

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/260019645>

Female Reproductive Investment in the Mesquite Lizard (*Sceloporus grammicus*) Species Complex (Squamata: Phrynosomatidae)

ARTICLE *in* THE SOUTHWESTERN NATURALIST · SEPTEMBER 2013

Impact Factor: 0.27 · DOI: 10.1894/0038-4909-58.3.335

CITATIONS

2

READS

94

5 AUTHORS, INCLUDING:



[Elizabeth Bastiaans](#)

State University of New York College at Oneo...

13 PUBLICATIONS 438 CITATIONS

SEE PROFILE



[Fausto R. Méndez-de-la-Cruz](#)

Universidad Nacional Autónoma de México

121 PUBLICATIONS 1,298 CITATIONS

SEE PROFILE



[Cynthia Dinorah Flores Aguirre](#)

Universidad Nacional Autónoma de México

2 PUBLICATIONS 2 CITATIONS

SEE PROFILE



[Barry Sinervo](#)

University of California, Santa Cruz

155 PUBLICATIONS 8,447 CITATIONS

SEE PROFILE

Female Reproductive Investment in the Mesquite Lizard (*Sceloporus grammicus*) Species Complex (Squamata: Phrynosomatidae)

Author(s): Elizabeth Bastiaans , Fausto Méndez de la Cruz , Karla Rodríguez Hernández , Cynthia Flores Aguirre , and Barry Sinervo

Source: The Southwestern Naturalist, 58(3):335-343. 2013.

Published By: Southwestern Association of Naturalists

DOI: <http://dx.doi.org/10.1894/0038-4909-58.3.335>

URL: <http://www.bioone.org/doi/full/10.1894/0038-4909-58.3.335>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

FEMALE REPRODUCTIVE INVESTMENT IN THE MESQUITE LIZARD (*SCELOPORUS GRAMMICUS*) SPECIES COMPLEX (SQUAMATA: PHRYNOSOMATIDAE)

ELIZABETH BASTIAANS,* FAUSTO MÉNDEZ DE LA CRUZ, KARLA RODRÍGUEZ HERNÁNDEZ,
CYNTHIA FLORES AGUIRRE, AND BARRY SINERVO

*Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, 1156 High St.,
Santa Cruz, CA 95064 (EB, BS)*

*Instituto de Biología, Universidad Nacional Autónoma de México, Circuito exterior sin número, Ciudad Universitaria,
Copilco, Coyoacán, México, DF 04510 (FMC)*

*Facultad de Ciencias, Universidad Nacional Autónoma de México, Universidad 3000, Circuito exterior sin número,
Ciudad Universitaria, Copilco, Coyoacán, México, DF*

*Present address of EB: Department of Ecology, Evolution, and Behavior, University of Minnesota, Twin Cities,
100 Ecology Building, 1987 Upper Buford Circle, Saint Paul, MN 55108*

**Correspondent: ejbastiaans@gmail.com*

ABSTRACT—Life-history theory is based on the idea that trade-offs exist in allocation of resources. The same energy cannot simultaneously fuel growth and reproduction or simultaneously increase size and number of offspring. Many genetic, physiological, and environmental variables influence how trade-offs manifest and whether they are detectable through phenotypic correlations. In most squamates, the absence of parental care enables estimation of reproductive investment using mass of offspring. This, as well as their diverse ecologies, makes squamates an attractive system for empirical tests of life history theory. Approximately 20% of squamates are viviparous, and long gestation periods limit most to one litter per year. Carrying offspring until an advanced developmental stage may increase the burden of the litter, and female abdominal volume may constrain litter size. These factors should intensify selection on female tactics of life history and enhance detectability of trade-offs. We compare life history of females in two species within the *Sceloporus grammicus* species complex, viviparous Mexican lizards from varied habitats. Each inhabits one of the primary ecosystems used by this taxon (chaparral and forest). Litter sizes were lower in the chaparral population, when adjusted for body size of the mother. A trade-off of size versus number of offspring was detected in the forest population but not in the chaparral population. The chaparral population varied more in average neonate mass between years, which may relate to local extinctions, likely linked to climate change, in Mexican montane lizards. Regardless of whether these differences represent adaptation or plasticity, our findings emphasize the importance of environmental influence on trade-offs in life history.

RESUMEN—La hipótesis de que existen compromisos en la asignación de recursos es la base de muchas teorías de historia de vida. La misma energía no puede apoyar simultáneamente el crecimiento somático y la reproducción, ni simultáneamente aumentar el número de crías y el tamaño de éstas. Muchas variables genéticas, fisiológicas y ambientales influyen en cómo se manifiestan los compromisos y si éstos son detectados por correlaciones fenotípicas. En la mayoría de las lagartijas, la ausencia del cuidado parental significa que la inversión reproductiva se puede estimar por la masa de los neonatos. Esto, junto con sus diversas ecologías, las hacen ideales para pruebas empíricas de la teoría de historia de vida. Aproximadamente el 20% de la Squamata es vivípara, y largos periodos de gestación limitan a la mayoría a una camada anual. Llevar las crías hasta un estadio avanzado de desarrollo puede aumentar el efecto de la carga y las restricciones por el volumen abdominal de la hembra pueden restringir el tamaño de la camada. Estos factores deben intensificar la selección sobre las estrategias de las hembras de historia de vida y aumentar la detectabilidad de los compromisos. Se compara la historia de vida por hembras de dos especies del complejo *Sceloporus grammicus*, lagartijas vivíparas mexicanas de ambientes variados. Cada especie se encuentra en uno de los dos ecosistemas principalmente usados por este complejo (matorral y bosque de pino). Las camadas contenían menos crías en la población del matorral, incluyéndose el tamaño corporal de la madre como covariable. Se detectó un compromiso entre el tamaño de la camada y la masa promedio de crías en la población del bosque, pero no en

la del matorral. La población del matorral varió más en la masa promedio de neonatos entre años, la cual podría relacionarse con extinciones locales, probablemente vinculadas al cambio climático, registradas en las lagartijas de las montañas de México. Aunque las diferencias representen adaptaciones o flexibilidad, nuestros resultados enfatizan la influencia del ambiente sobre los compromisos de historia de vida.

Life-history theory makes numerous predictions about how resources should be allocated to reproduction. The fundamental assumption underlying most of these predictions is that limited availability of resources creates trade-offs among growth, survival, and reproduction (Stearns, 1989; Roff, 2002), current and future reproduction (Lack, 1947; Stearns, 1989), and the size and number of offspring (Smith and Fretwell, 1974; Sinervo, 1990). While the mathematical predictions of life-history theory are clear (Smith and Fretwell, 1974; van Noordwijk and de Jong, 1986; Lloyd, 1987), the fit of empirical data to those predictions is often less so (Brown, 2003; Ji and Diong, 2006; Ji et al., 2008; Brown and Shine, 2009). Comparisons between closely related populations or species are often used to elucidate which ecological (Vitt and Price, 1982), physiological (Shine, 1992), and phylogenetic (Harvey and Keymer, 1991) factors influence how different organisms solve the difficulties posed by reproduction in a resource-limited world, as well as how closely these solutions will mirror theoretical predictions.

Squamate reptiles, in particular, are common study systems for such comparisons, because parental care of hatchlings or neonates is rare in this taxon (Shine, 2005). Thus, reproductive investment can often be estimated by measuring size of offspring or mass of eggs (e.g., Schwarzkopf, 1992; Ramírez-Bautista et al., 2004; Du et al., 2005a; Uller et al., 2009; Wang et al., 2011). The vast majority of comparative studies of life history in squamates have included predominantly or solely oviparous taxa (Sinervo and Licht, 1991; Uller and Olsson, 2007; Ji et al., 2008; Amat, 2008; Warne and Charnov, 2008; Uller et al., 2009; Brown and Shine, 2009; Wang et al., 2011). This is unsurprising, given that approximately 80% of all squamates are oviparous (Blackburn, 2006). However, several characteristics of viviparous squamates may recommend them as a study system for research on strategies of life history. The tight physiological and thermal control viviparous female squamates have over their offspring (Shine and Downes, 1999), combined with the independence of most neonates immediately after birth (Shine, 2005), mean that there is a clearly defined period over which female investment in offspring occurs. Also, viviparous female squamates are generally limited to one litter per reproductive season and are often highly burdened by their litters (Andrews et al., 1997; Shine, 2005), which likely intensifies selective forces on female strategies of life history in these organisms. This intense selection may produce either divergence among populations due to local adaptation or phenotypically plastic

strategies that allow females to adjust to local environmental conditions (Caswell, 1983).

The *Sceloporus grammicus* species complex currently includes at least three species of small, viviparous lizards, whose ranges collectively encompass most of Mexico: *S. grammicus*, *S. palaciosi*, and *S. anahuacus* (Lara-Gongora, 1983; Marshall et al., 2006; Wiens et al., 2010). Lizards of the *S. grammicus* species complex inhabit a range of habitats, from chaparral to high-altitude pine forests, and previous studies have found high levels of interpopulation and interspecific variation in life history traits such as litter size, body size, and timing of reproduction (Méndez de la Cruz 1989; Lemos-Espinal et al. 1998; Ramírez-Bautista et al. 2004; Jiménez-Cruz et al. 2005). However, most of these studies included relatively low numbers of individuals per population and sacrificed females before parturition occurred. Thus, they are less able to assess intrapopulation variation or the final stages of female reproductive investment.

The *S. grammicus* complex is highly karyotypically variable, and populations between which gene flow is reduced by chromosomal differences may specialize on separate ecological niches (Hall, 1973; Sites, 1983; Arévalo et al., 1993; Sites et al., 1995). Variation in characteristics of life history also occurs between populations with the same karyotype that occupy different habitats (Ramírez-Bautista et al., 2004). The genetic basis of many of the traits that vary between populations of the *S. grammicus* complex has not been established, so it is not clear whether divergence among populations in reproductive and life-history traits represents adaptation or phenotypic plasticity. However, given the important demographic consequences of variation in life history (Caswell, 1983) and the rapid anthropogenic change in habitat occurring in central México (Aguilar et al., 2003; Mas et al., 2004; Sinervo et al., 2010), detailed information about patterns of variation in life history within and among populations is of particular value. Rapid changes in life-history traits, due to either phenotypic plasticity or evolutionary change, have previously been associated with declining populations in diverse taxa (Bowen et al., 2003; Olsen et al., 2004), so studies that monitor individual populations across multiple reproductive seasons may promote more precise allocation of conservation resources to threatened areas.

The present study compares two populations of the *S. grammicus* species complex, one from the species *S. anahuacus* and one from the species *S. grammicus*. We maintained live females in the laboratory until parturition, which increased the number of lizards that could be examined from each study population and allowed us to

TABLE 1—Monthly average temperature and average precipitation during months relevant for reproduction in *Sceloporus grammicus* at Santiago Tolman and in *S. anahuacus* at Sierra del Ajusco, Mexico.

Month	Santiago Tolman		Sierra del Ajusco	
	Average temperature (°C)	Average precipitation (mm)	Average temperature (°C)	Average precipitation (mm)
February	11.7	9	7.8	16
March	14.1	19	9.1	17
April	15.5	37	10.3	43
May	16.0	65	10.5	96
June	15.9	110	10.1	196

assess variation in traits such as litter size, relative litter mass, and size of offspring within as well as between these populations. We performed the study in two successive reproductive seasons, which also enabled us to evaluate the variability in characteristics of life history between years.

MATERIALS AND METHODS—We collected lizards from two sites, representing two primary types of habitat used by lizards of the *S. grammicus* complex in central Mexico (Hall, 1973; Ramírez-Bautista et al., 2004). Cerro Gordo, near the town of Santiago Tolman, Mexico State (19.74°N, 98.81°W; 2,700 m above sea level), is classified as xerophytic chaparral dominated by *Opuntia*, *Bursera*, and *Prosopis* (Table 1; Ramírez-Bautista et al., 2004). *Sceloporus grammicus* near Santiago Tolman were previously identified as part of the low standard (2N = 31/32) chromosomal race (Ramírez-Bautista et al., 2004; Marshall et al., 2006) and primarily inhabit large *Opuntia* cacti. The second site was near Xalatlaco, in the Sierra del Ajusco, Mexico State (19.18°N, 99.32°W, 3600 m above sea level). Originally identified as part of the high standard (2N = 31/32, polymorphic for a fission of chromosome 1) cytotype of *S. grammicus* (Hall, 1973), these lizards were later reclassified as *S. anahuacus* (Lara-Gongora, 1983; Marshall et al., 2006). The site was more mesic than Santiago Tolman and was a pine (*Pinus*) forest with understory dominated by *Eupatorium*, *Senecio*, and *Festuca* (Table 1; Méndez de la Cruz, 1989). Lizards at this site primarily inhabited fallen pine logs and branches. Average monthly temperatures and precipitation in Table 1 were determined using climatic layers described by Hijmans et al. (2005).

Due to previously published information about reproductive cycles of these populations (Méndez de la Cruz, 1989; Ramírez-Bautista et al., 2004; Jiménez-Cruz et al., 2005), pregnant female *S. grammicus* were captured near Santiago Tolman in January 2008 (34 individuals) and January–February 2009 (25 individuals). We captured pregnant female *S. anahuacus* in the Sierra del Ajusco in April–May 2008 (47 individuals) and 2009 (27 individuals). This ensured that females from both locations were captured as close to their parturition dates as possible. We captured lizards by noosing and identified pregnant females by abdominal palpation. Upon capture, we measured snout–vent length (SVL) of each lizard to the nearest 0.5 mm, mass to the nearest 0.05 g with a Pesola© spring scale, and latitude and longitude of the location of capture with a Global Positioning System (GPS) receiver. All lizards were individually marked with unique toe clips.

Within 1 day of capture, we transported lizards to the Laboratorio de Herpetología at the Instituto de Biología,

Universidad Nacional Autónoma de México, in Mexico City, Distrito Federal, Mexico. Lizards were maintained in plastic terraria (22.5 × 14.6 × 13.5 cm) with a substrate of peat moss and a piece of cardboard as refuge. Heating lamps allowed females to maintain a body temperature of 32°C, the preferred body temperature of pregnant female *S. grammicus* (Andrews et al., 1997). We adjusted the photoperiod to correspond approximately (within 0.5 h) to the photoperiod lizards would experience in the field. Lizards were fed crickets (*Acheta domestica*) dusted with calcium and vitamin powders (Rep-Cal and Herptivite ©). Occasionally, their diets were supplemented with mealworm larvae (*Tenebrio molitor*). We checked terraria for the presence of neonates at least once daily and immediately removed them when they were present.

Within 1 day of birth, we measured SVL of neonates to the nearest 0.5 mm using a clear ruler. Mass of neonates was measured to the nearest 0.0001 g using an electronic balance, as was post-parturition mass of females. Sex of neonates was determined by examining the post-anal region for the two enlarged scales typical of males (Stebbins, 2003). Within 3 days of birth, females and neonates were released at the initial locations of capture of the females.

Relative litter mass (RLM, total mass of offspring in relation to the female body mass) is a common measure of reproductive investment in animals that do not exhibit parental care (Du et al., 2005; Shine, 2005). We calculated RLM as [(sum of masses of neonates in a clutch)/(post-parturition mass of female)] to avoid the statistical problems associated with alternative calculations that include female mass in the numerator and denominator (Shine, 1980; Seigel and Fitch, 1984; Fitch, 1985; Ford and Seigel, 1989b). We assessed normality of all response variables using normal quantile plots and goodness-of-fit tests before further analyses. Nonparametric statistics were used to assess female SVL and within-litter variance in mass of neonates, because these variables were not normally distributed. Average mass of neonates was log₁₀-transformed to achieve normality. We also assessed homogeneity of variances for all response variables using Bartlett's test before employing parametric statistics. For analyses that included litter size or total litter mass, we excluded females that gave birth to one or more stillborn offspring. Several individual females were captured in 2008 and 2009, resulting in nonindependent observations. To maintain independence of data points, these females were included in the dataset for 2009 but excluded from the dataset for 2008 (Zúñiga-Vega et al., 2008). As female body size is known to be an important influence on life history characteristics in many taxa, including squamate reptiles (Ford and Seigel, 1989a; Shine,

2005), we included it as a covariate in all analyses. We performed all statistical analyses using JMP 9.0 (SAS Institute, 2010).

RESULTS—We compared body size between populations using SVL, because this measure is more stable than body mass, especially in pregnant females (Ford and Seigel, 1989a; Zúñiga-Vega et al., 2008). Individuals from Santiago Tolman were significantly larger than those from the Ajusco (mean SVL \pm SE = 51.5 \pm 0.43 mm at Santiago Tolman, 48.0 \pm 0.47 mm at Ajusco; Wilcoxon rank sum test, $Z = 4.23$, $P < 0.0001$).

Relative litter mass was normally distributed (Shapiro-Wilk W Test, $W = 0.99$, $P = 0.58$, $n = 115$), so we used analysis of covariance (ANCOVA) to compare RLM between the two species, with female SVL and year included as covariables. We included all interaction effects in the initial model, performed each test, and then removed nonsignificant interactions in a stepwise procedure. The effect of year was not significant when species, female SVL, and their interaction were included as covariables ($F_{4,111} = 0.66$, $P = 0.42$), so we pooled data from 2008 and 2009. In the final model, there was a significant positive effect of female SVL on RLM (Fig. 1a; $F_{3,112} = 40.61$, $P < 0.0001$). This indicates that larger females invest proportionally more in their litter while pregnant. The effect of species was close to significance ($F_{3,112} = 3.70$, $P = 0.057$), with SVL-adjusted mean RLM (\pm SE) greater in *S. anahuacus* (0.44 \pm 0.02) than in *S. grammicus* (0.39 \pm 0.02). The interaction effect female SVL \times species was not significant ($F_{3,112} = 1.35$, $P = 0.25$).

We assessed reproductive trade-offs in size versus number of offspring by examining the relationship between litter size and average neonate mass (Smith and Fretwell, 1974). Body size of females can confound this relationship, however (Ford and Seigel, 1989a), so we accounted for this effect using ANCOVA, with female SVL as a covariate (Rowe, 1994). Litter size was not normally distributed according to the Shapiro-Wilk W test ($W = 0.95$, $P < 0.0001$). However, the distribution showed no obvious skewness or other deviations from normality, and a normal quantile plot indicated that the significant deviation from the normal distribution was likely due to the integer nature of litter size. We thus relied on the robustness of ANOVA models to minor deviations from normality in comparing litter size in *S. anahuacus* and *S. grammicus* (Quinn and Keough, 2002). Initially, we included species, female SVL, and year, as well as all interaction effects, as covariables. The effect of year was not significant ($F_{4,112} = 0.031$, $P = 0.86$), so the data were pooled. However, there were significant effects of female SVL and species (Fig. 1b, Table 2). Larger females had larger litters, and the SVL-adjusted mean (\pm SE) litter size of *S. anahuacus* (4.20 \pm 0.13) was greater than that of *S. grammicus* (3.50 \pm 0.16). The interaction effect of female SVL \times species was not significant (Table 2).

Average mass of neonates was log-normally distributed (Kolmogorov's $D = 0.061$, $P = 0.15$), so we log-

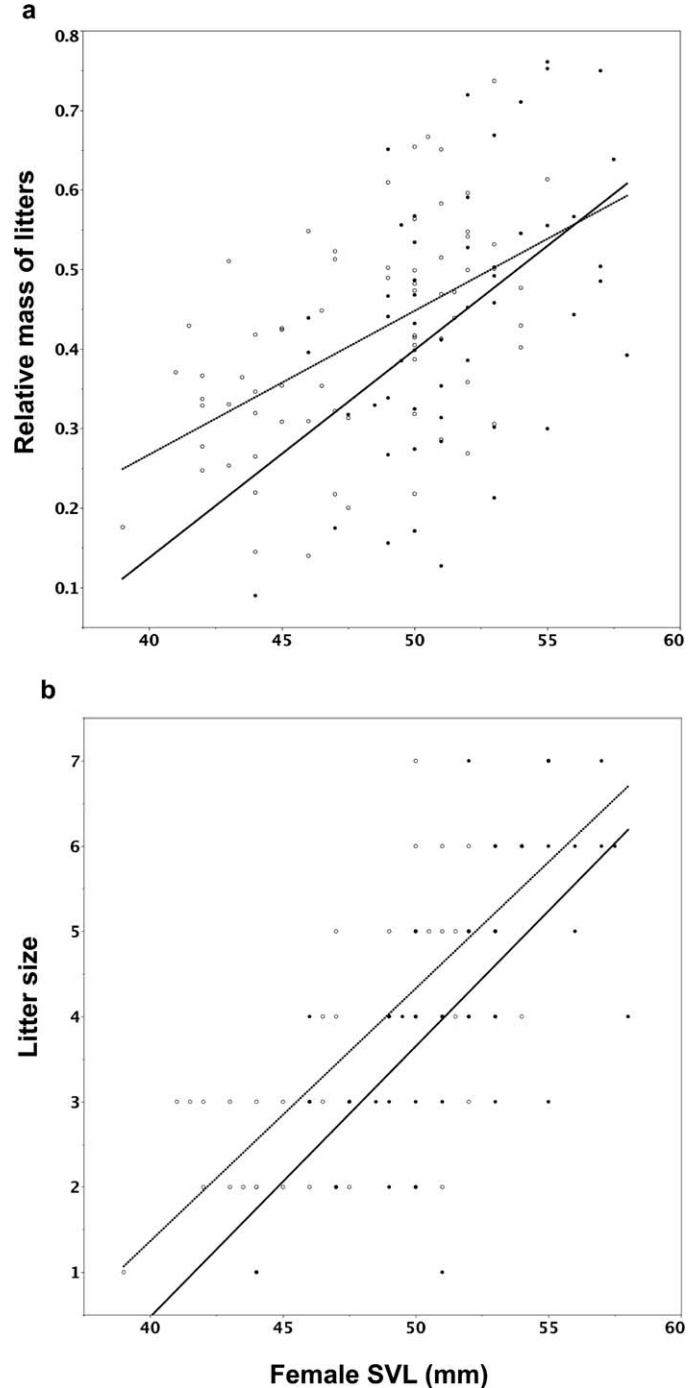


FIG. 1—Relationship of female snout-vent length (SVL) and a) relative mass of litters and b) litter size in *Sceloporus anahuacus* (open circles, dashed line) from Sierra del Ajusco and in *S. grammicus* (solid circles, solid lines) from Santiago Tolman, Mexico.

transformed it before using it as the response variable in an ANCOVA. We assessed the relationship between size and number of offspring in *S. grammicus* and *S. anahuacus* by including species, litter size, female SVL, year, and all two-way interactions in the initial model. We removed nonsignificant factors in a stepwise procedure, resulting

TABLE 2—Results of analysis of covariance showing the effects of female body size and species on litter size and the factors affecting average mass of neonates in *Sceloporus grammicus* at Santiago Tolman and in *S. anahuacus* at Sierra del Ajusco, Mexico. SVL = snout-vent length.

Analysis and source	Sum of squares	df	F	P
Body size, species, litter size				
Female SVL	130.100	1	131.80	<0.0001
Species	10.800	1	10.90	0.0013
Female SVL x species	0.150	1	0.15	0.6947
Error	111.600	113		
Mass of neonates				
Female SVL	0.045	1	25.30	<0.0001
Species	0.044	1	24.70	<0.0001
Year	0.030	1	17.00	<0.0001
Litter size	0.018	1	10.30	0.0018
Species x year	0.063	1	35.00	<0.0001
Species x litter size	0.012	1	6.60	0.0117
Error	0.200	110		

in a final model that included female SVL, species, year, litter size, species x year, and species x litter size, all of which were significant (Table 3). Larger females had larger neonates, and average mass of neonates was greater in *S. grammicus* than in *S. anahuacus*. Across years, average mass of neonates increased considerably in *S. grammicus* from 2008–2009 and decreased slightly in *S. anahuacus*. A post-hoc Tukey HSD test indicated that average mass of neonates in *S. grammicus* in 2009 was significantly greater than average mass of neonates in *S. grammicus* in 2008 and also significantly greater than average mass of neonates in *S. anahuacus* in 2008 or 2009 (all $P < 0.0001$). Average mass of neonates in *S. anahuacus* did not vary between years nor was it different from that in *S. grammicus* in 2008 (all $P > 0.05$).

The significant interaction of litter size and species indicates that the relationship between average size and number of offspring differs between the two populations, suggesting that trade-offs may manifest differently. We tested this in each population using ANCOVA with litter size, female SVL, year, and all interactions as factors. We removed nonsignificant factors in a stepwise procedure, resulting in a final model that included litter size, female SVL, year, and litter size x year. Female SVL was positively related to average mass of neonates (*S. anahuacus*, $F_{4,59} = 17.01$, $P = 0.0001$; *S. grammicus*, $F_{4,48} = 8.66$, $P = 0.005$), indicating that larger females had heavier offspring. As our previous analysis suggested, there was a significant effect of year on average mass of neonates in *S. grammicus* ($F_{4,48} = 48.33$, $P < 0.0001$) but not *S. anahuacus* ($F_{4,59} = 1.63$, $P = 0.2066$). There was a significant trade-off between size and number of offspring in *S. anahuacus* ($F_{4,59} = 12.21$, $P = 0.0009$ for effect of litter size; Fig. 2a), while no such trade-off was detected in *S. grammicus* ($F_{4,48} = 1.00$, $P = 0.3228$ for effect of litter size; Fig. 2b). The interaction between litter size and year was not significant in either species (*S. anahuacus*, $F_{4,59} = 1.40$, $P = 0.241$; *S. grammicus*, $F_{4,48} = 2.24$, $P = 0.1413$).

Variance in mass of neonates was calculated within each litter and compared between the two populations. Variance in mass of neonates within litters was neither normally nor log-normally distributed (Shapiro-Wilk $W = 0.68$, $P < 0.0001$; Kolmogorov's $D = 0.096$, $P = 0.0111$), so this comparison was performed using a Mann-Whitney U test. *Sceloporus grammicus* from Santiago Tolman exhibited considerably greater within-litter variance in neonate mass than did *S. anahuacus* from the Ajusco ($Z = 4.26$, $P < 0.0001$).

DISCUSSION—We found that female *S. grammicus* from Santiago Tolman were larger than female *S. anahuacus* from the Sierra del Ajusco. These results are consistent with measurements taken in the 1980s, which revealed that populations from lower elevations usually exhibit larger body size and faster rates of growth (Lemos-Espinal et al., 1998; Ramírez-Bautista et al., 2004). Numerous other studies have assessed the reproductive traits and annual cycles of populations of the *S. grammicus* complex in pregnant females sacrificed soon after capture (Guillette and Casas-Andreu, 1980; Lemos-Espinal et al., 1998; Ramírez-Bautista et al., 2004; Jiménez-Cruz et al., 2005; Hernández-Salinas et al., 2010). Measures of litter size and embryonic weight in these studies, while informative, may not present a complete picture of strategies of life history in females, as they do not account for any changes in mass of neonates that may occur late in development. Also, many of these studies compared life history across populations and years (e.g., Ramírez-Bautista et al., 2004). Given that we found significant variation between years in average mass of neonates in *S. grammicus*, it seems likely that results from comparisons that pool these data may be confounded by effects of population x year. By allowing parturition to occur in the laboratory and comparing the two populations we studied during the same two reproductive seasons, we can assess variation in strategies

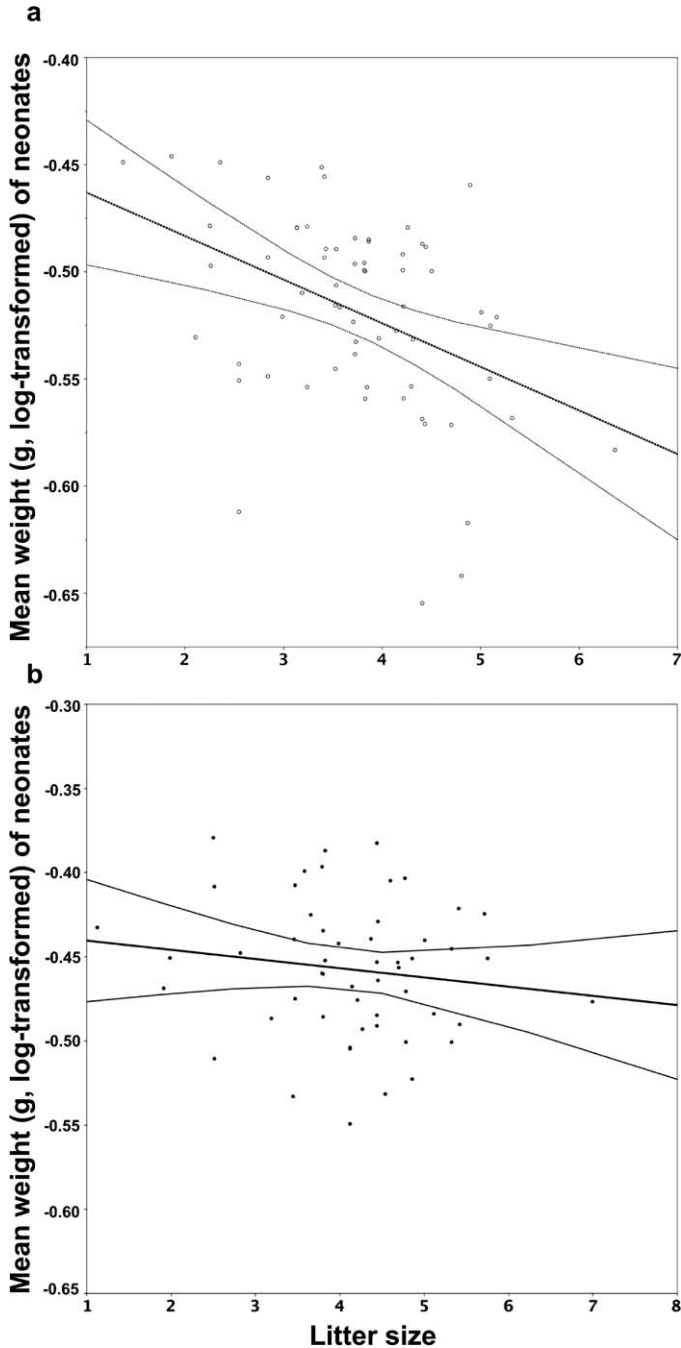


FIG. 2— Relationship of average mass of neonates and litter size in a) *Sceloporus anahuacus* from the Sierra del Ajusco and b) *S. grammicus* from Santiago Tolman, Mexico. Darker lines represent linear regression; lighter lines represent 95% confidence interval.

of full maternal investment of females within and between the populations.

The positive relationship between litter size and female SVL in both populations is consistent with previous research on this species complex (Guillette and Casas-Andreu, 1980; Lemos-Espinal et al., 1998; Ramírez-Bautista et al., 2004; Hernández-Salinas et al., 2010) as well as female squamates in general (Shine, 2005). The

greater litter size of *S. anahuacus* from the Ajusco, however, was contrary to some previous results for the *S. grammicus* complex, in which females collected from populations at lower elevations generally contained more embryos than those from populations at higher elevations (Guillette and Casas-Andreu, 1980; Lemos-Espinal et al., 1998; Ramírez-Bautista et al., 2004; Hernández-Salinas et al., 2010). It is possible that the inconsistencies between characteristics of life history of females at Santiago Tolman and females in other similar populations are a preliminary indication of decline or instability of the population at this location. While we did not formally assess density of populations at either Santiago Tolman or the Sierra del Ajusco, the greater sampling effort required at Santiago Tolman and the increase in sampling effort required at that site in 2009 over 2008 are consistent with this possibility.

Relative mass of litters or clutches has been frequently used to measure reproductive investment in females of species that do not exhibit parental care after parturition as well as to measure the physical burden gravidity or pregnancy imposes on females (Seigel and Fitch, 1984; Fitch, 1985; Shine and Schwarzkopf, 1992; Shine, 1992; Miles et al., 2000). However, most studies that have assessed what factors may influence relative mass of litters or clutches in squamates have been at the interspecific level. In such studies, single values of relative mass of litters or clutches are often assigned to entire species or populations (Vitt and Price, 1982), and levels of intraspecific or intrapopulation variance are low (Vitt and Price, 1982; Seigel and Fitch, 1984; Shine, 1992; Du et al., 2005). The high levels of variation we observed in *S. anahuacus* (range of 0.14–0.74) and *S. grammicus* (range of 0.09–0.76) indicate that these taxa may be exceptions to this pattern. The strong, positive correlations observed in both species between female SVL and relative mass of litters (Fig. 1a) may be related to the fact that individuals of this species complex grow most rapidly during their first 2 years of life and much more slowly thereafter (Zúñiga-Vega et al., 2008). This rapid early growth may result in a decreased investment in somatic growth and an increased proportional investment in reproduction over the lifespan of an individual (Pianka and Parker, 1975; Clutton-Brock, 1984). However, repeated measures of individual females would be required to rigorously test this hypothesis.

We observed greater average mass of neonates in *S. grammicus* from a chaparral habitat than in *S. anahuacus* from a forest habitat as well as an increase in average mass of neonates in the chaparral population from 2008–2009. These differences were apparent even when mass of neonates was adjusted by female SVL and litter size. The change in average neonate mass between years is likely too rapid to represent a response to selection, given the lifespan of these lizards (Lemos-Espinal et al., 1998; Zúñiga-Vega et al., 2008), so it is probable that it

represents a phenotypically plastic response to environmental variables. Other viviparous lizards can substantially modify the phenotypes, including body mass, of their offspring during gestation (Shine and Downes, 1999). However, considerable further investigation would be required to determine the extent to which this is possible in *S. grammicus*, as well as which, if any, environmental cues are responsible.

The relationship between size and number of offspring is a trade-off that has been intensively studied from theoretical and empirical perspectives (Smith and Fretwell, 1974; Lloyd, 1987; Sinervo, 1990; Sinervo and Licht, 1991; Olsson and Shine, 1997; Czesak and Fox, 2003; Uller and Olsson, 2007; Wang et al., 2011). The basic idea states that a limited amount of energy available for reproduction forces individuals to choose between dividing that energy among either a few large or many small offspring (Smith and Fretwell, 1974). However, this prediction relies on several assumptions, most notably that there is a fixed amount of energy available for reproduction and that a decision of an individual regarding how much energy to allocate to reproduction is made prior to the initiation of reproduction (Smith and Fretwell, 1974). While viviparous sceloporines do not exhibit the complex, mammal-like placenta of some other viviparous squamates (Blackburn et al., 1984; Villagrán et al., 2005), it is possible that some transfer of resources occurs between mothers and embryos during the gestation period of 5–6 months. If so, females may be able to adjust their reproductive investment in response to changing conditions during the reproductive season. Also, high levels of variation between individuals in acquisition of resources relative to variation in allocation of resources may obscure the trade-off between size and number offspring at the intrapopulation level (van Noordwijk and de Jong, 1986). This model predicts that trade-offs between size and number of offspring should be observed more often in populations with lower variance in size of offspring within litters (Brown, 2003), and the observation that variance in mass of neonates within litters was greater in *S. grammicus* than in *S. anahuacus* is consistent with this hypothesis. Recently, extinctions of numerous populations have been documented at the lower edges of the ranges of Mexican lizards at high elevations (Sinervo et al., 2010). We were not able to find *S. grammicus* at lower elevations near our site at Santiago Tolman, despite the fact that the species was once abundant there. While we did not formally assess density of populations in 2008 and 2009, greater sampling effort was required in 2009 to achieve a comparable sample size to the previous year.

Increasing temperatures may have caused some lizards at Santiago Tolman to spend more time in shaded refuges and less time foraging or seeking mates (Sinervo et al., 2010). If females at Santiago Tolman varied more in their genetic quality or body condition than did females from

the Sierra del Ajusco, perhaps because of this, the trade-off between size and number offspring may be masked (van Noordwijk and de Jong, 1986; Brown, 2003).

In summary, our comparison of *S. grammicus* from Santiago Tolman and *S. anahuacus* from the Sierra del Ajusco confirms many of the patterns observed in previous research. As in previous studies (Guillette and Casas-Andreu, 1980; Lemos-Espinal et al., 1998; Ramírez-Bautista et al., 2004; Hernández-Salinas et al., 2010), females from Santiago Tolman (chaparral habitat at lower elevations) had larger body sizes and gave birth earlier in the year than did females from the Ajusco (pine forest at higher elevations). The positive relationship between litter size and female SVL (Fig. 1b) also was not surprising because larger females have higher fecundity in other populations of the *S. grammicus* complex (Guillette and Casas-Andreu, 1980; Lemos-Espinal et al., 1998; Ramírez-Bautista et al., 2004; Zúñiga-Vega et al., 2008; Hernández-Salinas et al., 2010) as well as many other squamates (Shine, 2005).

However, the positive relationship between female SVL and relative mass of litters (Fig. 1a), implying that larger females invest proportionally more of their body mass in reproduction, provides a counterpoint to studies that have found low levels of variation in this measure within populations and species of other squamates (Du et al., 2005). The greater SVL-adjusted litter size in *S. anahuacus* (the species at higher elevations) as well as the slightly (although nonsignificantly) greater relative mass of litters we found in this population (Fig. 1), are contrary to the patterns observed in some previous research on the *S. grammicus* complex (Guillette and Casas-Andreu, 1980; Lemos-Espinal et al., 1998; Ramírez-Bautista et al., 2004; Hernández-Salinas et al., 2010). *Sceloporus grammicus* (the species at lower elevations) had greater average mass of neonates, and we observed a drastic increase in this measure in *S. grammicus* (but not in *S. anahuacus*) from 2008–2009. Our study does not address which of the phenotypic differences we observed are genetically based and which result from phenotypic plasticity. However, the fact that the change in mass of neonates we observed occurred over a single year and corresponded in time to a possible decline in the population at Santiago Tolman may indicate that changes in average mass of neonates are part of a plastic response to the environmental change that caused the decline.

Future studies could investigate this question in other populations of montane lizards near the lower boundaries of their altitudinal ranges, by documenting characteristics of life history in multiple successive reproductive seasons. The fact that numerous species of Mexican montane lizards have experienced rapid declines or local extinctions of populations at lower and intermediate elevations in recent years (Sinervo et al., 2010) makes such studies particularly urgent. Also, the lack of an observable trade-off between size and number of off-

spring in *S. grammicus* at Santiago Tolman (Fig. 2b) may have resulted from high levels of variability in acquisition of resources between individuals (van Noordwijk and de Jong, 1986; Brown, 2003). This may be a signature of populations that are declining due to environmental changes and also would be a fruitful avenue for future research.

For assistance with fieldwork, we thank A. Helios de la Vega, V. Jiménez Arcos, R. Lara Resendiz, D. Miles, E. Vásquez, and M. Villagrán Santa Cruz. We thank H. Monterde for assistance with husbandry of lizards. For helpful comments on the manuscript, we thank G. Bastiaans, M. Bastiaans, J. Marshall, K. McCully, R. Mehta, G. Morinaga, D. Paranjpe, C. Ravelo, S. Schlung, J. Yost, N. Ford, and two anonymous reviewers. This research was conducted with the approval of the University of California, Santa Cruz Chancellor's Animal Research Committee (code Sineb0902) and under permits issued by the Secretaría de Medio Ambiente y Recursos Naturales de México (folio FAUT0074). Funding for this research was provided by a UC Mexus grant to BS and a Science, Technology, Engineering Policy, and Society Institute Fellowship, a Fulbright United States Students grant, and a National Science Foundation grant I05-1110497 to EB.

LITERATURE CITED

- AGUILAR, A. G., P. M. WARD, AND C. B. SMITH, SR. 2003. Globalization, regional development, and mega-city expansion in Latin America: analyzing Mexico City's peri-urban hinterland. *Cities* 20:3–21.
- AMAT, F. 2008. Exploring female reproductive tactics: trade-offs between clutch size, egg mass and newborn size in lacertid lizards. *Herpetological Journal* 18:147–153.
- ANDREWS, R. M., F. R. MÉNDEZ DE LA CRUZ, AND M. VILLAGRÁN SANTA CRUZ. 1997. Body temperatures of female *Sceloporus grammicus*: thermal stress or impaired mobility? *Copeia* 1997:108–115.
- ARÉVALO, E., G. CASAS, S. K. DAVIS, G. LARA, AND J. W. SITES. 1993. Parapatric Hybridization between chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae): structure of the Ajusco Transect. *Copeia* 1993:352–372.
- BLACKBURN, D. G. 2006. Squamate reptiles as model organisms for the evolution of viviparity. *Herpetological Monographs* 20:131–146.
- BLACKBURN, D. G., L. J. VITT, AND C. A. BEUCHAT. 1984. Eutherian-like reproductive specializations in a viviparous reptile. *Proceedings of the National Academy of Sciences* 81:4,860–4,863.
- BOWEN, W., S. L. ELLIS, S. J. IVERSON, AND D. J. BONESS. 2003. Maternal and newborn life-history traits during periods of contrasting population trends: implications for explaining the decline of harbour seals (*Phoca vitulina*), on Sable Island. *Journal of Zoology* 261:155–163.
- BROWN, C. A. 2003. Offspring size-number trade-offs in scorpions: an empirical test of the van Noordwijk and de Jong model. *Evolution* 57:21–84.
- BROWN, G. P., AND R. SHINE. 2009. Beyond size–number trade-offs: clutch size as a maternal effect. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:1,097–1,106.
- CASWELL, H. 1983. Phenotypic plasticity in life-history traits: demographic effects and evolutionary consequences. *American Zoologist* 23:35–46.
- CLUTTON-BROCK, T.H. 1984. Reproductive Effort and Terminal Investment in Iteroparous Animals. *The American Naturalist* 123: 212–229.
- CZESAK, M. E., AND C. W. FOX. 2003. Evolutionary ecology of egg size and number in a seed beetle: genetic trade-off differs between environments. *Evolution* 57:11–21.
- DU, W., X. JI, Y.-P. ZHANG, X.-F. XU, AND R. SHINE. 2005. Identifying sources of variation in reproductive and life-history traits among five populations of a Chinese lizard (*Takydromus septentrionalis*, Lacertidae). *Biological Journal of the Linnean Society* 85:443–453.
- FITCH, H. S. 1985. Variation in clutch and litter size in New World reptiles. University of Kansas, Lawrence.
- FORD, N. B., AND R. A. SEIGEL. 1989a. Relationships among body size, clutch size, and egg size in three species of oviparous snakes. *Herpetologica* 45:75–83.
- FORD, N. B., AND R. A. SEIGEL. 1989b. Phenotypic plasticity in reproductive traits: evidence from a viviparous snake. *Ecology* 70:1,768–1,774.
- GUILLETTE, L. J., AND G. CASAS-ANDREU. 1980. Fall reproductive activity in the high altitude Mexican lizard, *Sceloporus grammicus microlepidotus*. *Journal of Herpetology* 14:143–147.
- HALL, W. 1973. Comparative population cytogenetics, speciation, and evolution of the iguanid lizard genus *Sceloporus*. Ph.D. dissertation, Harvard University, Cambridge, Massachusetts.
- HARVEY, P. H., AND A. E. KEYMER. 1991. Comparing life histories using phylogenies. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 332:31–39.
- HERNÁNDEZ-SALINAS, U., A. RAMÍREZ-BAUTISTA, A. LEYTE-MANRIQUE, AND G. R. SMITH. 2010. Reproduction and sexual dimorphism in two populations of *Sceloporus grammicus* (Sauria: Phrynosomatidae) from Hidalgo, Mexico. *Herpetologica* 66:12–22.
- HIJMANS, R. J., S. E. CAMERON, J. L. PARRA, P. G. JONES, AND A. JARVIS. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1,965–1,978.
- Ji, X., AND C.-H. DIONG. 2006. Does follicle excision always result in enlargement of offspring size in lizards? *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* 176:521–525.
- Ji, X., W. DU, Y.-F. QU, AND L.-H. LIN. 2008. Nonlinear continuum of egg size-number trade-offs in a snake: is egg-size variation fitness related? *Oecologia* 159:689–696.
- JIMÉNEZ-CRUZ, E., A. RAMÍREZ-BAUTISTA, J. C. MARSHALL, M. LIZANA-AVIA, AND A. N.-M. DE OCA. 2005. Reproductive cycle of *Sceloporus grammicus* (Squamata: Phrynosomatidae) from Teotihuacán, México. *Southwestern Naturalist* 50:178–187.
- LACK, D. 1947. The significance of clutch-size. *Ibis* 89:302–352.
- LARA-GONGORA, G. 1983. Two new species of the lizard genus *Sceloporus* (Reptilia, Sauria, Iguanidae) from the Ajusco and Ocuilan Sierras, Mexico. *Bulletin of the Maryland Herpetological Society* 19:1–14.
- LEMONS-ESPINAL, J. A., R. BALLINGER, AND G. R. SMITH. 1998. Comparative demography of the high-altitude lizard, *Sceloporus grammicus* (Phrynosomatidae), on the Iztaccihuatl Volcano, Puebla, México. *Great Basin Naturalist* 58:375–379.
- LLOYD, D. G. 1987. Selection of offspring size at independence and other size-versus-number strategies. *American Naturalist* 129:800–817.
- MARSHALL, J., E. ARÉVALO, E. BENAVIDES, J. L. SITES, AND J. W. SITES.

2006. Delimiting species: comparing methods for Mendelian characters using lizards of the *Sceloporus grammicus* (Squamata: Phrynosomatidae) complex. *Evolution* 60:1,050–1,065.
- MAS, J.-F., A. VELÁZQUEZ, J. R. DÍAZ-GALLEGOS, R. MAYORGA-SAUCEDO, C. ALCÁNTARA, G. BOCCO, R. CASTRO, T. FERNÁNDEZ, AND A. PÉREZ-VEGA. 2004. Assessing land use/cover changes: a nationwide multirate spatial database for Mexico. *International Journal of Applied Earth Observations & Geoinformation* 5:249–261.
- MÉNDEZ DE LA CRUZ, F. 1989. Estudio comparativo de la reproducción, tipología y aloenzimas de dos poblaciones cercanas de *Sceloporus grammicus* (Reptilia: Iguanidae) de la Sierra del Ajusco, México. PhD dissertation, Universidad Nacional Autónoma de México, Distrito Federal, México.
- MILES, D. B., B. SINERVO, AND W. A. FRANKINO. 2000. Reproductive burden, locomotor performance, and the cost of reproduction in free ranging lizards. *Evolution* 54:13–86.
- VAN NOORDWIJK, A., AND G. DE JONG. 1986. Acquisition and allocation of resources—their influence on variation in life-history tactics. *American Naturalist* 128:137–142.
- OLSEN, E. M., M. HEINO, G. R. LILLY, M. J. MORGAN, J. BRATTEY, B. ERNANDE, AND U. DIECKMANN. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428:932–935.
- OLSSON, M., AND R. SHINE. 1997. The limits to reproductive output: offspring size versus number in the sand lizard (*Lacerta agilis*). *American Naturalist* 149:179–188.
- PIANKA, E. R., AND W. S. PARKER. 1975. Age-specific reproductive tactics. *American Naturalist* 109:453–464.
- QUINN, G. P., AND M. J. KEOUGH. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge, United Kingdom.
- RAMÍREZ-BAUTISTA, A., E. JIMÉNEZ-CRUZ, AND J. MARSHALL. 2004. Comparative life history for populations of the *Sceloporus grammicus* complex (Squamata: Phrynosomatidae). *Western North American Naturalist* 64:175–183.
- ROFF, D. A. 2002. *Life history evolution*. Sinauer, Sunderland, Massachusetts.
- ROWE, J. W. 1994. Reproductive variation and the egg size-clutch size trade-off within and among populations of painted turtles (*Chrysemys picta bellii*). *Oecologia* 99:35–44.
- SCHWARZKOPF, L. 1992. Annual variation of litter size and offspring size in a viviparous skink. *Herpetologica* 48:390–395.
- SEIGEL, R. A., AND H. S. FITCH. 1984. Ecological patterns of relative clutch mass in snakes. *Oecologia* 61:293–301.
- SHINE, R. 1980. “Costs” of reproduction in reptiles. *Oecologia* 46:92–100.
- SHINE, R. 1992. Relative clutch mass and body shape in lizards and snakes: is reproductive investment constrained or optimized? *Evolution* 46:828–833.
- SHINE, R. 2005. Life-history evolution in reptiles. *Annual Review of Ecology, Evolution, and Systematics* 36:23–46.
- SHINE, R., AND S. J. DOWNES. 1999. Can pregnant lizards adjust their offspring phenotypes to environmental conditions? *Oecologia* 119:1–8.
- SHINE, R., AND L. SCHWARZKOPF. 1992. The evolution of reproductive effort in lizards and snakes. *Evolution* 46:62–75.
- SINERVO, B. 1990. The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution* 44:279–294.
- SINERVO, B., AND P. LICHT. 1991. Proximate constraints on the evolution of egg size, number, and total clutch mass in lizards. *Science* 252:1,300–1,302.
- SINERVO, B., F. MÉNDEZ DE LA CRUZ, D. B. MILES, B. HEULIN, E. BASTIAANS, M. VILLAGRÁN-SANTA CRUZ, R. LARA-RESENDIZ, N. MARTÍNEZ-MÉNDEZ, M. CALDERÓN-ESPINOSA, R. N. MEZA-LÁZARO, H. GADSDEN, L. J. ÁVILA, M. MORANDO, I. J. DE LA RIVA, P. V. SEPULVEDA, C. F. ROCHA, N. IBARGÜENGOYÍA, C. A. PUNTRIANO, M. MASSOT, V. LEPETZ, T. A. OKSANEN, D. G. CHAPPLE, A. M. BAUER, W. R. BRANCH, J. CLOBERT, AND J. W. SITES. 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328:894–899.
- SITES, J. W. 1983. Chromosome evolution in the iguanid lizard *Sceloporus grammicus*. I. Chromosome polymorphisms. *Evolution* 37:38–53.
- SITES, J. W., N. H. BARTON, AND K. M. REED. 1995. The genetic structure of a hybrid zone between two chromosome races of the *Sceloporus grammicus* complex (Sauria, Phrynosomatidae) in Central Mexico. *Evolution* 49:9–36.
- SMITH, C. C., AND S. D. FRETWELL. 1974. The optimal balance between size and number of offspring. *American Naturalist* 108:499–506.
- STEARNS, S. C. 1989. Trade-offs in life history evolution. *Functional Ecology* 3:259–268.
- STEBBINS, R. C. 2003. *A field guide to western reptiles and amphibians*. Houghton Mifflin Harcourt, New York.
- ULLER, T., AND M. OLSSON. 2007. Offspring size-number trade-off in a lizard with small clutch sizes: tests of invariants and potential implications. *Evolutionary Ecology* 23:363–372.
- ULLER, T., G. M. WHILE, E. WAPSTRA, D. A. WARNER, B. A. GOODMAN, L. SCHWARZKOPF, T. LANGKILDE, P. DOUGHTY, R. S. RADDER, D. H. ROHR, C. M. BULL, R. SHINE, AND M. OLSSON. 2009. Evaluation of offspring size-number invariants in 12 species of lizard. *Journal of Evolutionary Biology* 22:143–151.
- VILLAGRÁN, M., F. R. MÉNDEZ, AND J. R. STEWART. 2005. Placentation in the Mexican lizard *Sceloporus mucronatus* (Squamata: Phrynosomatidae). *Journal of Morphology* 264:286–297.
- VITT, L. J., AND H. J. PRICE. 1982. Ecological and evolutionary determinants of relative clutch mass in lizards. *Herpetologica* 38:237–255.
- WANG, Z., Y. XIA, AND X. JI. 2011. Clutch frequency affects the offspring size-number trade-off in lizards. *PLoS ONE* 6:e16585.
- WARNE, R. W., AND E. L. CHARNOV. 2008. Reproductive allometry and the size-number trade-off for lizards. *American Naturalist* 172:E80–E98.
- WIENS, J. J., C. A. KUCZYNSKI, S. ARIF, AND T. W. REEDER. 2010. Phylogenetic relationships of phrynosomatid lizards based on nuclear and mitochondrial data, and a revised phylogeny for *Sceloporus*. *Molecular Phylogenetics and Evolution* 54:150–161.
- ZÚÑIGA-VEGA, J. J., F. R. MÉNDEZ-DE LA CRUZ, AND O. CUELLAR. 2008. Body growth in one montane population of *Sceloporus grammicus* (Sauria, Phrynosomatidae) in Central Mexico. *Amphibia-Reptilia* 29:127–134.