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EFFECTS OF ELEVATION ON LITTER-SIZE VARIATION AMONG LIZARD POPULATIONS IN THE *SCELOPORUS GRAMMICUS* COMPLEX (PHRYNOSOMATIDAE) IN MEXICO

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ABSTRACT.—We examined the effect of elevation on litter-size variation in viviparous lizards of the *Sceloporus grammicus* complex in 10 states of Mexico. Female snout–vent length (SVL) decreased with increasing elevation, and absolute litter size based on embryos also tended to decrease with increasing elevation. However, after controlling for variation in female body size, we found that litter sizes tended to be relatively larger at higher elevation. Elevation therefore appears to influence litter size in these lizards; however, relatively little of the variation is explained by elevation; thus, other factors are likely making substantial contributions to the observed litter-size variation. The *S. grammicus* complex appears to be a good model system for examining the underlying causes of geographic and elevational variation in lizard life histories.

RESUMEN.—Examinamos el efecto del altitud en la variación del tamaño de camada de las lagartijas vivíparas del complejo *Sceloporus grammicus* en 10 estados de México. La LHC de las hembras disminuyó con la altitud, y el tamaño absoluto de camada, calculado con base en el número de embriones, también tendió a disminuir. No obstante, después de controlar la variación en el tamaño corporal de las hembras, encontramos que los tamaños de camada tendieron a ser relativamente más grandes en altitudes mayores. La altitud, por tanto, parece influir en el tamaño de camada de estas lagartijas; sin embargo, la altitud explica relativamente poco de la variación, por lo que, es probable que otros factores contribuyan substancialmente a la variación observada en el tamaño de camada. El complejo *S. grammicus* parece ser un buen sistema para estudiar las causas fundamentales de la variación geográfica y altitudinal en la historia de vida de las lagartijas.

Intraspecific studies among many populations of lizards have revealed geographic variation in life history characteristics, such as litter size, and age and size at maturity (Tinkle and Ballinger 1972, Howland 1992, Niewiarowski 2001). Elevation can play an important role in determining intraspecific life history variation in lizards (Ballinger 1979, Grant and Dunham 1990, Adolph and Porter 1993, 1996, Ballinger et al. 1996, Sears 2005). Previous studies of a variety of lizard species have found apparent elevational effects on litter or clutch size; the litter or clutch sizes have both been shown to increase or decrease with elevation depending on the species (Rocha et al. 2002, Smith et al. 2003, Jin and Liu 2007, Rojas-González et al. 2008). However, most of these studies compare only one pair or just a few populations from each elevation.

We examined elevational effects on litter-size variation in several populations within the *Sceloporus grammicus* complex. Previous studies have examined intraspecific variation in life history traits of *S. grammicus;* however, these studies either examined high-elevation populations only (Lemos-Espinal et al. 1998) or did not explicitly examine elevational variation (Ramírez-Bautista et al. 2004). We predict a decrease in litter size as elevation increases (i.e., one can speak of an optimization of litter size correlated with snout–vent length of females; Ramirez-Bautista et al. 2006, Hernández-Salinas et al. 2010). This relationship may result from the different environments in which these lizards occur. One possible explanation for these reproductive traits in the environments which *S. grammicus* inhabits stems from life history evolutionary theory based on *r* strategy, which could be supported because *S. grammicus* does invade (colonize) new habitats in its range (Morales 1988).

Our data were compiled from unkaryotyped museum samples; therefore, all individuals were simply taken to be members of the *S. grammicus* complex rather than assigned to a chromosome race, subspecies, or species. Given the apparent close phylogenetic relationships and the nebulous species boundaries between groups within this species complex (Arévalo et al. 1991, Marshall et al. 2006), we feel that our comparison of litter sizes is appropriate for examination of the potential role of elevation in

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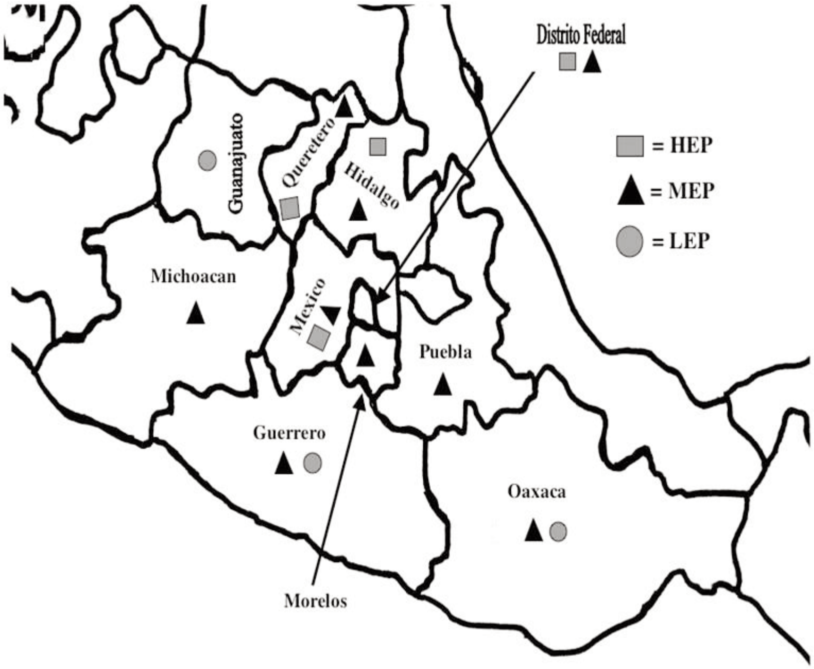

Fig. 1. Map of Central Mexico showing localities where samples were collected. Samples were pooled and categorized by political state boundaries and elevation: HEP = high-elevation population, MEP = medium-elevation population, and LEP = low-elevation population.

explaining litter-size variation in these lizards (i.e., the confounding effects of phylogenetic constraints should be minimal compared to the proximate variation or local adaptation).

STUDY AREA

We conducted our study of populations belonging to the *Sceloporus grammicus* complex in 30 localities (Table 1) from 10 states of Mexico (Puebla [PUE], Distrito Federal [DF], Estado de México [EDOMEX], Querétaro [QRO], Hidalgo [HGO], Morelos [MOR], Guanajuato [GTO], Michoacán [MICH], Oaxaca [OAX], and Guerrero [GRO]; Table 1). Populations were pooled based on their elevation, (1) high-elevation populations (HEPs; 2800–3420 m; EDOMEX, QRO, and DF); (2) medium-elevation populations (MEPs; 2000–2700 m; OAX, HGO, DF, and EDOMEX); and (3) low-elevation populations (LEPs; 1000–1875 m, PUE, GTO, GRO, MOR, MICH, and OAX; Fig. 1, Table 1).

General vegetation type was oak-pine forest for HEPs; oak-pine, pine, scrub, and xerophytic and tropical forest for MEPs; and pine, scrub, and xerophytic and tropical forest for LEPs (Rzedowski 1978; Table 1). The climate of the localities where specimens were collected varied according to vegetation type and altitude (Table 1). Mean annual precipitation ranged from 683.7 to 820.7 mm in low-elevation sites (30 years), 454.0 to 1041.2 mm in medium-elevation sites (37 years), and 859.3 to 1892.6 mm in high-elevation sites (13 years) (García 1981).

METHODS

Females analyzed in this study were taken from the Colección Nacional de Anfibios y Reptiles (CNAR) and the Colección de Anfibios y Reptiles del Museo de Zoología de la Facultad de Ciencias (MZFC) of the Universidad Nacional Autónoma de México (UNAM). Specimens were collected in the years 1975–1995. We organized adult females (n = 215) and neonates (n = 170) by state and elevation groups (HEP, MEP, and LEP; Fig. 1). For each female we used a caliper to measure snout–vent length (SVL) to the nearest 0.1 mm. In addition, we recorded the number of embryos in each oviduct (or uterus; Ramírez-Bautista et

TABLE 1. Environmental characteristics of the study localities: state, elevation category (HEP = high-elevation population; MEP = medium-elevation population; LEP = low-elevation population), vegetation type, altitude, climate, and coordinates. BJ = Benito Juárez, GAM = Gustavo A. Madero, SM = Santuario Mapethé, OJ = Omitlán de Juárez, NCP = Northeast Pachuca City, PNEC = Parque Nacional El Chico, SPY = San Pedro Yolox, SC = Santiago Comaltepec, NDM = Nejapa de Madero, SCT = Santa Cruz Tepototutla, NCO = Northeast Oaxaca City.

Locality	State	Altitude (masl)	Elevation category	Vegetation type	Climate	Latitude	Longitude
Ajusco	DF	3200	HEP	pine-oak	temperate	19°15′30″	99°19′26″
Capulin	EDOMEX	3090	HEP	pine-oak	temperate	19°30′27″	99°16′30″
no data	QRO	2800	HEP	no data	no data	no data	no data
BJ	DF	2300	MEP	xerophytic, pine	temperate	19°25′02″	99°10′05″
Coyoacan	DF	2300	MEP	xerophytic, pine	temperate	19°20′56″	98°09′59″
GAM	DF	2350	MEP	scrub, xerophytic, pine	temperate	19°25′02″	99°10′05″
Iztapalapa	DF	2400	MEP	xerophytic, pine	temperate	19°21′30″	99°05′38″
Tlalpan	EDOMEX	2700	MEP	xerophytic, pine, oak	temperate	19°30′04″	99°06′41″
Teotihuacán	EDOMEX	2294	MEP	xerophytic, pine, oak	temperate	19°41′10″	98°54′09″
Chignaupan	PUE	2209	MEP	pine-oak	subhumid	19°50′17″	98°01′72″
Ajacuba	HGO	2000	MEP	scrub, xerophytic	semidry	20°05′32″	99°07′24″
Apulco	HGO	2207	MEP	scrub, xerophytic, pine	temperate	20°21′32″	98°21′55″
Tulancingo	HGO	2256	MEP	scrub, xerophytic, pine	temperate	20°05′20″	98°23′19″
Pachuca	HGO	2370	MEP	scrub, xerophytic	temperate	20°06′59″	98°48′01″
SM	HGO	2410	MEP	scrub, xerophytic, pine	temperate	20°38′40″	99°07′28″
OJ	HGO	2500	MEP	pine-oak	temperate	20°10′11″	98°38′31″
NCP	HGO	2600	MEP	scrub, xerophytic	temperate	20°54′28″	99°11′33″
PNEC	HGO	2700	MEP	pine-oak	temperate	20°08′20″	98°41′34″
Tetipac	GRO	2000	MEP	tropical forest	subhumid	18°38′29″	99°42′20″
SPY	OAX	2025	MEP	tropical forest, pine	humid	17°31′57″	96°33′25″
SC	OAX	2200	MEP	tropical forest, pine	humid	17°33′50″	96°32′27″
Oaxaca	OAX	2500	MEP	tropical forest, pine	humid	no data	no data
NDM	OAX	2600	MEP	tropical forest	humid	16°34′31″	95°47′46″
Teocelo	MOR	2500	MEP	no data	no data	no data	no data
no data	MICH	2500	MEP	no data	no data	no data	no data
Chilpancingo	GRO	1360	LEP	tropical forest, scrub	subhumid	17°33′07″	99°30′23″
Taxco	GRO	1735	LEP	tropical forest	subhumid	18°33′05″	99°35′58″
SCT	OAX	1875	LEP	tropical forest	subhumid	17°44′49″	96°37′33″
NCO	OAX	1563	LEP	tropical forest, pine	subhumid	17°06′23″	96°12′31″
Xichú	GTO	1700	LEP	scrub, pine, xerophytic	temperate	21°17′53″	100°01′43″

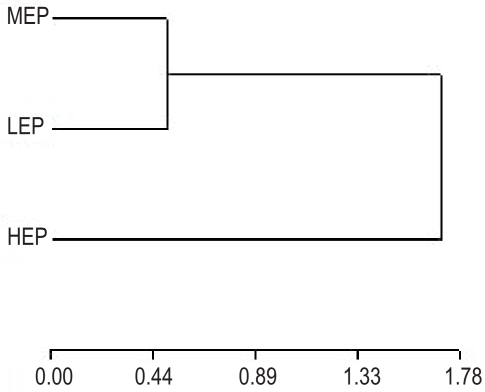

Fig. 2. Cluster analysis showing populations grouped by elevation: HEP = high-elevation population, MEP = medium-elevation population, and LEP = low-elevation population.

al. 2004, Hernández-Salinas et al. 2010) and the elevation where each individual was collected.

We used ANOVA to analyze the variation of female SVL among population groups. An ANCOVA was also performed using female SVL as a covariate, litter size as the dependent variable, and elevation group as the independent variable. Correlation analysis was used to determine how litter size was related to female SVL in all groups (based on elevation). In addition, we performed a similarity analysis (cluster analysis) to see how the elevation groups (elevation) clustered in relation to litter size and female SVL. We performed a post hoc Tukey's HSD test to compare neonate SVL (n = 170 from 6 populations) among elevation groups.

Finally, we used linear regression to examine the relationship between elevation and female SVL and between elevation and litter size. Because litter size can be affected by female SVL, we used the residuals (of the litter size on female SVL regression) in another regression with elevation to examine the relationship independent of body size effects. Standard parametric statistical tests were used whenever assumptions were met. Statistical analyses were performed with Infostat 1.1.

RESULTS

Female body size differed among elevation groups ($F_{2,212} = 32$, $P < 0.001$). Mean SVL of females was lower in HEPs (49.1 mm, SE = 0.77, range 37.0–58.0, n = 39) than in MEPs (55 mm, SE = 0.50, range 40.0–69.0, n = 155) and LEPs (57.4 mm, SE = 1.07, range 46.0–68.0, n = 25).

A similarity analysis with SVL and litter size among elevation groups showed 2 groups: (1) HEP females with smaller SVL and litter size and (2) MEP and LEP females with larger SVL and litter size (Fig. 2). In addition, a similarity analysis among populations (30 localities in 10 states) generated 6 different groups. The first corresponded to the population from Guanajuato (GTO-LEP); the second included Querétaro and Michoacán populations (QRO-HEP and MICH-MEP); the third included Puebla, Oaxaca, and Morelos populations (PUE-MEP, OAX-LEP, OAX-MEP, and MOR-MEP); the fourth included Hidalgo populations (HGO-MEP); the fifth included both medium- and high-elevation populations of the Estado de México (EDOMEX); and the last group included Guerrero and Distrito Federal populations (GRO-LEP, GRO-MEP, DF-MEP, and DF-HEP; see Table 1 for localities and elevation categories for each state).

Snout–vent length of neonates at birth varied among elevation groups (ANOVA: $F_{2,167} = 23.51$, $P = 0.001$). Mean SVL for HEPs was lower (23.0 mm, SE = 0.45, range 15.0–32.0, n = 125) than that of LEPs (29.8 mm, SE = 0.64, range 24.0–32.0, n = 15) and MEPs (27.7 mm, SE = 0.64, range 19.0–32.0, n = 30). A Tukey's HSD test showed that SVL of neonates differed between HEPs and LEPs ($P = 0.001$) and between HEPs and MEPs ($P = 0.01$), but not between LEPs and MEPs ($P > 0.05$). SVL of offspring from EDOMEX-HEP (19.9 mm, SE = 0.43, range 15–30, n = 72) was smaller than SVL of offspring from DF-MEP (27.2 mm, SE = 1.08, range 19.8–32, n = 10) and DF-HEP (27.2 mm, SE = 0.43, range 21–32, n = 53) populations. However, the larger SVLs were from GTO-LEP (29.8 mm, SE = 0.64, range 25–32, n = 15), MOR-MEP (29.1 mm, SE = 0.56, range 26–32, n = 11), and HGO-MEP (29 mm, SE = 1.28, range 22–32, n = 9) populations (Fig. 1).

Litter size was correlated with female SVL from HEPs ($r^2 = 0.35$, $P = 0.001$), MEPs ($r^2 = 0.27$, $P = 0.001$), and LEPs ($r^2 = 0.17$, $P = 0.02$; Fig. 3). The residuals of the litter size on female SVL regression showed a marginally significant increase with elevation (residuals = 0.76 + 0.0003 SVL; $n = 215$, $r^2 = 0.014$,

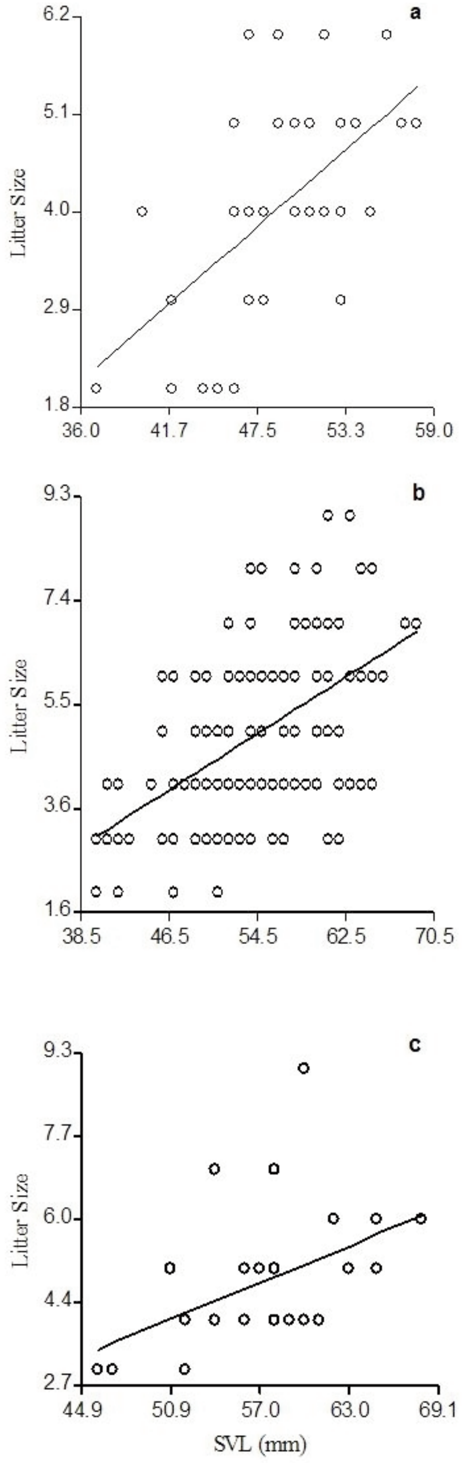

Fig. 3. Relationship of litter size to SVL for female lizards of the *Sceloporus grammicus* complex from Mexico: **a,** high-elevation population; **b,** medium-elevation population; and **c,** low-elevation population.

$P = 0.007$). An ANCOVA showed differences in litter size among elevation groups ($F_{2,215} = 32.6$, $P = 0.001$). Tukey's HSD test showed no significant difference in litter size between HEPs (4.0, SE = 0.19) and LEPs (4.1, SE = 0.28; $P = 0.66$). However, litter size from MEPs was higher (5.1, SE = 0.13) than from HEPs ($P = 0.001$) and LEPs ($P = 0.001$).

DISCUSSION

Female SVL differed among HEPs, LEPs, and MEPs. Females from low-elevation groups had a larger mean SVL than females from high-elevation groups. The difference in SVL is a pattern that has been observed in another *Sceloporus grammicus* population from different elevations (Ramirez-Bautista et al. 2006, Hernández-Salinas et al. 2010). The pattern could result from evolutionary adaptation of the lizards to their local environments (Guillette 1982, Ramírez-Bautista et al. 2004). Smaller SVL in HEPs could be related to a need for faster growth rate, earlier maturity, and shorter reproductive periods at higher elevations than for MEPs and LEPs (Fig. 2). Other studies on *S. grammicus* have shown that populations from high-elevations have smaller absolute litter sizes than populations from low elevations (Lemos-Espinal et al. 1998, Ramírez-Bautista et al. 2004, 2006). As in other populations of *S. grammicus*, this pattern is also found in populations of various species from tropical and temperate environments (e.g., *Sceloporus jarrovi* and *Sceloporus ochoterenae* [Smith et al. 1994, 2003], *Mabuya agilis* [Rocha et al. 2002], and *Xenosaurus platyceps* [Rojas-González et al. 2008]).

Offspring from HEPs were smaller than those from MEPs or LEPs. Such a pattern could be related to environmental factors such as temperature and precipitation. Smaller neonate SVLs in HEPs could also be related to a shorter embryonic development period than found in MEPs and LEPs; embryonic development occurred during the cool winter months (October–March) and birth occurred from March through August when temperature and food resources are higher. These factors permit the neonates to have a faster growth rate and to reach sexual maturity at a smaller SVL (Lemos-Espinal et al. 1998, Ramírez-Bautista et al. 2004, Iraeta et al. 2006).

Another factor to consider is the availability of food resources during embryonic development, which could obviously affect birth size (Guillette and Casas-Andreu 1980, Guillette 1982). However, it should be noted that SVL of adults and neonates showed extensive variation even within elevational groups, which may indicate that populations in the same geographical and environmental area differ morphologically because of adaptations in reproductive strategies (Fig. 1; Tinkle et al. 1970). This could indicate that although some population means get smaller with increased elevation, the populations also share similarities in SVL and litter size with geographically close populations (Table 1). However, we do not mean that *S. grammicus* does not show any phenotypic plasticity associated with the SVL, such as reproductive patterns of females and litter size. These data could indicate that populations of the *S. grammicus* complex are in the process of speciation (Leyte-Manrique et al. 2006). Such speciation processes have been shown in the *S. grammicus* complex from genetic and molecular evidence (Arévalo et al. 1991, Marshall et al. 2006).

The larger mean litter size associated with MEPs could mean that these populations experience a higher predation pressure than HEPs and LEPs and that increased litter size is a response to this environment (Ramírez-Bautista et al. 2004). In addition, MEP neonates were larger than HEP or LEP neonates, again possibly reflecting higher predation pressure on neonates in the MEP population. Other studies of *S. grammicus* populations from high elevations have shown that offspring, adults, and litter sizes are smaller than those from LEPs (Lemos-Espinal et al. 1998, Ramírez-Bautista et al. 2004). Taken together, these studies suggest that life history variation among elevational groups tends to be greater than variation within elevational groups, at least for some traits.

Elevation is known to be important in influencing intraspecific life history variation in lizards (Ballinger 1979, Michaud and Echternacht 1995, Jin and Liu 2007). Life history variation along an elevational gradient arises from proximate environmental factors (Grant and Dunham 1990, Sears 2005), genetic or ultimate factors (Smith et al. 1994, Ballinger et al. 1996), or the interaction of proximate and genetic factors (Iraeta et al. 2006). Environmental factors and the influence of these factors on the evolution of life histories, specifically reproductive strategies as observed in this study, indicate that adaptive processes in local conditions (Shine 2005) respond in variation of litter size and female SVL at different elevations. The temperature gradient associated with elevation is possibly the most important environmental factor and influences not only litter size but also reproductive cycles and embryonic development. The temperature factor is somehow also expressed in the phenotypic variation females exhibit in SVL (Shine 2005, Du et al. 2005) as reported in this study.

Indeed, the general relationships of litter size and elevation and the variation in the relationship between SVL and litter size among populations (Fig. 3) suggest that elevation and other factors (not analyzed in this study; i.e., habitat use, diet, population dynamics, sexual behavior, and geographical distance) are likely playing a large role in the variation of litter size in the *S. grammicus* complex observed in this study.

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