, Adolph 1990a). We quantified seasonal and geographic variation in activity times for each study site by walking transects throughout the activity season (March–December), starting shortly after sunrise and ending after sunset. We noted the time at which the first and last active lizards were observed. Days on which cloud cover obscured the site at dawn or dusk were excluded from analysis. Observations are based on a total of 152 field days from September 1984 through June 1987.

To estimate the time available for daily activity of hatchlings during the summer and fall, we made observations on the earliest dates that we observed hatchlings at each site. We estimated the latest dates of hatching by combining information on incubation times and observed dates of oviposition by females in the wild and in the laboratory. Incubation time in the field was estimated as the time between the first observed oviposition event and the first date hatchlings were observed. We then estimated the latest date at which eggs would hatch at each site, based on the latest date a female was observed to oviposit. We estimated the maximum amount of time available for daily activity by computing an average day length that would be experienced by hatchlings. A separate estimate was computed for the "first" and "last" lizards to hatch by restricting the analysis of seasonal changes in daily activity to those dates delimited by our estimates of the date of "first" and "last" hatching.

Care of gravid females and eggs

We collected gravid female lizards from each study site in June 1986 and transported them to the laboratory in Seattle within 5 d of collection. In the laboratory, females were housed individually in plastic terraria with a damp substrate of peat moss and sand and were provided water and food ad libitum (*Achaeta* crickets, dusted periodically with Vionate commercial vitamin supplement and calcium). Females were kept in an environmental chamber with a 12L:12D photoperiod provided by natural spectrum fluorescent and ultraviolet lights under a cycling temperature regime (12 h at 34°C, 12 h at 15°C). Terraria were checked at least once per day for eggs. Eggs were incubated individually within covered 100 mL plastic cups filled with moistened vermiculite. This substrate was maintained at a water potential of approximately −200 kPa (Tracy et al. 1978) and was replaced every 7 d. The cups were enclosed within sealed plastic bags and incubated at 27°C, with one exception. Several clutches of eggs from the low-elevation population of *S. occidentalis* were incubated at 24°C to determine whether incubation temperature affected growth rate. When incubation was nearly complete, we checked eggs daily for hatchlings. Hatching success was >80% for both species.

Effect of the thermal environment on growth

Treatment of hatchlings followed Sinervo and Adolph (1989) and Sinervo (1990a). We weighed each hatchling and gave it a unique toe-clip mark. Hatchlings were housed individually in plastic terraria (21 × 13 × 11 cm) with a sand substrate and several pieces of bark for cover and kept in an environmental chamber with an air temperature of 15°C. A 75-W incandescent light bulb placed over one corner of the terrarium provided a thermal gradient (20°–40°C) in which the lizards could thermoregulate. For the first 3 d after hatching, this heat source was provided for 9 h/d. Previously we found that hatchlings usually maintain a T_b between 31° and 33°C in this experimental design (Sinervo and Adolph 1989, Sinervo 1990a). Animals were fed 1 1/2- to 2-wk-old crickets dusted with vitamins ad libitum and were provided water ad libitum.

At 3 d of age, each hatchling was weighed and assigned at random to one of four activity-time treatments: 6, 9, 12, or 15 h of access to radiant energy per day. Hatchlings from a single clutch were distributed across treatments to allow us to determine whether growth rates varied among sibships (see Table 1 for sample sizes). Background illumination by natural spectrum fluorescent lights provided all animals with

TABLE 1. Number of sibships (i.e., groups of clutchmates) and sample sizes of hatchlings for each population obtained from eggs that were incubated at 27°C. Additional hatchling *S. occidentalis* from low elevation in California (*N* = 29) were obtained from eggs incubated at 24°C. Lizards that died during the course of the 3-wk growth experiment (*N* = 17) or lizards that were grossly deformed (*N* = 3, missing digits) are excluded.

Population*	Sibships	Hatchlings
S. occidentalis		
CA, low	24	73
CA, mid	10	55
OR	9	52
S. graciosus		
CA, mid	13	29
CA, high	17	43

* CA = California, OR = Oregon. Low, mid, and high refer to elevation.

the same photoperiod (15L : 9D). Animals were weighed once per week for 3 wk.

Effect of food limitation on growth

Hatchling *S. occidentalis* (*N* = 7, low-elevation California population) and *S. graciosus* (*N* = 7, mid- and high-elevation California populations) were reared with restricted access to food. Over a 3-wk period after hatching, these lizards were maintained on a 4-d feeding cycle: 2 d with food ad libitum alternating with 2 d without food; water was always available. Thus, these hatchlings received about half the usual amount of food. Potential activity time for food-restricted animals was 9 h/d. We compared growth rates of these animals to those hatchlings from the same populations receiving food ad libitum in the 9-h treatments (*N* = 33 *S. occidentalis*, *N* = 23 *S. graciosus*). Food-limited hatchlings were weighed at 0, 3, 7, 14, and 21 d of age, as in the main experiment.

Statistical analysis of growth rate

We analyzed growth rates on a mass-specific basis (Sinervo and Adolph 1989, Sinervo 1990a, b). Growth in mass was expressed as

mass-specific growth rate

$$= [\ln(\text{mass}_{t_2}) - \ln(\text{mass}_{t_1})]/(t_2 - t_1)$$

$$= \Delta\ln(\text{mass})/\Delta t,$$

where t_1 and t_2 denote successive times of measurement. In the limit (as $\Delta t \rightarrow 0$), $\Delta \ln(\text{mass})/\Delta t \rightarrow d[\ln(\text{mass})]/dt$. This expression, $d[\ln(\text{mass})]/dt$, can be rewritten as $(d[\text{mass}]/\text{mass}) \, dt$, which is growth rate expressed on a mass-specific basis (in grams per gram per day), i.e., daily change in mass as a proportion of current mass (= relative growth rate; Brody 1945). Hereafter, growth rate refers to mass-specific growth rate.

Preliminary analysis revealed no effect of hatchling

sex (*P* > .05), so females and males were pooled for subsequent analysis. We estimated growth rates for each individual as the regression slope of ln(mass) against age and used these growth rates as variates in analyses (Sinervo and Adolph 1989). Because growth rate in some populations varied nonlinearly with potential activity time we considered the four treatments as factors (rather than as a linear covariate) when comparing species, populations, and families. Population and species were used as factors in intraspecific and interspecific comparisons. To determine whether significant nonlinear effects were present, we also calculated growth rate for each population as a quadratic function of potential activity time. We used ln-transformed hatchling mass as a covariate in all analyses because of the allometric effects of hatchling size on growth (Sinervo 1990b) and because hatchling size varied among families, populations, and species.

RESULTS

Seasonal and geographic differences in daily activity in natural populations

In the field activity times varied seasonally in all populations (Fig. 1). Daily activity periods were relatively short early and late in the season and longest during the middle of the summer. Activity patterns also differed among habitats, in two ways: both the length of the activity season in days and daily activity time (in hours per day) on any given date decreased with altitude and with latitude (*P* < .01, Kruskal–Wallis test).

Among-site differences in activity time were especially pronounced for hatchlings because of the phenology of oviposition and hatching. Neonates in cooler environments had fewer, shorter days of activity between hatching and the end of the activity season (Fig. 1, Table 2). Hatchling *S. occidentalis* in Oregon had (on average) 6.2–7.8 h/d of activity time; similarly, high-elevation *S. graciosus* in California had 6.2–7.5 h/d. In contrast, low-elevation California *S. occidentalis* could be active up to 9.4–10.1 h/d, averaged across the season. The earliest hatchlings at low elevation could experience up to 13 h/d of activity. Activity patterns at mid-elevation (California) were intermediate.

General effect of thermal environment on growth rates

In the laboratory, mass-specific growth rates increased significantly as access to radiant energy increased (Fig. 2). The form of this response differed among species and among some populations of *S. occidentalis*. Growth rates for *S. occidentalis* hatchlings from California (low- and mid-elevation populations pooled) increased linearly with potential activity time (Fig. 2A; linear term, *P* < .04; quadratic term NS, *P* > .28). In contrast, growth rates of *S. occidentalis* from Oregon (linear term, *P* < .003; quadratic term, *P* <

.001) and both populations of *S. graciosus* from California (linear term, $P < .03$; quadratic term, $P < .05$) varied with potential activity time in a curvilinear fashion, approaching a plateau in the 9-, 12-, and 15-h treatments (Fig. 2A). Absolute growth rates (in grams per day) showed the same trends (Table 3).

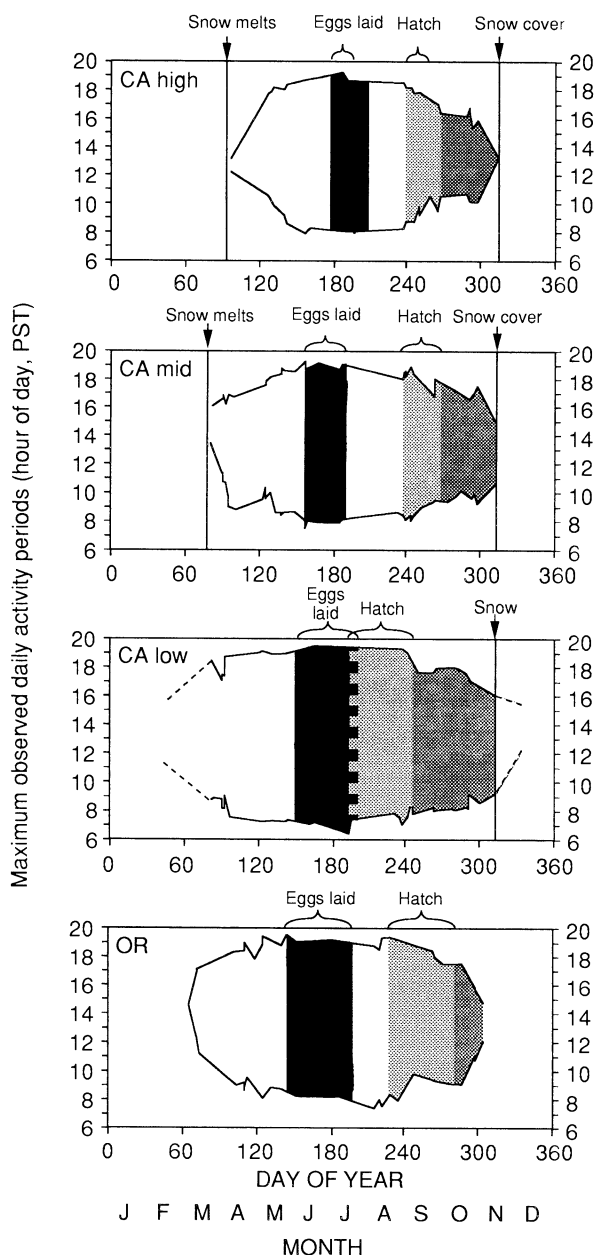### Combined effects of thermal environment and hatchling size on growth

In the laboratory, initial hatchling size varied among populations: hatchling *S. occidentalis* from Oregon were much smaller than California *S. occidentalis,* which were slightly smaller than *S. graciosus* (Table 4). Growth in *Sceloporus* hatchlings is size dependent: within pop-

TABLE 2. Estimates of length of fall activity period, and average amount of time available for activity on a daily basis, for "first" and "last" hatching lizards.*

Site†	Growing season length (d)		Maximum daily activity time (h)	
	"First hatch"	"Last hatch"	"First hatch"	"Last hatch"
CA, high	70	<40	7.5	6.2
CA, mid	70	<50	8.4	6.7
CA, low	130	>90	10.1	9.4
OR	80	<30	7.8	6.2

* "Hatching" dates determined from field observations of hatchlings and oviposition events.

† CA = California, OR = Oregon. Low, mid, and high refer to elevation.

ulations, smaller hatchlings have higher mass-specific growth rates, although their absolute growth rates are lower (Sinervo 1990*b*). Thus, comparisons of mass-specific growth rates are confounded by variation in initial size. This effect can be seen by comparing growth rates in Fig. 2A, which are uncorrected for body size differences, with the size-adjusted growth rates in Fig. 2B. The effect of size is particularly evident in *S. occidentalis* from Oregon. Without correcting for size effects, Oregon hatchlings have growth rates similar to *S. occidentalis* from California. In contrast, their size-adjusted growth rates are comparable to those of *S. graciosus* from California. To account for these size effects in subsequent analyses of growth rate, we used ln(hatchling mass) as a covariate.

Population comparisons of growth rate

S. graciosus from mid- and high-elevation populations in California did not differ in growth rate or in the response across activity-time treatments (Fig. 2B, effect of potential activity time: $F_{3, 63} = 2.89$, $P < .04$, population effect: $F_{1, 63} = 0.47$, $P > .49$; interaction

←

FIG. 1. Seasonal and geographic patterns of maximum observed daily activity periods (interval between times first and last lizards sighted, Pacific Standard Time) for *Sceloporus* lizards, as a function of calendar day. The end of the activity season is typically abrupt and is coincident with the first major snowfall at mid- and high elevation in California. The end of the activity season is not as abrupt at low elevation in California, where snow in the fall may or may not arrive until December, snow does not persist during the winter, and lizards are active during brief bouts of warmer weather. The range of oviposition dates (black) at each site reflects in part the number of clutches laid at each site. Clutch frequencies per season are: one at high elevation in California; one at mid-elevation in California, although some *S. occidentalis* can lay two; two to three clutches at low elevation in California; and two clutches in Oregon (B. Sinervo and S. C. Adolph, *personal observations*). The range of hatching dates reflects the range of oviposition dates. The time available for activity is much longer for the first lizard to hatch (light and dark shading) than for the last lizard to hatch (dark shading).
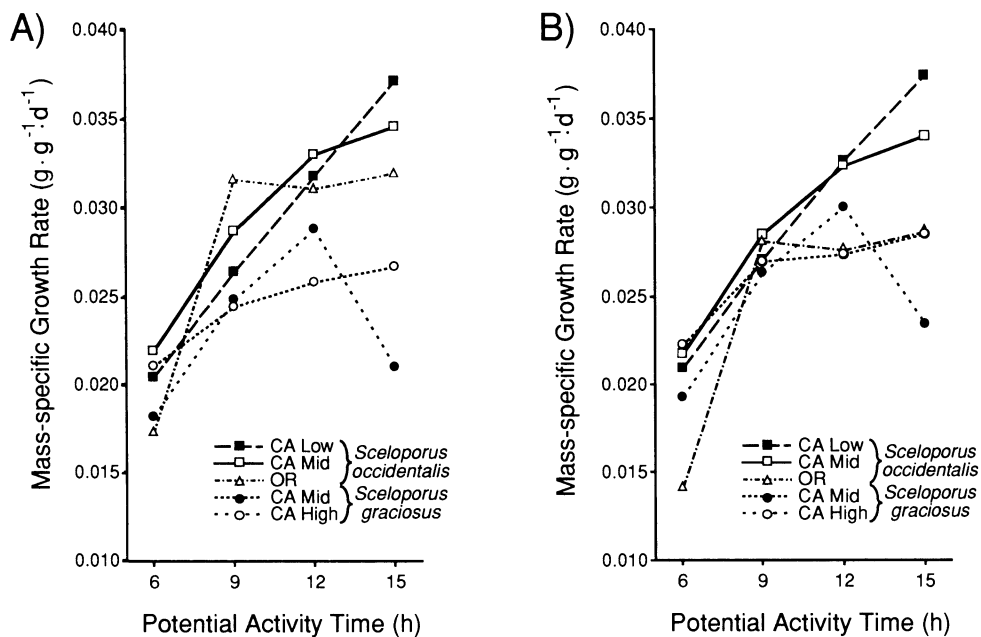
FIG. 2. (A) Sensitivity of mass-specific growth rate of hatchling *Sceloporus* lizards to potential daily activity time in laboratory experiments. The growth rates in (A) are confounded by among-population and interspecific differences in hatchling size. (B) Sensitivity of size-adjusted mass-specific growth rate of hatchling *Sceloporus* lizards to potential activity time (h/d). Effects of hatchling size were adjusted in each population using the following regression equation: $G = 0.0205 - 0.0167 \times \ln(H)$, where G is mass-specific growth rate and H is initial hatchling mass ($r = 0.29$, $N = 280$).

effect: $F_{3, 63} = 0.68$, $P > .57$; covariate ln[hatchling mass]: $F_{1, 63} = 0.74$, $P > .39$). Likewise, *S. occidentalis* from low- and mid-elevation populations did not differ in overall growth rate or in growth response across activity-time treatments (Fig. 2B, effect of potential activity time: $F_{3, 117} = 12.33$, $P < .00001$, population effect: $F_{1, 117} = 0.47$, $P > .49$; interaction effect: $F_{3, 117} = 0.45$, $P > .50$; covariate ln[hatchling mass], $F_{1, 117} = 23.13$, $P < .00001$). However, *S. occidentalis* from Oregon and the low-elevation California site differed in both overall growth rate and growth response across activity-time treatments (Fig. 3A, effect of potential activity time: $F_{3, 115} = 14.68$, $P < .00001$, population effect: $F_{1, 115} = 11.85$, $P < .00001$; interaction effect: $F_{3, 115} = 2.60$, $P = .055$; covariate ln[hatchling mass]: $F_{1, 115} = 21.42$, $P < .00001$). Thus, whereas there has been no local differentiation among populations of either *S. graciosus* or *S. occidentalis* at different eleva-

tions, populations of *S. occidentalis* from different latitudes (Oregon vs. California) have diverged substantially in overall growth rate and in the functional response of growth to different thermal environments. These differences are largely due to the differences in the curvature of the growth response for Oregon *S. occidentalis*, which exhibits a plateau at longer activity-time treatments.

Interspecific comparisons of growth rate

California *S. occidentalis* had higher growth rates overall, and were more sensitive to the potential activity time, compared to *S. graciosus* (Fig. 3B, effect of potential activity time: $F_{3, 187} = 18.77$, $P < .00001$, population effect: $F_{1, 187} = 4.14$, $P < .04$; interaction effect: $F_{3, 187} = 2.95$, $P < .04$; covariate ln[hatchling mass]: $F_{1, 187} = 24.71$, $P < .00001$). However, *S. occidentalis* from Oregon and *S. graciosus* from Califor-

TABLE 3. Average absolute growth rate (g/d) (mean ± 1 SE) of *Sceloporus* hatchlings as a function of potential daily activity time (access to heat lamps, h).

Population*	Potential daily activity time (h)			
	6	9	12	15
S. occidentalis (CA, low)	0.0627 ± 0.0016	0.0719 ± 0.0018	0.0770 ± 0.0030	0.0852 ± 0.0029
S. occidentalis (CA, mid)	0.0663 ± 0.0023	0.0770 ± 0.0021	0.0815 ± 0.0036	0.0842 ± 0.0028
S. occidentalis (OR)	0.0631 ± 0.0017	0.0676 ± 0.0017	0.0676 ± 0.0027	0.0718 ± 0.0043
S. graciosus (CA, mid)	0.0604 ± 0.0025	0 0731 ± 0.0030	0.0785 ± 0.0028	0.0791 ± 0.0078
S. graciosus (CA, high)	0.0619 ± 0.0017	0.0709 ± 0.0017	0.0722 ± 0.0027	0.0668 ± 0.0043

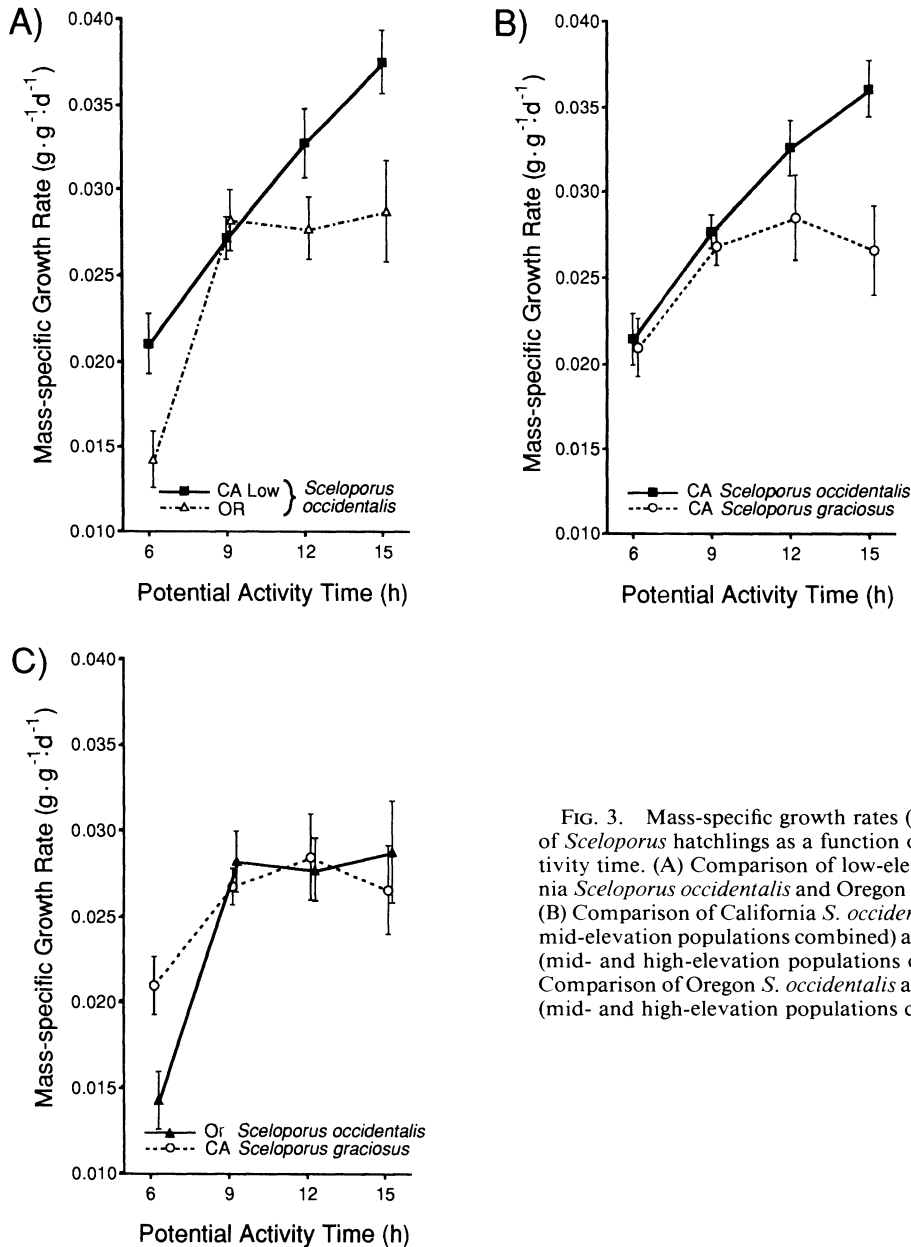* CA = California, OR = Oregon. Low, mid, and high refer to elevation.

FIG. 3. Mass-specific growth rates (means $\pm$ 1 SE) of *Sceloporus* hatchlings as a function of potential activity time. (A) Comparison of low-elevation California *Sceloporus occidentalis* and Oregon *S. occidentalis*. (B) Comparison of California *S. occidentalis* (low- and mid-elevation populations combined) and *S. graciosus* (mid- and high-elevation populations combined). (C) Comparison of Oregon *S. occidentalis* and *S. graciosus* (mid- and high-elevation populations combined).

nia did not differ in either overall growth rate or in growth response across different thermal environments (Fig. 3C, effect of potential activity time: $F_{3, 71} = 10.88$, $P < .00001$, population effect: $F_{1, 71} = 0.17$, $P > .68$; interaction effect: $F_{3, 71} = 1.96$, $P > .13$; covariate ln[hatchling mass]: $F_{1, 71} = 10.37$, $P < .002$).

Consequences of growth rate and initial size for juvenile size

Both growth rate and initial hatchling size affect body size at a given age. For example, *S. occidentalis* from Oregon were much smaller than all California popu-

lations at 21 d because of their small size at hatching and their slower growth rates in all treatments (Fig. 4). In other cases, the effects of hatchling size and growth on overall size were more subtle. In the short-day treatments (6 and 9 h), *S. graciosus* and California *S. occidentalis* had comparable growth rates. At 21 d, *S. graciosus* was larger than *S. occidentalis* at 21 d under short activity-time treatments (Fig. 4) because of its slightly larger size at hatching (Table 4). However, in the long-day treatments (12 and 15 h), higher growth rates allowed *S. occidentalis* from low elevation to overcome their initial size disadvantage, so that they were larger than *S. graciosus* at 21 d (Fig. 4).
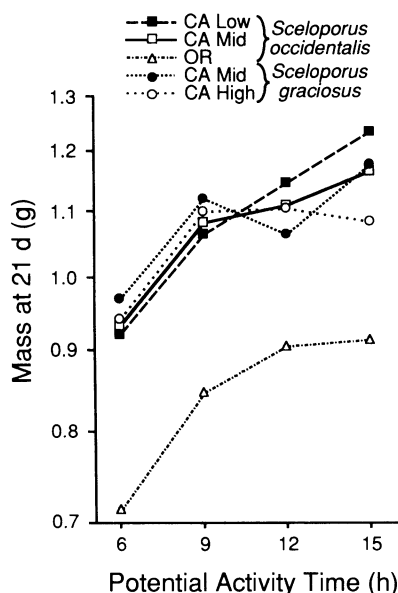
FIG. 4. Joint effects of potential activity time (Fig. 2) and hatchling size (Table 4) on mass at age 21 d (ln-transformed axes for mass) for populations of *Sceloporus*. Significant treatment × population interaction effect ($P < .05$) indicates that *S. graciosus* hatchlings from California are larger at 21 d of age in the low activity-time treatments whereas *S. occidentalis* hatchlings from California are larger at 21 d in the high activity-time treatments. The much smaller size of Oregon hatchlings at 21 d in all treatments is largely due to their smaller size at hatching.

TABLE 4. Hatchling mass (mean ± 1 SE) for experimental subjects from each source population of *Sceloporus occidentalis* and *S. graciosus*. The only pairwise comparison of hatchling size that is not significant is the comparison of high- and mid-elevation hatchling *S. graciosus*.

Population*	Hatchling mass (g)	N
S. occidentalis (CA, low)	0.712 ± 0.0095	73
S. occidentalis (CA, mid)	0.673 ± 0.0097	55
S. occidentalis (OR)	0.567 ± 0.0137	52
S. graciosus (CA, mid)	0.747 ± 0.0137	29
S. graciosus (CA, high)	0.769 ± 0.0121	43

* CA = California, OR = Oregon. Low, mid, and high refer to elevation.

Effect of family membership on growth rate

Sibships of *S. occidentalis* were large enough to test for among-family variation in growth rate (excluding families with three or fewer members, which were not represented in all four treatments). In two of three populations, family membership explained a significant proportion of the variation in growth rate (Oregon: effect of family: $F_{7, 31} = 5.41$, $P < .001$, activity time: $F_{3, 31} = 13.74$, $P < .00001$, covariate ln[hatchling mass]: $F_{1, 31} = 0.54$, $P > .46$; California mid-elevation, effect of family: $F_{7, 41} = 4.52$, $P < .001$, activity time: $F_{3, 41} = 8.08$, $P < .001$, covariate ln[hatchling mass]: $F_{1, 41} = 0.31$, $P > .58$; California low elevation, effect of family: $F_{8, 34} = 2.18$, $P = .05$, activity time: $F_{3, 34} = 10.50$, $P < .00001$, covariate ln[hatchling mass]: $F_{1, 34} = 5.29$, $P < .03$). The percentage of variation attributable to either family membership or environmentally induced treatment effects was generally large (Oregon: family = 34%, activity time = 37%; California mid-elevation: family = 33%, activity time = 25%; California low elevation: family = 20%, activity time = 36%).

We detected significant family × treatment interaction for the population from mid-elevation in California (effect of family: $F_{6, 20} = 10.28$, $P < .0001$, activity time: $F_{3, 20} = 13.00$, family × activity time:

$F_{18, 20} = 3.57$, $P < .005$, covariate ln[hatchling mass]: $F_{1, 20} = 7.86$, $P < .02$) and marginally significant family × treatment interaction for the population from Oregon (effect of family: $F_{6, 18} = 12.11$, $P < .0001$, activity time: $F_{6, 18} = 13.00$, family × activity time: $F_{18, 18} = 2.09$, $P = .06$, effect for covariate ln[hatchling mass] was not significant and was not used in the ANOVA model). Small sibship sizes precluded a similar analysis of a family × treatment interaction for the population from low elevation in California. The variation in the shapes of reaction norms among families reflects underlying genotype × environment effects. The substantial variation in growth response among families of *S. occidentalis* from mid-elevation in California and among families from Oregon is illustrated in Fig. 5.

Effect of food limitation on growth rate

Restricting access to food (2 d with food, 2 d without food) significantly reduced hatchling growth rates (Table 5) of both *S. occidentalis* (effect of food limitation $F_{1, 37} = 6.45$, $P < .02$, covariate ln[hatchling mass]: $F_{1, 37} = 2.16$, $P > .15$) and *S. graciosus* (effect of food limitation $F_{1, 37} = 18.31$, $P < .0001$, covariate ln[hatchling mass]: $F_{1, 37} = 3.16$, $P > .09$). The effect of a 50% reduction in food was similar to that of a 50% decrease in available activity time (Table 5, from 12 to 6 h): each reduced mass-specific growth rate by ≈0.01 $g \cdot g^{-1} \cdot d^{-1}$.

Effect of incubation temperature on growth rate

Hatchling *S. occidentalis* (low-elevation population) that were incubated at 24°C did not have significantly different growth rates compared to hatchlings from the same population that were reared at 27°C (effect of potential activity time: $F_{3, 95} = 12.37$, $P < .00001$, effect of incubation temperature: $F_{1, 95} = 0.01$, $P > .94$; interaction effect: $F_{3, 95} = 1.75$, $P > .16$; covariate ln[hatchling mass]: $F_{1, 95} = 12.78$, $P > .01$). Additional information on the possible effect of incubation temperature is available from our earlier study, in which *S. occidentalis* eggs from low elevation in California were incubated at 30°C and hatchlings were reared under 6, 9, or 12 h/d of potential activity (Sinervo and Adolph 1989). Inspection of our previous results in
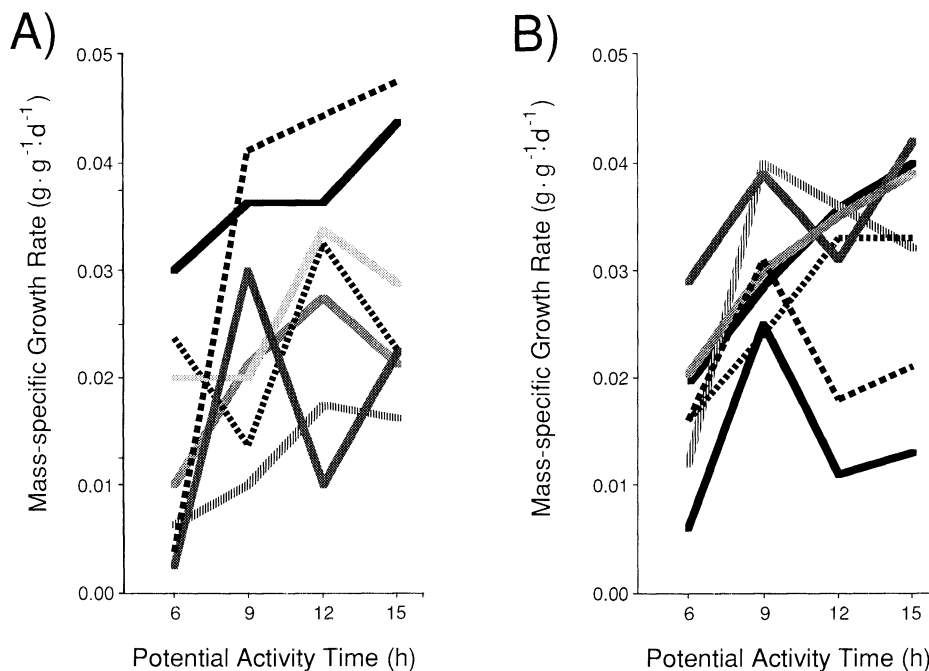
FIG. 5. Among-family variation in growth rates for *Sceloporus occidentalis* from: (A) mid-elevation in California and (B) Oregon. Each line represents the hatchlings from a single clutch; values for each treatment are the mean of sibs in that treatment. Only those families with at least one member in each treatment were used. Note that certain families grow best under short days (e.g., 9 h potential activity time per day) and some families grow best under longer days (e.g., 12–15 h).

comparison to those of the present study reveals no apparent difference in growth rate for hatchlings incubated under these slightly elevated temperatures. These comparisons, although limited to one population from California, suggest that growth rates of hatchlings are probably much more sensitive to current thermal environments than to the temperatures they experienced during incubation.

DISCUSSION

Mechanistic basis for variation in growth rates with potential activity time

Thermal opportunity exerted a strong proximate effect on growth rate in hatchling *Sceloporus* lizards. Similar effects occur in other reptiles and amphibians (Lillywhite et al. 1973, Avery 1984; C. R. Peterson, *personal communication*) and are consistent with mechanistic models based on physiology and bio-

physics (Porter 1989). *Sceloporus* growth rates varied up to twofold over the range of thermal environments lizards encounter in nature on a seasonal basis. This suggests that if food is sufficiently available in natural environments, lizards with longer potential activity days should grow faster than lizards experiencing short days. Several studies have reported this pattern of variation in wild lizard populations, either at different seasons or among different populations (Davis 1967, Tinkle 1972). Consequently, growth rates measured in the wild cannot be used to infer genetic differences among populations or species; they may instead reflect geographic variation in thermal environments and/or food availability (Andrews 1982).

Two mechanisms probably underlie the dependence of growth rate on potential activity time observed in this experiment. First, lizards with longer potential activity times were able to spend more time at their

TABLE 5. Mass-specific growth rates of food-limited and food-unlimited *Sceloporus* lizard hatchlings. Hatchlings receiving unlimited food had food available ad libitum every day, whereas animals receiving restricted food were on a 4-d feeding cycle (food ad libitum for 2 d, followed by no food for 2 d).

	Growth rate ($g \cdot g^{-1} \cdot d^{-1}$)			
	Unlimited food		Restricted food	
Population*	Mean ± 1 SE	N	Mean ± 1 SE	N
S. occidentalis (CA, low)	0.0266 ± 0.0026	33	0.0164 ± 0.0016	7
S. graciosus (CA, mid and high pooled)	0.0248 ± 0.0012	23	0.0147 ± 0.0026	7

* CA = California. Low, mid, and high refer to elevation.

preferred T_b ($\approx 31°$–$34°C$; Sinervo and Adolph 1989, Sinervo 1990a). In this T_b range, rates of physiological processes involved in food digestion, food assimilation, metabolism, and conversion to somatic tissue are typically high compared to rates at nighttime T_b (Avery 1973, Bennett and Gleeson 1976, Skoczylas 1978, Harwood 1979, Buffenstein and Louw 1982, Waldschmidt et al. 1986, 1987, Tsuji 1988a, b, Van Damme et al. 1991, Beaupre et al. 1993a, b). Long-day lizards would have been able to experience higher average rates of these processes, and hence higher growth rates, per day. Second, lizards in long-day treatments had more time available for foraging and food intake (Avery et al. 1982, Avery 1984, Karasov and Anderson 1984, Waldschmidt et al. 1986, Van Damme et al. 1991). These mechanisms are complementary rather than alternatives: sustaining higher growth rates would require both higher processing rates and higher food harvesting rates (Congdon 1989). This is illustrated by the slower growth rates of food-limited lizards (Table 5). In these animals, a 50% reduction in food (2 d with food, 2 d without food) reduced mass-specific growth rate by the same amount (≈ 0.01 $g \cdot g^{-1} \cdot d^{-1}$) as a 50% reduction in activity time (from 12 to 6 h/d).

The sensitivity of *Sceloporus* growth rates to potential activity time has both physiological and behavioral components (Sinervo and Adolph 1989, Sinervo 1990a). Our previous studies suggest that behavioral differences are at least partly responsible for interspecific and interpopulational differences in growth response observed in this study (Figs. 2 and 3). Growth rates of *S. occidentalis* from California increased linearly with potential activity time. *S. occidentalis* from the low-elevation population maintain high T_b and are active and alert throughout the day, whether in short or long activity-time treatments (Sinervo and Adolph 1989, Sinervo 1990a). In contrast, *S. occidentalis* from Oregon and *S. graciosus* from California (mid-elevation) voluntarily curtail activity, particularly under long-day conditions, spending a substantial fraction of the day in retreat sites (under bark or buried in the sand; Sinervo and Adolph 1989, Sinervo 1990a). Body temperatures of these inactive lizards are lower than T_b's of active lizards (Sinervo and Adolph 1989, Sinervo 1990a). In addition, growth rates and selected T_b's covary among families of *S. occidentalis* and between Oregon and California populations (Sinervo 1990a). These observations are consistent with a positive genetic correlation between these traits (Sinervo 1990a). Daily patterns of activity and thermoregulation therefore act as a behavioral filter between environmental thermal opportunities and growth physiology. A different experimental design (one that imposes a temporal T_b pattern on the animals) might help to disentangle the relative contributions of physiology (maximum growth rate) and behavior (activity patterns leading to realized growth rates) to variation in growth rates. However, such a design might still not eliminate

differences in behavior; lizards could still choose to be inactive or not to feed during the warm part of the daily cycle.

A recent study by Gerwien and John-Alder (1992) suggests a possible hormonal basis for correlated variation in growth and activity. They surgically removed thyroid glands of yearling *S. undulatus,* then released them into field enclosures. Thyroidectomized lizards had reduced growth rates and activity patterns relative to sham-operated controls. This intriguing result points to thyroid hormone levels as a possible control mechanism for both behavior and growth rate of sceloporine lizards.

Evidence for genetic variation in growth rates

Our laboratory experiments provide evidence for genetically based differences in average reaction norms of growth rates between *S. occidentalis* and *S. graciosus* from California and between California and Oregon populations of *S. occidentalis*; reaction norms differed most under long potential activity days. We did not find intraspecific population differences in growth response in either *S. occidentalis* or *S. graciosus* from different elevations in southern California. In addition, previous studies (Sinervo and Adolph 1989, Sinervo 1990a, b) and the current study (Fig. 3C) provide evidence of among-family variation in growth rate. In this study we found significant family × treatment interaction effects for populations of *S. occidentalis* from Oregon and mid-elevation in California (Fig. 5). This variation in norms of reaction among genotypes within a population (genotype × environment interaction) provides the requisite material for evolution of reaction norms among populations. The response of the different families to thermal environment appears to be complex. However, closer inspection reveals families that grow best under intermediate potential activity times (e.g., 9 h/d) and families that grow best under longer amounts of potential activity time (e.g., 12–15 h/d). This variation in norm of reaction among families parallels variation in norm of reaction found among different populations of *S. occidentalis* and among different species of *Sceloporus* in that most of the variation in reaction norms occurs at long days of activity. Thus, within populations of *S. occidentalis* there appear to be "short-day specialist" genotypes and "growth opportunist" genotypes.

Maternal effects are an alternative explanation to genetic differences for the observed variation in growth rates. However, previous work on *Sceloporus occidentalis* indicates that maternal effects are largely determined by egg size (Sinervo 1990a), which is strongly correlated with hatchling size in these populations (Sinervo 1990a; S. C. Adolph and B. Sinervo, *unpublished data*). Because our statistical analyses included hatchling size as a covariate, they are likely to have eliminated most of the maternal effects on growth rate. Therefore, the differences in growth response between

families, populations, and species are likely to reflect genetic differences, perhaps due to differences in selective regimes in different environments. Genetic variation in growth rates among individuals within a population may be common; most studies of reptilian growth report wide variability in individual growth rates, even under relatively constant conditions (Andrews 1982).

Several studies of growth rates in other *Sceloporus* populations have revealed population differences that are likely to be partly genetic. Ballinger (1979) found that juveniles from a high-elevation population of *S. jarrovi* grew faster than juveniles from a low-elevation population when raised in outdoor enclosures at low elevations. Ferguson and Brockman (1980) measured hatchling growth rates for laboratory-reared hatchlings of *S. undulatus* and *S. graciosus* in a laboratory thermal gradient similar to the one used in our study. Growth rates differed among three populations of *S. undulatus*, and *S. graciosus* grew more slowly than all three populations of *S. undulatus*. In addition, lizards from all four populations grew faster in the laboratory than did their counterparts in the field, demonstrating proximate influences on growth (i.e., due to differences between laboratory and field environments). Ferguson and Talent (1993) raised hatchling *S. undulatus* to reproductive maturity in the laboratory and found that lizards from Utah and Oklahoma populations differed in growth rates, body proportions, age at maturity, and size at maturity. Sidereal age at maturity for these laboratory-reared animals was just 4–5 mo, compared to 1–2 yr in the wild, again demonstrating proximate effects. Niewiarowski and Roosenberg (1993) performed reciprocal field transplant experiments using *S. undulatus* from New Jersey and Nebraska. Nebraska hatchlings, when transplanted to New Jersey, had reduced growth rates comparable to native New Jersey hatchlings. However, New Jersey hatchlings transplanted to Nebraska did not have the higher growth rates of native Nebraska hatchlings. Biophysical estimates of potential activity time (using copper models) were 2–2.5 h/d longer in Nebraska than New Jersey. Thus, Nebraska hatchlings are more sensitive to thermal opportunity than are New Jersey hatchlings. These studies and our results suggest that both proximate and genetic sources of variation in growth rates are common for free-living *Sceloporus* lizards, and that population × environment interactions may be common as well.

Ecological context of intra- and interspecific differences in hatchling growth

S. occidentalis and *S. graciosus* from California have similar growth rates under short days, but *S. occidentalis* grows faster under long days. In general, this difference corresponds to the differences in thermal opportunities these two species experience in nature. In California, *S. graciosus* typically lives at higher elevations than does *S. occidentalis* (Stebbins 1985, Adolph 1990a) and therefore averages fewer hours of potential activity per day compared to *S. occidentalis* (Fig. 1, Table 2). Altitudinal differences in thermal environments are particularly pronounced for hatchlings, because of variation in the phenologies of oviposition, incubation, and hatching. At the low-elevation site, hatchlings of *S. occidentalis* appear in mid-July and early August (Fig. 1). These animals experience potential activity times averaging 9.4–10.1 h/d across the remaining activity season, and midsummer hatchlings routinely experience up to 13 h/d of potential activity (Fig. 1, Table 2). At mid-elevation, both species hatch in late August and September, when potential activity time averages 6.7–8.4 h/d and rarely exceeds 10 h/d. Hatchling *S. graciosus* at high elevation appear in late August to October and grow under potential activity times averaging 6.2–7.5 h/d; they rarely experience 9 h/d. The thermal environment experienced by hatchling *S. occidentalis* in Oregon closely resembles that of *S. graciosus* at high elevation in California: hatchlings emerge in late August through October and have potential activity times averaging 6.2–7.8 h/d.

These general environmental differences are paralleled by differences in the sensitivity of growth rate to potential activity time: *S. graciosus* is a "short-day specialist," whereas *S. occidentalis* in California is a "growth opportunist" (Fig. 2). The linear reaction norm of California *S. occidentalis* would permit high growth rates across a range of thermal environments. In contrast, the reaction norms of Oregon *S. occidentalis* and California *S. graciosus* would allow fast growth under short activity days, but show diminishing returns as potential activity time increases. Hatchlings in these populations rarely experience activity times >10 h/d. On a large scale, therefore, growth responses appear to be appropriate to the thermal environments to which hatchlings are most commonly exposed.

On the other hand, we detected no significant differences in hatchling growth response between conspecific populations of either species from different elevations in California (Fig. 3, Table 3), although they inhabit different thermal environments. These environmental differences are particularly pronounced for *S. occidentalis* hatchlings from the desert low-elevation site compared to those from the montane mid-elevation site. The lack of population differentiation on a local scale argues against a purely adaptive explanation for interspecific and geographic patterns of hatchling growth response, as does the difference in growth response between sympatric *S. occidentalis* and *S. graciosus*, which inhabit the same thermal environment. Lack of population differentiation could result from gene flow. We have no direct measurements of gene flow between these populations, and indirect evidence from other traits is equivocal. For example, laboratory-reared juveniles from these California populations do not differ intraspecifically in habitat selection, sug-

gesting lack of genetic differentiation among populations (Adolph 1990b). On the other hand, eggs from low- and mid-elevation populations of S. occidentalis differ significantly in laboratory measures of the thermal dependence of incubation time and of water uptake rates, and dorsal color patterns differ genetically between these populations (S. C. Adolph and B. Sinervo, unpublished data). These observations suggest that genetic differentiation in heritable traits between these populations is possible.

Evolution of growth rate and hatchling size in seasonal environments

The relationship between growth and fitness is undoubtedly complex. First, growth rates per se could be the direct target of natural selection for early maturity. Second, evolution of growth rates could result from selection on body size (e.g., size-specific mortality risk). Finally, growth rate could evolve because of selection on the physiological and behavioral processes that underlie growth.

For Sceloporus lizards with long activity seasons, maturation in 1 yr is feasible for fast growers. However, in shorter activity seasons, a wider range of growth rates may permit maturity at age 2 yr, whereas maturing in 1 yr may be virtually unattainable. Indeed, we have never observed maturation in 1 yr by S. occidentalis from mid-elevation in California or in Oregon and have observed only one female S. graciosus mature in her 1st yr at mid-elevation, during 1984–1987 (B. Sinervo and S. C. Adolph, unpublished data). However, S. occidentalis at low elevations commonly mature in 1 yr. Thus, the fitness advantage of high growth rates may be greater in populations with long growing seasons. Similarly, fast growth may be more important for S. occidentalis, because they reach sexual maturity at a larger size than S. graciosus.

Body size affects a variety of performance-related traits in lizards, including sprint speed (Garland 1985, Sinervo and Adolph 1989, Sinervo and Huey 1990, Sinervo and Losos 1991), ability to hold territories (Rand 1967, Trivers 1972, Brattstrom 1974, Ferner 1974, Ruby 1981, Ferguson et al. 1982, Stamps 1983, 1988), and dispersal distance (Doughty 1991). Body size of juvenile lizards can influence survival during the activity season (Fox 1978, Fox et al. 1981, Ferguson and Fox 1984, Sinervo et al. 1992) and during winter dormancy (Ferguson and Bohlen 1978, Bauwens 1981). High overwinter mortality has been observed in S. undulatus (Jones and Ballinger 1987) and may be similarly high for juveniles in our study populations, because they have a prolonged (4–7 mo) period of winter inactivity during cold conditions.

Both initial size and growth rate interact to determine juvenile size (Fig. 4). For example, under short-day treatments (6 and 9 h/d) S. graciosus attained a slightly larger body size at age 21 d compared to California S. occidentalis, because of their comparable growth rates and slightly larger initial size. Under long-day treatments (12 and 15 h/d), however, low-elevation S. occidentalis hatchlings were largest at 21 d, because their higher growth rates overcame their smaller initial size. Mid-elevation S. graciosus and S. occidentalis were approximately the same size at age 21 d, because differences in their initial sizes and growth rates balanced out. In the field, hatching phenology would also affect size of juveniles entering hibernation. Field observations indicate similar hatching dates for sympatric (mid-elevation) S. graciosus and S. occidentalis. However, eggs of S. graciosus have shorter incubation times (by ≈10%) compared to eggs of S. occidentalis at all temperatures that we have studied in the laboratory (24°, 27°, and 30°C, S. C. Adolph and B. Sinervo, unpublished data). The combination of extended incubation times at high elevations, smaller initial size, and reduced thermal opportunities for growth could explain why S. occidentalis are not found at higher elevations; their upper elevational limit in the San Gabriel Mountains is ≈2300–2400 m, just above our mid-elevation site. The larger hatchling size of S. graciosus may partially compensate for the reduced opportunities for growth at high elevations.

Hatchling S. occidentalis from Oregon are small and they grow slowly; in addition, northern adults are smaller than southern adults (Fitch 1978, Sinervo et al. 1991). The smaller size of northern hatchlings entails reduced locomotor performance, as demonstrated by allometric engineering experiments (Sinervo 1990a, b, Sinervo and Huey 1990, Sinervo et al. 1991). In addition, a field study of S. occidentalis in Washington has documented directional natural selection favoring small eggs and hatchlings (B. Sinervo et al., unpublished data). Northern populations of S. occidentalis also show lower sprint speeds of hatchlings (Sinervo and Huey 1990) and gravid females (Sinervo et al. 1991), including effects not attributable to body size or relative clutch mass. Relaxed selection for large size and locomotor performance is consistent with arguments that predation rates are lower in the north (Pianka 1970). On the other hand, Wilson (1991) found no consistent relationship between mortality rate and latitude among seven populations of the sceloporine lizard Uta stansburiana in California, Oregon, and Washington.

The contribution of activity to growth implies that juvenile growth rates could represent an evolutionary compromise between the costs and benefits of activity, particularly predation risk (Huey and Slatkin 1976, Rose 1981). Among populations of S. undulatus, increased annual opportunity for activity is associated with higher annual mortality (Adolph and Porter 1993). Studies of other sceloporine lizards indicate links between daily activity patterns and mortality risk (Fox 1978, 1983, Marler and Moore 1988, 1989, Wilson 1991; B. Wilson, personal communication). Because the trade-off between growth rate and activity level in Sceloporus is reflected in an underlying genetic corre-

lation (Sinervo 1990*b*), these traits would be expected to evolve in a correlated fashion. Interspecific and interpopulation differences in growth rates and associated activity patterns could reflect different balances between the costs and rewards of activity. Indeed, lizards in natural populations may not be active as often as the thermal environment would allow (Porter et al. 1973, Simon and Middendorf 1976, Rose 1981).

A related issue concerns the possible relationships between food availability, metabolism, energy allocation, and growth. Where food is limited, increases in average daily T_b could have a negative effect on growth rates by increasing energy expenditure without a compensatory increase in energy intake. This might be particularly important in deserts and other hot, arid environments. For example, Grant and Dunham (1990) have presented evidence that thermal environments and resource availability interact to determine altitudinal variation in life history traits of *Sceloporus merriami*. Capacity for rapid growth may entail high metabolic rates (e.g., Brody 1945, Case 1978), which would be disadvantageous when food is limited. Gerwien and John-Alder (1992) suggested that thyroid hormone levels could function as a control mechanism for energy allocation to growth; this could work either as a short-term response to nutritional status or as an evolved response to a particular environmental condition. Indeed, surgical removal of the thyroid gland in eastern fence lizards (*S. undulatus*) reduces both growth rate and standard metabolic rate (SMR; Gerwien and John-Alder 1992). Moreover, individual variation in SMR is positively correlated with individual variation in growth rate after the effects of body mass and treatment (thyroidectomy vs. sham) are removed, indicating a close functional link between incremental variation in metabolism and growth (Gerwien and John-Alder 1992). The interactions between growth, metabolism, energy allocation, and the endocrine system remain largely unexplored in lizards and other reptiles and merit further study.

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