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COMPARATIVE LIFE HISTORY FOR POPULATIONS OF THE *SCELOPORUS GRAMMICUS* COMPLEX (SQUAMATA: PHRYNOSOMATIDAE)

Aurelio Ramírez-Bautista^{1,3}, Elsa Jiménez-Cruz¹, and Jonathon C. Marshall²

ABSTRACT.—A Teotihuacán population of the *Sceloporus grammicus* complex was compared with other previously studied populations (Parque Nacional Zoquiapan [PNZ], Monte Alegre Ajusco [MAA], Pedregal San Angel [PSA], Cantimplora [CA], Capulín, Laguna, Paredon, Michilia, and south Texas) for variations in several life history characteristics (SVL at sexual maturity, reproductive period, ovulation and gestation time, and litter size). Mean body size at sexual maturity of females from Teotihuacán was larger than PNZ, MAA, CA, and Capulín. Reproductive period (vitellogenesis, ovulation, gestation, and birth) for the Teotihuacán population was the shortest of all populations. In the Teotihuacán population, gestation time was similar to the Capulín and MAA populations but was shorter than all other populations except the Michilia population. Embryonic development at ovulation varied among populations, with Teotihuacán and Capulín showing earlier stages (stages 1) at ovulation than all other populations. Teotihuacán, PSA, PNZ, and Texas all showed similar litter size, which were larger than Laguna, Paredon, MAA, Capulín, and CA populations. Differences in reproductive characteristics of these populations could indicate phylogenetically constrained, reproductively isolated populations, or they may be explained as merely responses to different environments.

Key words: Reptilia, Squamata, Phrynosomatidae, *Sceloporus grammicus*, reproduction, México, chromosome races, polytypy.

In the last 3 decades, following contributions by Tinkle (1969), Tinkle et al. (1970), and Ferguson et al. (1980), several studies have documented variation in life histories, population dynamics, and demography both among lizard species (Ballinger 1973, Dunham 1980) and among populations of a single species (Ballinger 1979, Ferguson et al. 1980, Dunham 1982, Benabib 1994, Lemos-Espinal et al. 1998). Geographic variation of life history characteristics for some species has been studied extensively. Examples of such species include *Sceloporus undulatus* (Ferguson et al. 1980), *S. variabilis* (Benabib 1994), *S. grammicus* (Lemos-Espinal et al. 1998), *Urosaurus bicarinatus* (Ramírez-Bautista et al. 1995), and *U. ornatus* (Dunham 1982). Variations in the life histories found in these studies are possibly adaptations to different environmental pressures (local environments), but data about roles played by resource availability, predators, and climate on the regulation of populations at that time were nonexistent (Ferguson et al. 1980). Many studies of lizard life histories have attempted to obtain empirical data to test current hypotheses of life history evolution (Tinkle et al. 1970, Vitt

and Congdon 1978, Dunham 1982), but this approach is limited by the paucity of intraspecific studies.

Intraspecific studies on reproductive patterns have revealed geographic variation in life history characteristics such as clutch size, egg size, fecundity, and age at maturity among populations. Among congeners variation also exists in components of reproductive cycles, such as length of the reproductive season, litter size, gestation time (viviparous species), and snout-vent length (SVL) at sexual maturity (e.g., *S. variabilis* [Benabib 1994]; *S. grammicus* [Martínez 1985, Lemos-Espinal et al. 1998]; *S. jarrovi* [Goldberg 1971]). Variation in these reproductive characteristics might be related to environmental factors such as food availability (Ballinger 1977, Dunham 1982), duration of appropriate environmental conditions (Benabib 1994), or phylogenetic history (Dunham and Miles 1985).

Chromosome races of the *Sceloporus grammicus* complex inhabit a range of habitats across the Mexican Plateau (Fig. 1), from deserts to high-elevation mountain environments (Arévalo et al. 1991). The few populations that have

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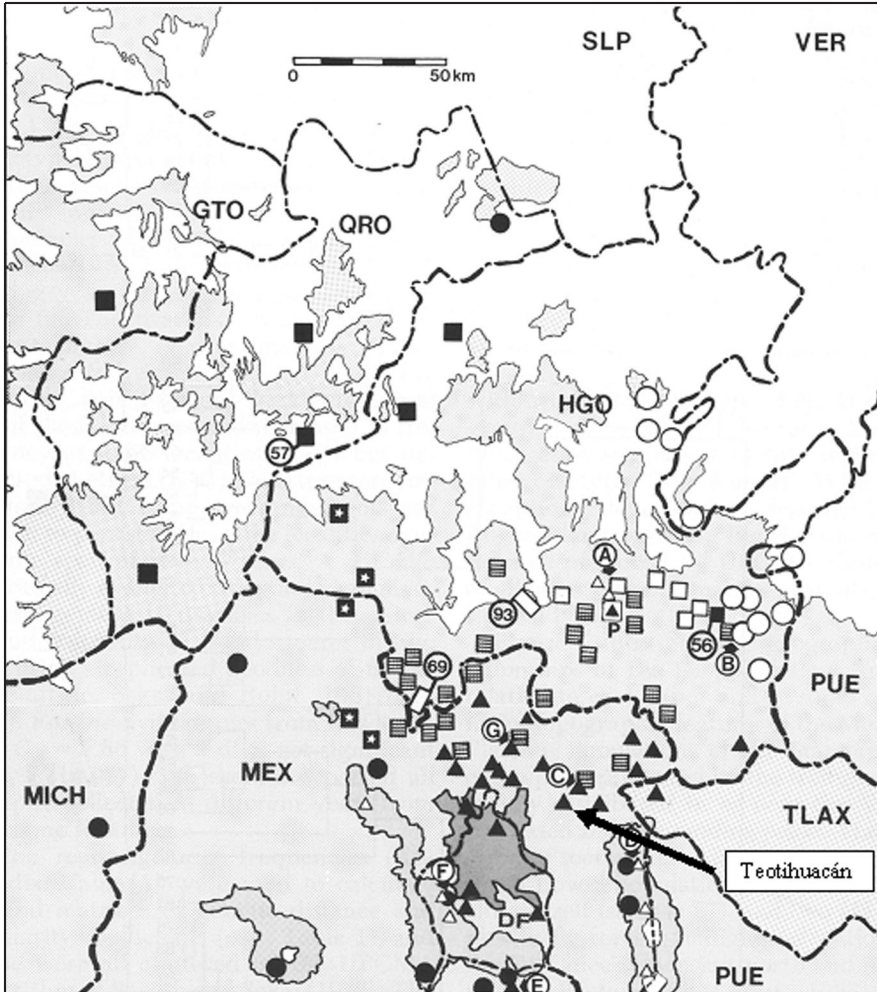


Fig. 1. Map of distribution range of 7 chromosomal races of the *S. grammicus* complex in central México (taken from Arévalo et al. 1991). Sample site used in our study (Teotihuacán) is indicated by the solid black arrow. In Arévalo et al. (1991), solid triangles = standard race, open triangles = high standard, solid circles = F6, open circles = F5, solid squares = F5+6, open squares = FM3, square with star embedded = FM1, and thatched square = FM2. Sites of questionable race status = open circle and locality number. Capital letters enclosed in circles show hybrid zones between certain races. Dark shading delimits México City; 2000-, 3000-, and 4000-m contours are identified by extensive gray shading, limited fine-grained gray, and white "island" volcanic peaks, respectively.

been studied all exhibit reproductive activity in which gametogenesis, courtship, and mating occur in the fall, and pregnancy proceeds over winter with parturition during the following early spring (Guillette and Casas-Andreu 1980, Lemos-Espinal et al. 1998). The objective of this study is to compare the reproductive characteristics of a new population, Teotihuacán, with other previously studied populations of the *Sceloporus grammicus* complex.

MATERIALS AND METHODS

Data from the Teotihuacán population were obtained between October 1984 and September 1985 at Santiago Tolman, Teotihuacán (19°41'N, 98°52'W), state of México, at an elevation of 2294 m. The climate of the area is seasonally temperate, with highest temperatures and rainfall occurring in summer. Mean annual precipitation is 559.6 mm, and vegetation type

is mesquite grassland and pine forest (Rzedowski 1978). Climatic and meteorological data for a 15-year period (1969–1984) were recorded at the Estación Meteorológica at San Martín de las Pirámides and at García (1981).

Monthly sample sizes from Teotihuacán were 6 to 10 females, although in some months (November and December) up to 14 adult females were collected. All adult lizards collected had an SVL large enough to indicate they were sexually mature (Ramírez-Bautista and Vitt 1997, 1998). We sampled 118 females, measuring snout-vent length to the nearest 0.1 mm. The smallest female (44.1 mm) showing vitellogenic follicles or embryos in the uterus was used as an estimation of the minimum size (in SVL) at sexual maturity (Ramírez-Bautista et al. 1995, 1996, 1998). Gonads and fat bodies of females were removed and weighed to the nearest 0.0001 g.

Clutch size was determined by counting embryos in the oviducts of adult females during the reproductive season. We calculated relative clutch mass (RCM; Vitt and Congdon 1978) as mass of embryos (embryonic stages from 34 to 40) / (females mass – clutch weight). We calculated a Pearson's product-moment correlation coefficient to test for a relationship between clutch size and SVL of females.

We compare these reproductive characteristics with other populations from the *S. grammicus* complex (sensu lato Sites 1993). Guillette and Casas-Andreu (1980) studied some reproductive characteristics of a population from PNZ (19°41'N, 98°42'W), state of México, in 1978–79. The pine woodland habitat at an elevation of 3200 m had an annual precipitation of 1169.3 mm. Ortega and Barbault (1984) performed a similar study from December 1980 to December 1981 for a population from Michilia (24°1'N, 104°40'W), Durango. This oak-pine forest habitat at 2480 m received an average of 576 mm of annual precipitation. Guillette and Bearce (1986) studied populations from southern Texas and the lowlands of Tamaulipas (26°4'N, 98°17'W) at an elevation of 38 m in an oak forest that received 423.8 mm of annual precipitation. Martínez (1985) studied 2 populations: Pedregal San Angel (PSA; 19°26'N, 99°81'W), Distrito Federal, where the habitat, an oak-pine forest at an elevation of 2400 m, had 840 mm of precipitation annually, and La Cantimplora (CA; 19°15'N, 99°11'W), in pine woodland at an elevation of

3300 m and an annual precipitation of 790.5 mm. Méndez-De la Cruz (1988) studied 2 populations: Monte Alegre Ajusco (MAA; 19°13'N, 99°17'W), at an elevation of 3200 m, and El Capulín (19°11'N, 99°19'W), at an elevation of 3400 m. Annual precipitation for both locations was 1340 mm, and habitat was pine forest. Lemos-Espinal et al. (1998) studied 2 populations: Laguna (3700 m) and El Paredón (4400 m), located in the Campo Experimental Forestal San Juan Tetla (19°10'N, 98°36'W), state of México; the pine forest habitat had 1187.5 mm of annual precipitation. Table 1 summarizes habitat data for each location.

Where possible, populations (Table 2) were assigned to a chromosomal race according to criteria established by Sites and Davis (1989), Sites (1993), and Arévalo et al. (1991, 1993). The species *Sceloporus anahuacus* and *S. palaciosi* are based on the Lara-Góngora (1983) description, although further study is needed to firmly establish species rank for each.

RESULTS

Variation in Climate

Teotihuacán and localities of 9 populations compared in this study differ dramatically in amount and variability of annual precipitation (Table 1). Over 82% of mean annual precipitation falls in the 6 months (May–October) during which 5 populations of *S. grammicus* (Teotihuacán, Michilia, Texas, PSA, and CA) are in reproductive activity. However, other populations (PNZ, MAA, Capulín, Laguna, and Paredon) receive greater average annual precipitation as their seasonal distribution of rainfall is more extended (April–October; García 1981).

Snout-Vent Length at Sexual Maturity

Mean body sizes of sexually mature females differed greatly between populations (ANOVA; $F_{5,295} = 45.08$, $P < 0.005$; Table 2). Female body size from the Teotihuacán population was larger than that from PNZ, MAA, CA, Capulín, and PSA, but the PSA populations showed similar size ($P > 0.05$). Snout-vent length at sexual maturity was larger at PSA than at Laguna, Paredon, Michilia, PNZ, MAA, Capulín, and CA (Table 2).

Reproductive Traits

Reproductive activity (vitellogenesis, ovulation, gestation time, and birth) varied among

TABLE 1. General habitat description including average annual precipitation and temperature for 10 localities sampled for reproductive studies of the *S. grammicus* complex. PNZ (Parque Nacional Zoquiapan), MAA (Monte Alegre, Ajusco), PSA (Pedregal San Angel), and CA (Cantimplora) data were taken from García (1981; data for a 15-year period).

	Laguna	Paredon	Michilita	S. Texas	PNZ	MAA	Capulín	PSA	CA	Teotihuacán
Altitude (m)	3700	4400	2480	—	2000–3200	3200	3400	2400	3300	2200
Plant community	Pine	Pine	Oak/Pine	Oak	Pine	Pine	Pine	Oak/Pine	Pine	Mesquite grassland/Pine
Precipitation (mm)	1187.5	1187.5	576	423.8	1169.3	1340	1340	840	790.5	559.6
Temperature (°C)	13.1	13.1	17.4	23.3	11.1	12.0	12.0	15.1	12.0	14.8

TABLE 2. Reproductive characteristics from different female populations of the *S. grammicus* complex: SVL MMS = snout-vent length minimum and maximum at sexual maturity; N = sample size. Chromosomal races are given with each population and are based on ranges established by Sites and Davis (1989), and Arévalo et al (1991, 1993), HS (high-elevation standard, 2n = 32, *S. anahuacas*), S (standard, 2n = 32, *S. grammicus*), F6 (fixed fission of metacentric chromosome 6, 2n = 34, *S. palaciosi*), F5+6 (fixed fissions in chromosome 5 and 6, 2n = 36, *S. g. disparilis*). Mean is followed by $\pm 1 s_x$.

Population	Laguna ¹ (HS)	Paredon ¹ (HS)	Michilita ² (S)	S. Texas ³ (F5+6)	PNZ ⁴ (F6)	MAA ⁵ (HS)	Capulín ⁵ (HS)	PSA ⁶ (S)	CA ⁶ (S)	Teotihuacán ⁷ (S)
Vitellogenesis	Aug–Sept	Aug–Sept	Aug–Dec	Jul–Sept	Jul–Sept	Jul–Sept	Jul–Sept	May–Aug	May–Jul	Oct–Nov
Ovulation	Oct	Oct	Jan	Oct–Nov	Sept	Oct–Nov	Oct–Nov	Sept	Sept	Nov
Gestation time	Oct–May	Oct–May	Jan–May	Nov–May	Sept–May	Nov–April	Nov–April	Sept–April	Oct–May	Nov–April
Litter size	3.64 ± 0.09	3.31 ± 0.13	6.2 ± 1.7	5.4 ± 0.06	5.2 ± 0.25	3.51 ± 0.16	3.72 ± 0.14	5.3 ± 0.19	3.7 ± 0.17	5.09 ± 0.24
Range	2–5	2–4	3–9	3–7	3–7	2–6	2–6	2–11	2–6	2–9
SVL (mm)	—	—	—	—	48.5 ± 0.07	48.8 ± 0.61	44.5 ± 0.6	53.04 ± 0.55	45.01 ± 0.32	55.2 ± 0.45
SVL MMS	39–52	39.2–50	44–60	—	42.3–61.2	37.9–54	38.6–50	40–62	34–55	44.1–72.3
N	67	54	46	21	48	54	60	24	26	62

¹Lemos-Espinal et al. 1998

²Ortega and Barbañt 1984

³Guillette and Bearce 1986

⁴Guillette and Casas-Andreu 1980

⁵Méndez-De la Cruz 1988

⁶Martínez 1985

⁷This study

these 10 populations of the *S. grammicus* complex. The Teotihuacán population showed a shorter reproductive period (7 months, October–April; Table 2) than Laguna, Paredon, and Michilia (10 months, August–May), MAA (10 months, July–April), Texas and PNZ (11 months, July–April), PSA (12 months, May–April), and CA (13 months, May–May). Gestation times from Teotihuacán (6 months), Capulín (6 months), Michilia (5 months), and MAA (6 months) populations were all shorter than Texas (7 months), Laguna, Paredon, PSA, and CA (all 8 months), and PNZ (9 months) populations.

Embryonic Development at Ovulation

Developmental stages of eggs at ovulation varied among populations. At Teotihuacán egg development varied from stage 1 to stage 8 (ovulation occurred in November), at Michilia all eggs were at stage 4 (ovulation in January), at Texas, stage 12 (November), at PZN, stage 2 (September), at MAA eggs were either in stage 2 or 3 (November), at El Capulín eggs varied from stage 1 to 4 (November), and at PSA and CA eggs showed stage 5 development (September). Snout-vent length at birth was measured in only 3 populations; for the Teotihuacán population it ranged from 18.0 mm to 22.0 mm, and for both Paredon and Laguna populations SVL at birth ranged from 19.0 mm to 20.0 mm.

Litter Size

Litter size differed significantly among populations (ANOVA; $F_{9,295} = 54.8$, $P < 0.001$). Multiple comparisons revealed that mean litter size for Teotihuacán, PSA, PZN, and Texas populations did not vary significantly ($F_{1,155} = 2.32$, $P > 0.05$; Table 2), but these populations showed larger litter size than Laguna, Paredon, MAA, Capulín, and CA ($F_{8,249} = 23.5$, $P < 0.001$). Largest litter size was from the Michilia population (6.2 ± 1.7 ; $P < 0.05$). However, litter size was significantly correlated with SVL in some populations such as Teotihuacán ($r = 0.78$, $P < 0.001$), PNZ ($r = 0.68$, $P < 0.001$; Guillette and Casas-Andreu 1980), Michilia ($r = 0.88$, $P < 0.01$; Ortega and Barbault 1984), Texas ($r = 0.78$, $P < 0.001$; Guillette and Bearce 1986), MAA ($r = 0.62$, $P < 0.05$; Méndez-De la Cruz 1988), Capulín ($r =$

0.76 , $P < 0.05$; Méndez-De la Cruz 1988), Laguna ($r = 0.85$, $P < 0.0001$; Lemos-Espinal et al. 1998), and Paredon ($r = 0.89$, $P < 0.001$; Lemos-Espinal et al. 1998). This pattern indicates that litter size is proportional to maternal body size in all populations.

Fat Body Cycle

The Teotihuacán and Texas populations were the only studies used to analyze reproductive activity with fat body cycle in females. Reproductive cycle of females from the Teotihuacán population did not show any relationship between \log_{10} gonadal mass and \log_{10} fat body mass ($R^2 = 0.016$, $F_{1,117} = 1.83$, $P > 0.05$), and a similar pattern is shown in the Texas population (Guillette and Bearce 1986).

Relative clutch mass was measured only from the Teotihuacán population, and it was 0.338 ± 0.024 (0.015 – 0.80; $N = 57$). Relative clutch mass was correlated with female SVL ($r = 0.449$, $F_{1,55} = 13.88$, $P < 0.0005$), and there was significant variation in RCM among months (ANOVA; $F_{5,55} = 17.28$, $P < 0.0001$). Females exhibited an RCM during November ($\bar{x} = 0.162 \pm 0.021$, $N = 13$) and December ($\bar{x} = 0.233 \pm 0.025$, $N = 11$) lower than following months, which increased significantly from January ($\bar{x} = 0.360 \pm 0.037$, $N = 10$) to April ($\bar{x} = 0.555 \pm 0.061$, $N = 4$; $P < 0.0001$).

DISCUSSION

Reproduction in the *S. grammicus* complex females (sensu Sites 1993) is characterized by viviparous fall reproductive activity (Guillette and Casas-Andreu 1980, Ortega and Barbault 1984). This type of reproductive cycle is similar to other viviparous temperate zone species at high elevations, such as *S. bicanthalis* (Guillette 1982), *Barisia imbricata* (Guillette and Casas-Andreu 1987), *B. monticola* (Vial and Stuart 1985), *Eumeces copei* (Guillette 1983, Ramírez-Bautista et al. 1996), and *E. lynx* (Ramírez-Bautista et al. 1998). However, fall reproduction is also known to occur in lowland species, such as *Gerrhonotus liocephalus* (Flury 1949), *Eumeces egregius* (Mount 1963), *Sceloporus cyanogenys* (Crisp 1964), *S. poinsetti* (Ballinger 1973), *S. grammicus* (Ortega and Barbault 1984), *S. grammicus disparilis* (Guillette and Bearce 1986), and *S. jarrovi* (Ramírez-Bautista et al. 2002). These data suggest that fall reproduction could be an adaptation to factors other

than high elevation (Guillette and Casas-Andreu 1980, 1987, Guillette 1982, Guillette and Bearce 1986).

Fall reproduction occurs at both low and high elevation in several species within different generic lineages, such as *Sceloporus* (Phrynosomatidae), *Barisia* (Anguidae), and *Eumeces* (Scincidae). Within each of these species, groups inhabiting mountain habitats of México have independently evolved a similar set of reproductive characteristics (Guillette and Casas-Andreu 1980, Guillette and Bearce 1986, Ramírez-Bautista et al. 1998). The advantage of a fall reproductive strategy is the production of young at a time when resources are abundant (spring), which is particularly advantageous in environments (temperate and tropical zones where this type of reproduction occurs) with short growing seasons (Guillette 1983).

Snout-Vent Length at Sexual Maturity

Life history characteristics of *S. grammicus* from Teotihuacán vary from those of populations previously studied from different environments (Table 2). Mean SVL at sexual maturity for females from Teotihuacán was larger than for other populations (Table 2). These data could be related to time available for growth before reaching sexual maturity or different growth rates and food availability or both (Ballinger 1977, 1979, Ramírez-Bautista and Vitt 1997).

Gestation times for Teotihuacán and Michilia populations (November–April and January–May, respectively) were as short as or shorter than gestation in all other populations (Table 2). Parturition occurs in April and reproduction begins in October for Teotihuacán. These data indicate that females reach sexual maturity at age 7 months for Teotihuacán and 8 months for Michilia. These data also suggest that females from these populations have more time to grow, reaching sexual maturity at a larger size than populations in other species (Smith et al. 1994). However, even though the Teotihuacán population has the largest SVL at maturity and long growth period before maturity, this trend is not supported by comparisons with other populations in our study. For instance, PSA has the 2nd largest SVL but has nearly the shortest growth period.

Females of *S. jarrovi* from low-altitude populations grow faster than females from high-

altitude populations (Smith et al. 1994). This pattern could correspond to the Teotihuacán population, because it is the lower-altitude locality (Table 1). Larger females from the Teotihuacán population might be the result of greater food availability and/or a greater amount of time spent in feeding (reproductive activity [vitellogenesis] is later in Teotihuacán than in other populations). However, growth rates of *S. grammicus* from different environments (Laguna and Paredon) were similar regardless of food availability and environmental temperature (Lemos-Espinal and Ballinger 1995). Although growth rates in lizard species have been correlated with food, precipitation, and temperature of the environment, for the Teotihuacán and other populations additional factors appear to influence SVL at sexual maturity. Although precipitation (559.6 mm) and temperature (14.8°C) from Teotihuacán are low, the area nevertheless has resources (insects) as abundant as or more abundant than in all other areas (Table 1).

Reproductive Traits

This study indicates a marked difference in reproductive activity between the Teotihuacán and other populations. For example, reproductive period was shorter at Teotihuacán than at any other population. While gestation time was similar to that of other populations such as El Capulín, Michilia, and MAA, it was shorter than Texas, Laguna, Paredon, PSA, CA, and PZN. Developmental stages of eggs at ovulation also varied among populations; for example, in Teotihuacán and Capulín females ovulation occurs at an earlier stage (stage 1) than in the other populations. Variation in these characteristics among populations might be explained by the major influence of the environment, as occurs in other lizard species (Ballinger 1979, Dunham 1980, Ferguson et al. 1980, Ramírez-Bautista et al. 1995). Shorter reproductive period (vitellogenesis, ovulation, and gestation time) for the Teotihuacán population could be explained by the following: (1) length of the vegetative growing season may be shorter since precipitation is lower than in other populations with longer reproductive period (Table 1), and/or (2) late reproduction (vitellogenesis: October–November) would allow lizards more time for growing, and they could have larger body size at sexual maturity (as occurs in this population). Cost of a shortened reproductive period may

be small compared with the advantage gained by a longer growth period and larger SVL at maturity in the Teotihuacán environment.

Litter size varied among populations and increased with female body size at all localities (Guillette and Casas-Andreu 1980, Ortega and Barbault 1984, Guillette and Bearce 1986, Lemos-Espinal et al. 1998). This phenomenon is characteristic of many phrynosomatids such as *Urosaurus bicarinatus* (Ramírez-Bautista et al. 1995), *U.* (Dunham 1982), *S. spinosus* and *S. horridus* (Valdéz-Gonzalez and Ramírez-Bautista 2002), *S. jarrovi* (Ballinger 1973), and *S. variabilis* (Benabib 1994). Variation in litter size among localities could be explained by among-sites variation in densities and survivorship; for example, litter size from Michilia was higher (6.2 ± 1.7) than that of Laguna (3.64 ± 0.09) and Paredon (3.31 ± 0.13), whereas densities of these populations were 42 adult individuals \cdot ha $^{-1}$, 74 individuals \cdot ha $^{-1}$, and 146 individuals \cdot ha $^{-1}$, respectively (Lemos-Espinal et al. 1998, Ortega et al. 1999).

We could not compare the RCM for the Teotihuacán population because no previous study has been carried out in other populations. This study showed that values of RCM increased with an increase in embryonic development. Vitt and Price (1982) tested differences in RCM between phrynosomatid and teiid lizards and found that in *Sceloporus*, RCM is higher ($\bar{x} = 0.256 \pm 0.009$) than in *Cnemidophorus* ($\bar{x} = 0.148 \pm 0.006$) species. RCM for *S. grammicus* prior to birth ranged from 0.360 (January) to 0.555 (April); this pattern is similar to that of other species such as *S. jarrovi* (0.150–0.388 [Parker 1973]; 0.138–0.468 [Ramírez-Bautista et al. 2002]).

In comparing life history traits with chromosome races, we note some general trends. First, some populations that belong to the same chromosome race (Laguna, Paredon, and El Capulín in the HS race) show similar life history characteristics; however, PSA (also an HS) does not (Table 2). In other populations of the chromosomes races S, F6, F5+6 (Michilia, Cantimplora, Teotihuacán, Parque Nacional Zoquiapan, Monte Alegre Ajusco, and south Texas), life history trait similarity did not seem to group according to chromosome race (Table 2). The small sampling of populations and the absence of a rigorous testing (i.e., principal components analysis) are cause for care in interpretation of the above data. If these trends

do prove valid, they might be explained by the HS race showing similar life history characteristics due to the evolutionary history of that race, and the smaller differences (vitellogenesis and gestation time) could be a local adaptation. The other populations (chromosomes races S, F6, F6+6) vary in life history characteristics; these differences could be a complex of local adaptation tending toward evolutionary divergence (i.e., genetic differences between populations). Again, more in-depth analysis is needed to determine whether life history traits among populations are due to phylogenetic constraint or local adaptation and which environmental factor(s) are exerting the greatest influence. Such an analysis was not possible for the above study, because data for each individual were available only for the Teotihuacán population. This study provides a very general comparison of life history traits between populations and at the same time gives an in-depth description of life history traits for a new population.

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