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ECOLOGY OF GROWTH OF THE HIGH ALTITUDE LIZARD
***SCOLOPORUS GRAMMICUS* ON THE EASTERN**
SLOPE OF IZTACCIHUATL VOLCANO, PUEBLA, MÉXICO

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ABSTRACT

Growth in the lizard *Sceloporus grammicus* living at two altitudes on the Iztaccihuatl Volcano, Puebla, México, was studied from November 1984 to January 1992. Despite differences in the environmental conditions at these two elevations, individual lizards grew at similar rates at both study sites. Females in both populations grew slower and attained asymptotic size earlier in life than males (0.0025 mm per day and 49.7 mm snout-vent length for females vs. 0.0027 mm per day and 53.2 mm snout-vent length for males). Maximum growth rates were observed early in life in both sexes and sites. Growth in *Sceloporus grammicus* fits the von Bertalanffy growth model from 0 to 1.5 yrs. of age. Initial growth rates were between 0.10 and 0.15 mm per day in both sexes and sites. Rates decreased to less than 0.02 mm per day at maturity at both sites. Differential investment in feeding activities, social interactions and thermoregulation, differences in the number of predators and competitors, and absence of a hibernation period at both study sites are possible explanations for similar growth rates at both sites.

† † †

Growth is an important component of an organism's life history. Allocation of growth energy is compensatory with other life history traits (eg. reproduction, maintenance, storage; Fisher 1958). Williams (1966) observed that energy expended for reproduction may result in reduced growth. Gadgil and Bossert (1970) stressed that growth is one of the three major life history categories among which time-energy budgets are divided to maximize fitness.

Rapid growth rates are expected to evolve for organisms inhabiting environments with high resource supply/demand ratios, whereas low growth rates are expected to evolve in organisms inhabiting highly competitive environments with low resource supply/demand ratios (Pianka, 1970). This relative speed in growth rates leads to differences in body sizes within popula-

tions. A number of studies have shown a positive relationship between female body size and clutch size, such that larger, more rotund females have larger clutches than smaller and thinner females (Fitch, 1970; Tinkle, 1969; Tinkle et al., 1970; Vitt and Congdon, 1978), suggesting a selective advantage for large body size. Growth rates are also related to competitive ability, since contests for food or space are usually won by large individuals (Fox, 1983; Tokarz, 1985). Large individuals also usually have an advantage in predator avoidance. Smaller individuals are excluded from territories with optimal food supplies and are forced to forage more often and to spend more time when predators are apt to be hunting (Ferguson et al., 1982). In addition, female choice for larger males has been suggested as a causal factor for high male growth rates (Halliday and Verrel, 1988; Van Devender, 1978).

Growth has been studied extensively in lizards. Lizard growth rates vary with food availability (Andrews, 1976, 1979, 1982; Ballinger, 1977; Ballinger and Congdon, 1980; Case, 1976; Dunham, 1978; Ferguson and Brockman, 1980; Lewis, 1986; Mayhew, 1965; Medica et al., 1975; Schoener and Schoener, 1978; Stamps, 1977) 1982;). Differences in growth rates related to water supply have also been observed (Jenssen and Andrews, 1983; Nagy, 1973; Stamps and Tanaka, 1981). Lizard growth rates are also affected by temperature because temperature affects digestive rate and efficiency (Christian, 1986; Dunham et al., 1989; Grant and Dunham, 1990; Noeske and Meier, 1983; Sinervo and Adolph, 1989). Some studies have suggested a strong relationship between sexual selection and growth rates (Halliday and Verrel, 1988; Van Devender, 1978).

We examined body growth rates in two populations of the lizard *Sceloporus grammicus* occurring at two different altitudes. Growth rates were measured and

related to weather conditions, food availability, and lizard activity patterns, and were compared between sexes and among seasons through several years.

MATERIALS AND METHODS

Species studied: *Sceloporus grammicus* is a small, sexually dimorphic phrynosomatid (Frost and Etheridge, 1989) lizard that occurs from southern Texas, USA, to the state of Oaxaca, Mexico. On Iztaccihuatl Volcano, Puebla, México, *Sceloporus grammicus* occurs up to 4,600 m elevation. Adult males are larger than females (\bar{x} = 52 mm snout-vent length and 4.6 g body mass for males, versus \bar{x} = 49 mm snout-vent length and 4 g body mass for females) (Lemos-Espinal, 1992).

Study sites: Populations were located at two sites on the eastern slope of the Iztaccihuatl Volcano. These sites in Campo Experimental Forestal San Juan Tetla (CEFSJT), of the Instituto Nacional de Investigaciones Forestales y Agropecuarias de México (19°10'N, 98°36'W). At this latitude, the tree line is at 4,000 m elevation. The experimental station is 25 km southwest of the town of San Martín Texmelucan, and approximately 50 km west of Puebla City. The low elevation (3700 m) site (hereinafter Laguna) of approximately 4 ha is located in a *Pinus hartwegii* forest surrounding a natural ephemeral lake. Lizards occur primarily on logs and stumps, and occasionally under tree bark and in cracks of trunks or rocks. Neonates frequently are found on the sandy soil, in leaf litter or under surface debris. Laguna was studied monthly from November 1984 to June 1988 and from September 1990 to January 1992. The high elevation site (4400 m) (hereinafter Paredon) of approximately 1 ha is a volcanic rock formation surrounded by grassland of predominately *Festuca toluensis*. Lizards at this site live under rocks and in rock crevices. This site was studied monthly from November 1985 to June 1988 and from September 1990 to January 1992. Lizards were captured by hand or noose.

Rainfall data were obtained from a weather station located at 3,300 m elevation at the field station (Fig. 1). Maximum rainfall occurs in the summer (June–August), and rainfall decreases to very low values in the winter (December–February) and remains low until May. Therefore, the year can be divided into a wet season (May–October) and a dry season (November–April). Temperature data were obtained from maximum–minimum thermometers located at both study sites from May 1991 to April 1992.

Prey availability: Prey availability was estimated by setting sticky traps made of 10 wood squares (10 × 10 cm) coated with the adhesive Tanglefoot™. Sticky

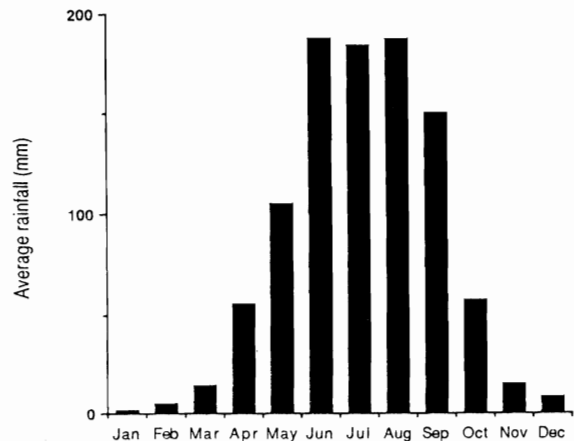


Figure 1. Average rainfall variation at Iztaccihuatl Volcano, Puebla, México. Data taken (January 1984–December 1991) from San Juan Tetla weather station (3,300 m elevation).

trap samples were taken monthly in the wet season from May through August 1991, and in the dry season from December 1991 through January 1992 at both sites. Sticky traps were randomly placed on each study site for 12 h from 0600 to 1800 h. At 1800 h traps were removed and number and size of arthropods (length × width) were recorded. The volume (V) of individual insects (assuming an ellipsoid shape) was estimated, using the equation for an ellipsoid.

Lizard Activity: Rates of lizard movements, feeding attempts, social displays and the number of 5-min periods in which a lizard was immobile were recorded for active male lizards during continuous 30-min observation periods (n = 32 periods) using methods of Grant and Dunham (1988). These rates are useful in estimating time budgets of lizard activity. In general, immobile behavior was an indication of thermoregulatory basking or ambush feeding behavior. These two behaviors could be distinguished by posture and degree of alertness. Also, thermoregulatory basking involved longer periods of immobility than did feeding behavior. Observations were made before noon in the summer and winter of 1991, 1992, and 1993. Sites and seasons (wet and dry) were compared using analysis of variance (ANOVA).

Growth Estimation: Lizards were captured by hand or noose (n = 3044). Lizards were permanently marked by clipping a unique combination of up to two toes for each foot. Before the lizards were released at the site of capture the following data were recorded: snout-vent length (SVL) to the nearest 0.1 mm using a caliper and a clear plastic ruler; body mass (BM) to the nearest 0.01 g using a Pesola® spring scale; sex; tail condition (broken, unbroken or regenerated); and site

Table 1. Regression statistics for growth curves. Initial growth rate (a); damping coefficient (b); asymptotic size (-a/b). Site: L = Laguna; P = Paredon.

Sex	Site	Season	N	R ²	a	b	-a/b
F	L	All	261	.71	.1294	.00257	49.58
F	L	Wet	144	.76	.1394	.00281	49.64
F	L	Dry	117	.64	.1094	.00219	49.97
F	P	All	323	.35	.1243	.00249	49.95
F	P	Wet	155	.42	.1600	.00320	50.03
F	P	Dry	168	.39	.0901	.00180	50.07
M	L	All	118	.76	.1547	.00294	52.62
M	L	Wet	63	.87	.1810	.00344	52.64
M	L	Dry	55	.63	.1232	.00230	53.59
M	P	All	158	.46	.1384	.00257	53.88
M	P	Wet	100	.53	.1509	.00280	53.90
M	P	Dry	58	.35	.1244	.00225	55.32

and date. Changes in length (dSVL) and growth interval length (dT) were used to calculate growth rates (GR = dSVL/dt). Only lizards with recapture intervals >30 and <100 days were used in parameter estimation. Average size during the interval (ASVL) was the average of first and last SVL.

Two frequently used growth models are the von Bertalanffy growth model (Fabens, 1965; von Bertalanffy, 1951, 1957) and the logistic-by-length growth model (Schoener and Schoener, 1978). Andrews (1982) discussed the difference between the von Bertalanffy and the logistic-by-length growth models. The von Bertalanffy model predicts the maximal rate of growth in length for the smallest size class and a decreasing rate of growth as size increases. In contrast, the logistic model predicts that the maximal rate of growth in length will be observed at 50% of the asymptotic length (Andrews, 1982).

The von Bertalanffy model predicts that growth rate in SVL is a linear function of body length:

$$GR = a - bASVL \dots\dots\dots 1$$

where a = initial growth rate, b = damping coefficient, and ASVL = average snout-vent length. ASVL is used rather than initial size because the GR is measured over a limited period and will underestimate instantaneous GR for the initial SVL (Van Devender 1978). Asymptotic size is predicted as Z = -a/b.

Equation # 1 can be expressed as:

$$GR = a [1 - (SVL/Z)] \dots\dots\dots 2$$

or

$$a - bASVL = a \{ a [1 - (SVL/Z)] \} \dots\dots\dots 3$$

which is Fabens (1965) derivation of the differential equation of the von Bertalanffy growth model. Knowing the size of neonate lizards (SVL₀), and using the values of Z and b obtained from GR = a - bASVL, the growth curve can be obtained by:

$$SVL = Z (1 - ke^{-bT}) \dots\dots\dots 4$$

where SVL is the size that the lizard has reached after

time T (since parturition) k is a constant that can be calculated if SVL₀ is known, and T is the number of days of growth (age).

k can be estimated as follows:

$$k = 1 - SVL_0/Z \dots\dots\dots 5$$

Fabens (1965) proposed the following equation to estimate SVL of a lizard at time t+d (SVL₂) in terms of its SVL at time t (SVL₁).

$$SVL_2 = Z - (Z - SVL_1) e^{-bd} \dots\dots\dots 6$$

where d is the time interval of growth.

In order to test the goodness of fit for the growth curves obtained, animals with known ages were compared with sizes predicted by the model. Linear regression was used to determine the relationship between GR and SVL. Separate regressions were calculated for each combination of sex, site, and season. The regressions were tested for statistical validity and compared using analysis of covariance (ANCOVA), using SVL as a covariate. Since our growth data followed the von Bertalanffy model, we do not detail the predictions of the logistic model here (see Andrews, 1982; Schoener and Schoener, 1978)

RESULTS

Growth and body size relationships

Growth rates: Growth rates for both populations of *Sceloporus grammicus* were maximal for the smallest size class and decreased as size increased, indicating a von Bertalanffy growth trajectory. Growth rates varied inversely with ASVL for males and females at both sites (Fig. 2). We used these data to calculate a predicted growth curve (age vs. SVL) and this agreed well with data from lizards of known age (Fig. 3; Table 1). Females from both populations grew slower than males ($P < 0.0001$, $F_{1,479} = 23.42$, for Laguna, and $P < 0.002$, $F_{1,379} = 9.36$, for Paredon). Growth curves for both sexes and sites indicated that female growth decreased with size more rapidly than did male growth

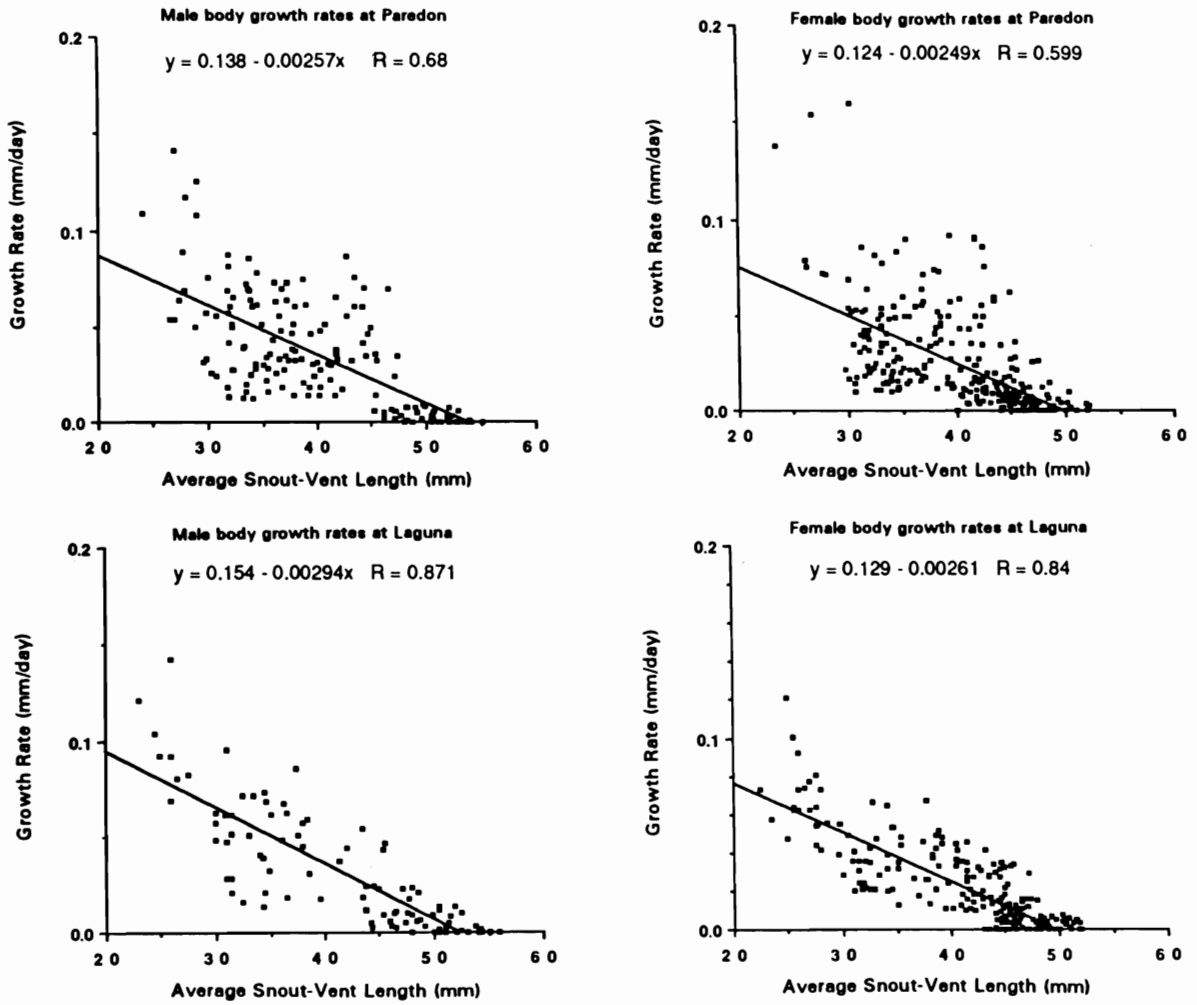


Figure 2. Growth in *Sceloporus grammicus* for females and males at both study sites. Each point represents growth rate (GR) and average snout-vent length obtained for lizards with recapture intervals of 30–100 days. Data are from both seasons (wet and dry).

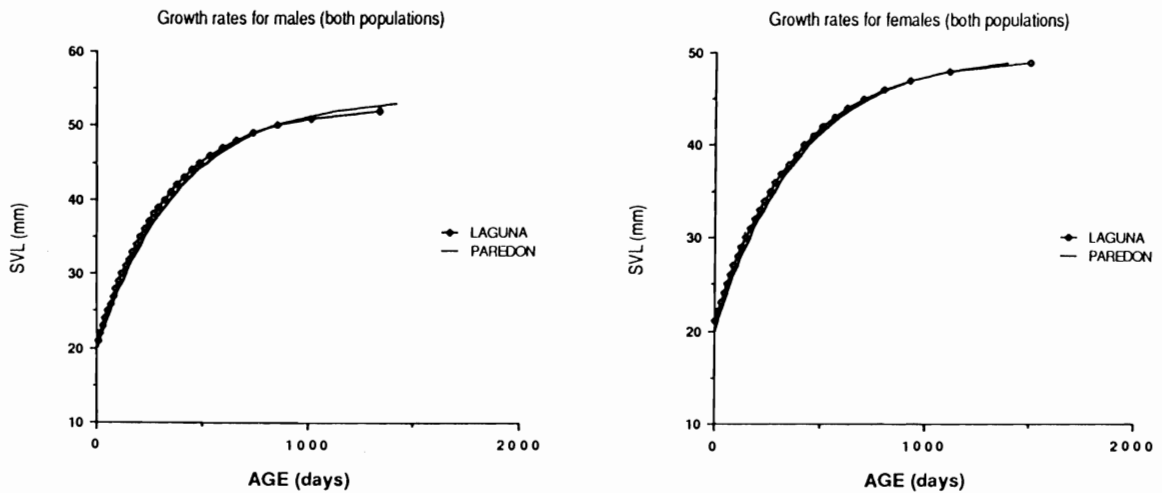


Figure 3. Size and age in *Sceloporus grammicus* for females and males at both study sites. Solid points represent the predicted growth curve from its corresponding regression line in Fig. 2. Open points are lizards marked within their first 3 months of life (20 mm SVL < lizard < 30 mm SVL) and capture later in the study.

Table 2. Variation in available prey of *Sceloporus grammicus*. Numbers represent volumes (ml) of insects on 10 Tanglefoot™ traps at each site per time sample. June E = early June; June L = late June. Data are means \pm one standard error and ANOVA for comparing data by sites.

Month	Laguna	Paredon	$F_{1,17}$	P
May	72.76 \pm 26.023	26.53 \pm 26.230	1.55	0.229
June E	129.57 \pm 21.885	54.64 \pm 4.430	12.47	0.0026***
June L	158.91 \pm 21.244	65.49 \pm 7.764	18.53	0.0005***
July	258.68 \pm 21.929	151.76 \pm 9.885	21.20	0.0003***
August	164.91 \pm 35.258	74.73 \pm 8.583	6.81	0.018**
December	6.53 \pm 1.233	2.12 \pm 0.652	10.56	0.0047**
January	5.22 \pm 1.227	2.15 \pm 0.713	4.92	0.0404*

(* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

(Fig. 4).

Growth rates between sites did not differ for either sex ($P > 0.05$, $F_{1,580} = 0.32$ for females, and $P > 0.05$, $F_{1,272} = 1.94$ for males). Although no significant difference was detected between growth rates of the same sex at different study sites, growth rates of lizards from Paredon have a much greater variability than those from Laguna ($R^2 = 0.35$ for females and $R^2 = 0.46$ for males at Paredon, VS $R^2 = 0.71$ for females and $R^2 = 0.76$ for males at Laguna). Growth rates of adult individual lizards (SVL > 40 mm) were not significantly different between wet and dry seasons for both sexes and sites (Laguna: $F_{1,110} = 0.24$, $P > 0.05$, for females, and $F_{1,43} = 0.88$, $P > 0.05$, for males; Paredon: $F_{1,99} = 1.2$, $P > 0.05$, for females, and $F_{1,46} = 1.33$, $P > 0.05$, for males).

Mean asymptotic sizes for females were 49.5 mm (SVL) at Laguna and 49.9 mm (SVL) at Paredon. Mean asymptotic sizes for males were 52.6 mm (SVL) at Laguna and 53.8 mm (SVL) at Paredon (Fig. 2).

Comparisons of individuals of known ages with ages predicted by the von Bertalanffy model (Fig. 3), clearly demonstrate that this model is reliable for animals less than or equal to 1.5 years of age. Beyond this age, model predictions are very poor. There is considerable overlap in sizes among lizards between 1.5 and 4 years of age. Strict applicability of the model is limited to individuals 1.5 years old or younger. Age determination of lizards older than 1.5 years should be verified by mark-recapture techniques.

Body-size relationships: Within a given site, males and females did not differ in the relationship of mass to SVL ($P > 0.05$, $t = 0.257$, $N = 1932$ for Laguna, and $P > 0.05$, $t = 0.855$, $N = 1112$ for Paredon, for t test of log-transformed data). However, the relationship of

mass to SVL differed between sites for females ($P < 0.05$, $t = 2.13$) and for males ($P < 0.005$, $t = 2.95$), for t test of log transformed data. Individual lizards at Laguna were slightly but not significantly heavier than individual lizards at Paredon (average BM = 3.71 g for Laguna, and 3.61 g for Paredon). Low altitude (Laguna) lizards of both sexes are relatively more robust at all SVLs compared to high altitude (Paredon) lizards.

Factors affecting growth

Weather conditions: Average minimum temperatures $2.03^\circ\text{C} \pm 0.635$ and $2.24^\circ\text{C} \pm 0.601$ at Laguna and Paredon, respectively (Fig. 5) were not significantly different ($P > 0.05$, $F_{1,52} = 0.06$). Average maximum temperatures were higher at Laguna than at Paredon ($13.09^\circ\text{C} \pm 0.873$ vs. $5.69^\circ\text{C} \pm 0.509$, $P > 0.0001$, $F_{1,52} = 53.53$). The average difference between maximum and minimum temperatures at Laguna ($11.05^\circ\text{C} \pm 1.162$) was significantly greater than at Paredon ($3.45^\circ\text{C} \pm 0.574$; $F_{1,52} = 34.37$, $P < 0.0001$). Although lizards at Laguna face the same minimum temperatures as lizards at Paredon, the former face higher maximum temperatures. However, individual lizards at Paredon are able to maintain similar body temperatures as individual lizards at Laguna by using microhabitats with great insolation.

Prey availability: The volume of available insects was significantly greater at Laguna for all the months sampled except May (Table 2). In addition, insect volumes were greater in summer than in winter for both sites. The increase in insect availability at Laguna probably results from the higher temperatures and higher rainfall in summer. In addition, a greater variability in insects collected in the adhesive Tanglefoot™ traps was observed at Laguna than at Paredon. Arthropod orders at Laguna included Diptera, Coleoptera, Hymenoptera, Hemiptera, Dermaptera, and Lepidoptera, along with some arachnoidea. Arthropod

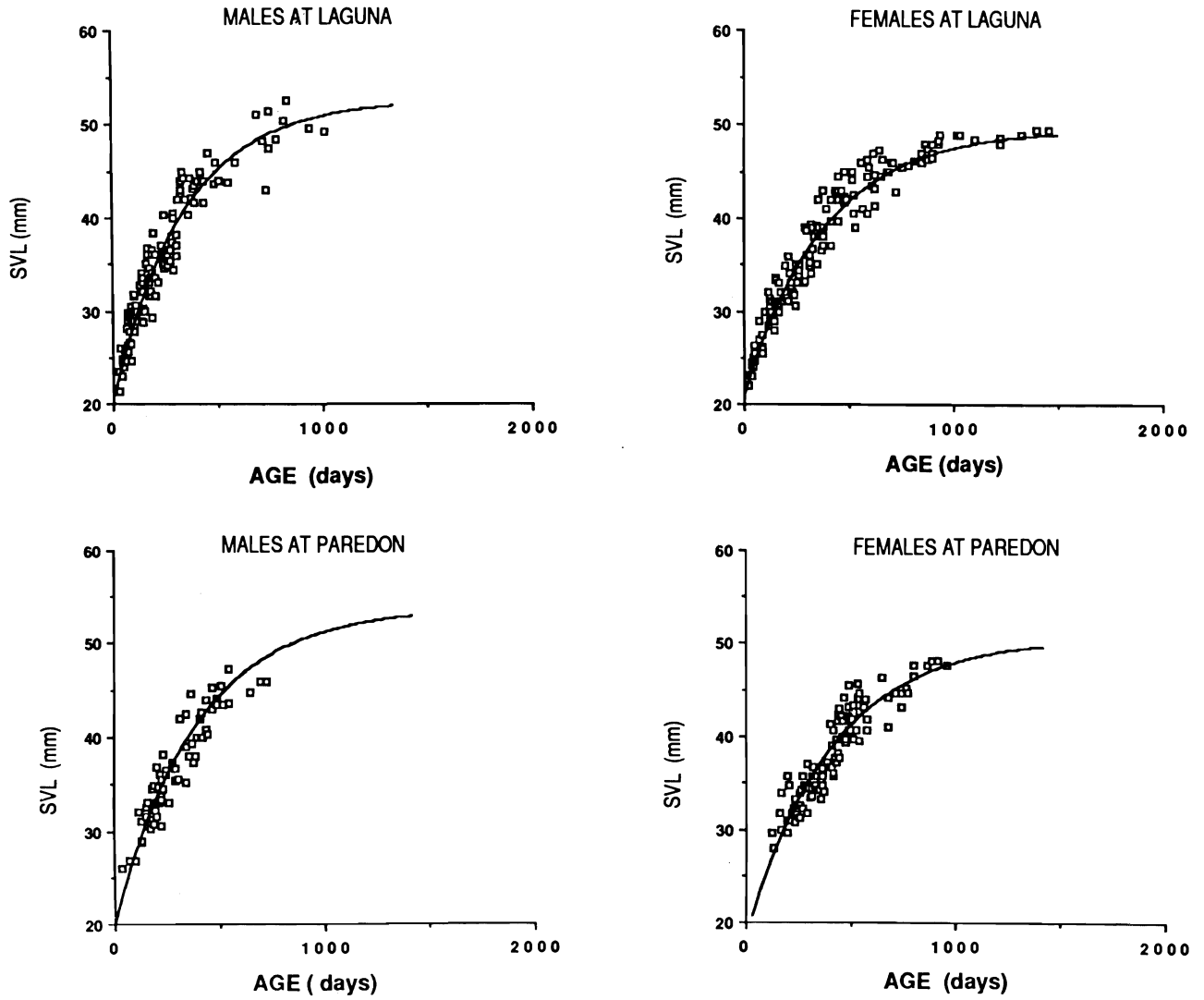


Figure 4. Size and age in *Sceloporus grammicus* for females and males at both study sites. Curves are the integral form for regression of all seasons in Table 1.

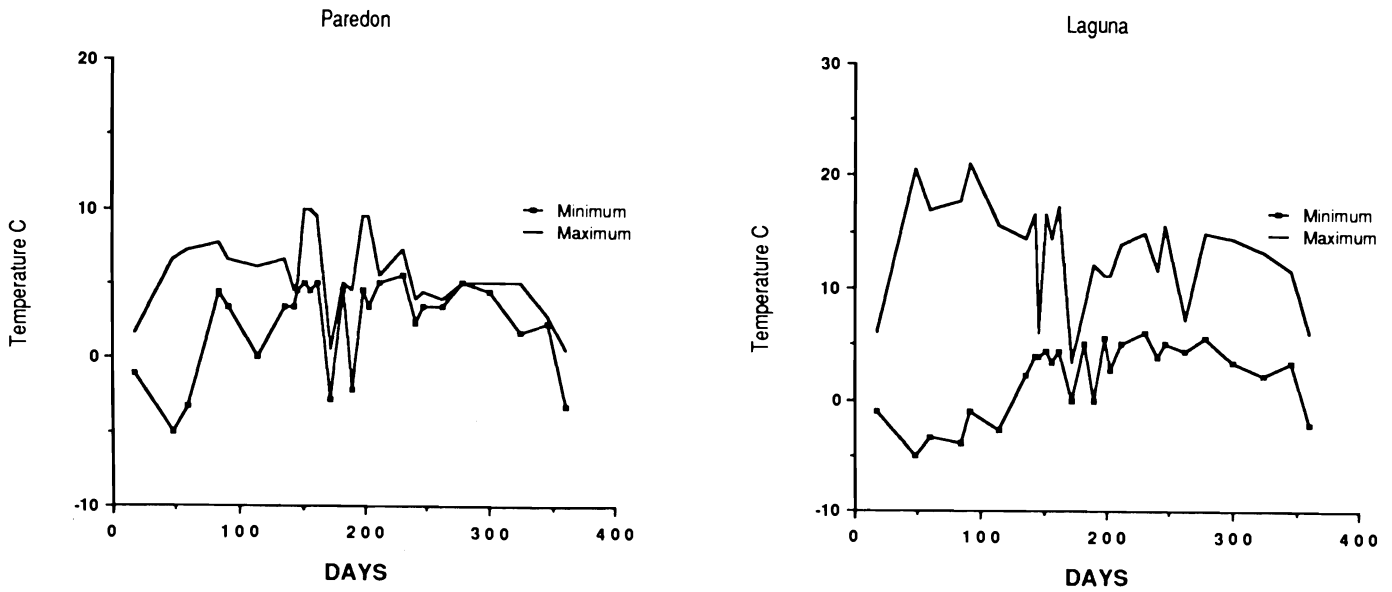


Figure 5. Variation of minimum and maximum temperatures at low (Laguna, 3,700 m) and high (Paredon, 4,400 m) altitude study sites on Iztaccihuatl Volcano, Puebla, México. X-axis in days from January to December (0 = January 1).

Table 3. Behaviors of *Sceloporus grammicus* during 30-min observation periods. Data are means \pm one SE. All data have units of number per 30-min except total distance which has units of m per 30-min. The term "5-min immobile" refers to the number of complete 5-min periods per 30-min observations during which no movement or behavior occurred. Based on 74 observation periods at Laguna (3,700 m in elevation) and 42 observation periods at Paredon (4,400 m in elevation), for summer (May, June, July, August 1991, 1992, 1993), and 15 observation periods at Laguna (3,700 m in elevation) and 17 observations periods at Paredon (4,400 m in elevation), for winter (December 1991, January, December 1992, and February 1993).

	Laguna		Paredon	
	Summer	Winter	Summer	Winter
Discrete movements	21.0 \pm 0.51	7.5 \pm 0.36	10.2 \pm 0.54	3.3 \pm 0.37
Total distance moved (m)	16.9 \pm 0.56	5.5 \pm 0.52	6.7 \pm 0.49	2.05 \pm 0.31
Feeding attempts	14.2 \pm 0.3	11.3 \pm 0.47	11.1 \pm 0.48	5.7 \pm 0.31
Displays	22.9 \pm 1.23	4.9 \pm 0.58	26.4 \pm 1.73	4.06 \pm 0.51
5 minutes immobile	0.14 \pm 0.04	1.2 \pm 0.11	1.14 \pm 0.06	2.18 \pm 0.2

orders at Paredon were Diptera, Coleoptera and Hymenoptera.

Lizard activity: In general, lizards at Laguna allocated more time to feeding and social interactions than lizards at Paredon (Table 3). Lizards at Paredon spent more time thermoregulating as reflected in the greater time spent immobile. There are significant differences in lizard activity patterns between summer and winter at each site. Summer activity patterns entailed more time spent in feeding and social interactions. These activities declined in winter with an increased amount of time spent thermoregulating. Increased thermoregulation in winter occurred at both high and low altitude sites. Thermoregulatory behavior by individual lizards at Paredon allowed similar active body temperature at both study sites (\bar{x} = 31.58°C \pm 0.11SE at Laguna, and 31.22°C \pm 0.16SE at Paredon, $F_{1,536} = 3.67$, $P > 0.05$), which may account for the similar growth rates.

DISCUSSION

Lizard food availability (insect abundance) is highly correlated with weather conditions, such as rainfall (Ballinger, 1977; Dunham, 1978). Grant and Dunham (1988, 1990) demonstrated that lizard growth rates are the result of interactions between food abundance, thermal environment and length of the growing season. Greater availability of insects at Laguna should result in greater growth if food availability limits growth, or in increased robustness. Heavier lizards at Laguna compared to Paredon might be the result of greater food availability combined with greater amounts of time spent in feeding activities.

The data obtained in this study suggest that populations living in different environments can attain similar growth patterns regardless of differences in food availability, time spent in feeding activities, social in-

teractions and thermoregulation, or differences in weather conditions as long as thermoregulatory opportunities allow maintenance of similar patterns of body temperatures. Some comparative studies in lizard growth rates have shown no differences in growth rates in populations of a species. Tinkle (1967) found similar growth rates of *Uta stansburiana* from Colorado and Texas. Grant and Dunham (1990) reported that individual growth rates for the desert lizard *Sceloporus merriami* did not differ significantly between populations at 560 m and 1609 m elevation at Big Bend National Park, Texas. However, growth rates of an intermediate population (1036 m elevation) were significantly higher than those for the two other populations because of longer activity periods (relative to the highest elevation site) and more insect availability (relative to the lowest elevation site). Walter (1991) demonstrated that growth rates of the lizard *Agama tuberculata*, of comparable age-size categories, were not significantly different between two sites at 690 m and 2215 m in elevation in the western Himalayas. However, all these studies demonstrated differences in age at maturity between populations living at different elevations due to a longer growing season in one of the sites. In contrast, *Sceloporus grammicus* populations in this study have similar ages at maturity (i.e. between 13 and 14 months; Lemos-Espinal 1992).

In spite of differences in patterns of food availability, time invested in feeding activities, social interactions, and thermoregulation, and differences in weather conditions, populations of *Sceloporus grammicus* at Laguna and Paredon had similar growth rates and body sizes. Several hypotheses may explain this similarity in growth. First, thermoregulation at Paredon may require lower energetic expenditure than at Laguna as there are no shaded areas. Lizards at this site can find a safe basking spot more easily than lizards at Laguna that live in a heavily shaded forest environment.

Moreover, individual lizards at Laguna deal with a greater number of possible competitors and predators. At Laguna *Sceloporus grammicus* coexist with another insectivorous lizard (*Sceloporus bicanthalis*), one frog (*Hyla plicata*), and 20 insectivorous birds which are potential competitors (Perez and Lemos-Espinal, 1988). In addition, possible predators of *Sceloporus grammicus* at Laguna include *Crotalus triseriatus*, *Thamnophis scalaris*, *Falco columbarius*, and *Falco sparverius*. On the other hand, at Paredon, there are no amphibians or other reptiles, and the only possible bird competitors that we observed were *Junco phaeonotus* and *Sialia mexicana*. Only one potential predator (*Falco sparverius*) occurs at Paredon. There is a greater probability of being eaten by a predator for individual lizards at Laguna than at Paredon, based on three indices of predation (tail-break frequency, flushing distance, and number of missed lizards per 24 hrs) (Lemos-Espinal, 1992). These combined data suggest that individual *Sceloporus grammicus* at Laguna face greater biotic interactions with predators and competitors than individuals at Paredon. Thus, even though maximum environmental temperatures are lower and food availability is reduced at Paredon, lizards at this site may suffer less interspecific competition and may spend less time avoiding predators than lizards at Laguna. As a result, lizards at both sites may be maintaining equivalent thermal conditions to enable similar growth rates at the two altitudes.

Another possibility is that the minimum amount of food required to attain the observed growth rate is present at Paredon and the additional food at Laguna represents an excess that cannot be put into individual growth. However, if this were the case, Laguna might be expected to support a denser population. This appears not to be the case (Lemos-Espinal, 1992).

The geographical position of our populations on Iztaccihuatl Volcano may be an important factor. Those comparative studies that have found differences in growth rates resulting from differences in the length of the growing season have been carried out at latitudes higher than 30° N (Grant and Dunham, 1988; 1990; Tinkle, 1967; Walter, 1991). The present study was conducted at 19° N, with a gradient of 700 m between sites, and with no significant differences between minimum temperatures. Perhaps populations living at these elevations do not experience sufficient differences to diverge in life history traits such as growth rates.

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