

ORIGINAL ARTICLE

Habitat use in eight populations of *Sceloporus grammicus* (Squamata: Phrynosomatidae) from the Mexican Plateau

Adrian LEYTE-MANRIQUE,¹ Uriel HERNÁNDEZ-SALINAS,² Aurelio RAMÍREZ-BAUTISTA,³ Vicente MATA-SILVA⁴ and Jonathon C. MARSHALL⁵

¹Laboratorio de Biología, Instituto Tecnológico Superior de Salvatierra, Salvatierra, Guanajuato, Mexico, ²Instituto Politécnico Nacional, CIIDIR Unidad Durango, Sigma 119, Fraccionamiento 20 de Noviembre II, Durango, Durango 34220, México,

³Laboratorio de Ecología de Poblaciones, Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, Km 4.5 carretera Pachuca-Tulancingo, 42184, Mineral de la Reforma, Hidalgo, Mexico, ⁴Department of Biological Sciences, The University of Texas at El Paso, El Paso, Texas, USA and ⁵Department of Zoology, Weber State University, 1415 Edvalson Street, Ogden, Utah, USA

Abstract

Studies on habitat use have often helped explain observed variation in morphology, behavior and reproductive characteristics among populations within a single species. Here we analyze morphological and ecological characteristics of individuals from the *Sceloporus grammicus* species complex from 7 different localities (CER, El Cerezo; PAC, Pachuca; HUI, Huichapan; EZA, Emiliano Zapata; SMR, San Miguel Regla; LMJ, La Mojonera; and LMZ, La Manzana) in the state of Hidalgo, and one locality (Cahuacán) in the State of Mexico. A canonical correspondence analysis (CCA) showed that females from PAC, EZA, LMZ, HUI, SMR and CAH populations use similar microhabitats characterized mostly by bare soil, in females from LMJ and CER use microhabitats characterized primarily by vegetation and rocks. Females were observed using 12 different types of perches. With regard to perch height use, the CCA showed that females from PAC, LMJ, LMZ, SMR, CER and CAH populations were correlated with height to nearest perch (HNP), in the rest of the females were not related to any perch use variable. In contrast, the CCA showed that males from PAC, LMJ and CAH were characterized by microhabitats with higher vegetal coverage, while males from LMZ and CER used microhabitats composed of bare soil, but males from HUI and SMR populations used microhabitats composed chiefly of bare soil and rocks. With respect to perch height use, the CCA showed that males from PAC, LMJ, EZA and LMZ were correlated with distance to the nearest perch, but the rest of the males were not correlated with any perch use variables. Males were observed in 9 different perch types. The males were larger than the females in all morphological variables analyzed. Moreover, in both sexes the snout–vent length is positively correlated with all morphological variables, and although both the slope and ordinate of the origin of all morphological variables were larger in males than females, the analysis of covariance indicated that there is no increase in the morphological variables with increasing SVL between sexes. Our results suggest that variation in habitat use and morphology among populations is an adaptive response (phenotypic plasticity) to the environmental conditions where these populations of *Sceloporus grammicus* occur.

Key words: canonical correspondence analyses, habitat use, morphology, populations, *Sceloporus grammicus*

Correspondence: Uriel Hernández-Salinas, Instituto Politécnico Nacional, CIIDIR Unidad Durango, Sigma 119, Fraccionamiento 20 de Noviembre II, Durango, Durango 34220, México.
Email: uhermandez3@gmail.com

INTRODUCTION

Studies on species distributed over broad geographic ranges often exhibit extensive variation in life-history characteristics across the species' populations, such as growth rate, snout–vent length (SVL) at sexual maturity, fecundity and survivorship (Michaud & Echternacht 1995). These traits allow the investigation of the ecological (e.g. predation and competition) and environmental factors (temperature, humidity and food) that influence phenotypic expression for each population (Goodman *et al.* 2008). For example, variation in habitat use among populations in the distribution of a species is a reflection of the respective selective pressures in each inhabited environment, which ensuingly modifies body size, body shape and behavior (Mesquita *et al.* 2015). These modifications allow us to group populations into ecomorphs or ecotypes (Michaud & Echternacht 1995; Losos *et al.* 2006). Studies on habitat use have been conducted for some lizard populations that have shown morphological variation according to microhabitat structure (Irschick *et al.* 1997; Vanhooydonck *et al.* 2000; Herrel *et al.* 2001). For example, the lizards of the genus *Anolis* Daudin from the Greater Antilles have shown morphological changes related to the use and diversification of their microhabitat, which has resulted in the proposal of discrete ecomorphs for each microhabitat type (Irschick *et al.* 1997). Another study of 4 populations of *Urosaurus ornatus* (Baird & Girard) showed a positive correlation between microhabitat use and body shape, indicating that these populations are well adapted to different microhabitat types (Herrel *et al.* 2001). However, in other lizard species a relationship has not been found between morphology and habitat characteristics. For example, Schulte II *et al.* (2004) did not find any relation between these characteristics in 25 *Liolaemus* Wiegmann species; this pattern was explained by similar habitats exploited by the species, which are profoundly homogeneous. Therefore, functional morphology is similar for all lizard species in all environments studied.

Irrefutably, studies on species with wide distributions yield a better understanding of morphological, physiological and ecological changes among populations that result from phenotypic plasticity or local adaptation (Schulte II *et al.* 2004; Ramírez-Bautista *et al.* 2005). In addition, within this context the differential use of microhabitat types by different populations of a species with a broad distribution, under different ranges of elevation, humidity and temperature, can eventually lead to genetic divergence and possibly to species radiation (Johnson *et al.* 2009; Hertz *et al.* 2013). For these rea-

sons, studying widely distributed species that inhabit very different microhabitats is extremely important.

The *Sceloporus grammicus* Wiegmann species complex has been an important system of study for phylogenetic and species delimitation analysis (Sites *et al.* 1992; Lara-Góngora 2004; Marshall *et al.* 2006), and life history evolution (Hernández-Salinas *et al.* 2010; Bastiaans *et al.* 2013a, 2014; Pérez-Mendoza & Zuñiga-Vega 2014). *S. grammicus* is a viviparous species widely distributed in Mexico (Arévalo *et al.* 1991), ranging across the hottest regions of the Mexican Plateau (Sites *et al.* 1992). Its wide geographic distribution in Mexico and high variation in morphological (Lara-Góngora 2004; Leyte-Manrique *et al.* 2006), ecological (Lemos & Ballinger 1995; Leyte-Manrique *et al.* 2007; Leyte-Manrique 2011), reproductive (Hernández-Salinas *et al.* 2010; Lozano *et al.* 2014, 2015), life history (Ramírez-Bautista *et al.* 2004, 2005; Pérez-Mendoza *et al.* 2013, 2014), demographic (Zuñiga-Vega *et al.* 2008; Pérez-Mendoza *et al.* 2013, 2014) and genetic characteristics (Arévalo *et al.* 1993, 1994; Marshall *et al.* 2006) indicate that this represents a species complex and a possible speciation scenario (Arévalo *et al.* 1991).

This species exploits a high diversity of environments, including temperate forests (pine forest, pine-oak forest and cloud forest) and scrub (xerophilic, submontane and crasicaule; Arévalo *et al.* 1991; Lara-Góngora 2004; Leyte-Manrique 2011). Populations of this species utilize different microhabitat types, such as rocks, trees, shrubs, ground and walls of abandoned houses (Lara-Góngora 2004). The diverse use of microhabitats in different species and groups of lizards has generated several predictions on morphological and ecological variations among populations. For example, in organisms that use vertical perches or branches of trees, individuals of small size and slender body with thin limbs are expected; in contrast, individuals that live in rocky habitats display dorsoventrally flattened bodies, which favors the use of crevices as shelter, and in addition have relatively short limbs that support the ability to turn (Herrel *et al.* 2002). It is important to mention that the populations in this study are a possible species complex experiencing a speciation event, but until a phylogenetic analysis proves otherwise, the eight populations of *S. grammicus* are worthy of study as a single species. Therefore, *S. grammicus* is regarded as an ideal model for comparative studies on morphological and ecological traits among populations (Sites *et al.* 1988). However, few studies on morphology and habitat use have been conducted among the diverse populations

of this possible species complex (Lara-Góngora 2004; Leyte-Manrique 2011). In this study, our objective is to document variation between populations by presenting quantitative data on microhabitat use and its relationship to morphology from eight distinct populations of *S. grammicus* from central Mexico.

MATERIALS AND METHODS

Study area

Fieldwork was carried out from February 2007 to December 2008 in eight geographic localities containing *S. grammicus* populations. Herein, these populations are adduced as follows: El Cerezo (CER: 20°10'09"N, 98°43'31"W), Pachuca (PAC: 20°03'06"N, 98°44'24"W), Huichapan (HUI: 20°26'N, 99°31'W), Emiliano Zapata (EZA: 19°51'30"N, 98°57'31"W), San Miguel Regla (SMR: 20°13'11"N, 98°33'39"W), La Mojonera (LMJ: 20°37'35"N, 99°02'33"W), and La Manzana (LMZ: 20°52'14"N, 99°13'20"W) from Hidalgo, and Cahuacán located in the State of Mexico (CAH: 19°33'N, 99°36'W; Table 1). Sampled months for each population were as follows: CER in June (2007), and April, June, August, October and December (2008); PAC: February, June, October and December (2007), and April and August (2008); HU: December (2007), and February, April and June (2008); EZA: August, October and December (2007), and February, April and

June (2008); SMR: April and December (2007), and February, April and June (2008); LMJ: June, August, October and December (2007), and February and April (2008); LMZ: August, October and December (2007), and February, April and June (2008); CAH: December (2007), and February (2008). During the months of survey, each population was sampled from 0900 to 1700 hours while ensuring that surveys occurred on sunny days, as individuals of *S. grammicus* show higher activity during these days (Ramírez-Bautista *et al.* 2014).

Vegetation types

To assess morphological characteristics along with microhabitat types and perch height preference by *S. grammicus* in these populations, we selected sampling areas while taking into consideration conditions such as vegetation type and annual precipitation (Table 1). Lizards from all sites were observed in their activity areas and characteristics of the microhabitat and perch height were recorded following the criteria used by Herrel *et al.* (2001) and Ramírez-Bautista & Benabib (2001). The eight populations of *S. grammicus* analyzed in this study were found in 3 different vegetation types: pine-oak forest, pine forest and xeric scrub (Rzedowski 1978: Table 1). Populations from CER, LMJ, LMZ and CAH inhabit pine-oak forest, while populations from PAC, HUI, and EZA are found in xeric scrub, and, finally, the population in SMR occupies a mixture of xeric scrub and pine forest.

Table 1 Environmental characteristics of localities for the eight populations of *Sceloporus grammicus* from Mexico

| Population | Municipality | Environmental characteristics | | | |
|---------------|-----------------------|-------------------------------|---------------|--------------------|------------------|
| | | Vegetation | Elevation (m) | Precipitation (mm) | Temperature (°C) |
| HIDALGO STATE | | | | | |
| PAC | Mineral de la Reforma | XER | 2348 | 387 | 14.2 |
| LMJ | Zacualtipán | POF | 2062 | 2047 | 13.6 |
| EZA | Tizayuca | XER | 2312 | 601 | 14.9 |
| LMZ | Zimapán | POF | 2507 | 1391 | 18.3 |
| HUI | Huichapan | XER | 2287 | 427 | 16 |
| SMR | Huasca de Ocampo | PF-XER | 2074 | 855 | 15.3 |
| CER | Mineral del Chico | POF | 2450 | 1503 | 14.9 |
| MEXICO STATE | | | | | |
| CAH | Cahuacán | POF | 2058 | 1200 | 12 |

Vegetation: POF, pine and oak forest; PF-XER, pine forest and xerophytic scrub; XER, xerophytic scrub. Annual mean temperature and precipitation for populations from the state of Hidalgo were taken from Pavón and Meza-Sánchez (2009) and for the population from the state of Mexico (CAH) from García (1973).

Microhabitat and perch height use

In this study, we considered two groups of variables to describe microhabitat and perch height use. The first group of variables describes the microhabitat use and comprises: (i) vegetation coverage (VC), with pastures and other non-woody plants included; (ii) rock coverage (RC); and (iii) bare soil coverage (BSC). These variables were taken in percentages and were determined from a surface area of 1 m² with the focal spot under observation as the center (focal spot is the point located in the center of the area of 1 m², where the lizard was observed; Herrel *et al.* 2001). To describe the perch height use we formed a second group of variables that consisted of: (i) type of perch (TP), considered as the site or place where lizards were observed or captured, such as branches, rocks, logs, *Agave* plants and walls of abandoned houses; (ii) perch height (PH): the distance from the ground to the point where the lizard was captured; and (iii) distance to nearest perch (DNP), which is the distance between the perch site where lizards were first observed to the other nearest perch; and (iv) height to nearest perch (HNP), which is the height of the nearest potential perch that the lizard could occupy. All measurements for these variables were taken with a standard measuring tape (Vanhooydonck *et al.* 2000).

To confirm that all data collected were properly scored, photographs were taken with a high-resolution camera covering the entire surface area (1 m²). Data from the microhabitat structure was transformed to arcsin. This transformation is suggested for percentage data, and, thus, allowed an increase in normality and at the same time as decreasing the interdependence of data (Sokal & Rohlf 1981). Variables of perch height were log₁₀-transformed to increase the possibility of a normal distribution. Normality of the data was performed by W Shapiro–Wilk test, recommended for sample sizes >150 (Shapiro *et al.* 1968; Zar 1999). The relationship among microhabitat use and perch height from the eight populations was evaluated with a canonical correspondence analysis (CCA; Ter Braak 1986). The CCA is a multivariate method that helps to explain how a group of individuals can relate with environmental variables (habitat structure and perch height). The CCA relates two matrices: matrix of dependent variables (e.g. matrix of sites by species or individuals) and matrix of independent variables (e.g. matrix of environmental variables: habitat structure and perch height). The relationship between both matrices is done by means of multivariate regression techniques (Ter Braak & Verdonschot 1995). In this study, this analysis was developed for males and

females separated by different microhabitat and perch height in the program CANOCO for Windows 4.56 (Ter Braak & Verdonschot 1995). The significance of the relationship of the individuals of both sexes and populations together with environmental variables was tested using the Monte Carlo test (1000 permutations). The results of the ordination diagram for each individual and population are represented by different symbols, while correlations with variables that characterize the habitat and perch use are shown with arrows.

Morphological analysis

For the morphological data, a total of 244 adult individuals (117 males and 127 females) were collected from the eight populations. For this study, only adult individuals were collected, and to verify that they belonged to this age class, males and females were sexed according to SVL (minimum size at sexual maturity; see Ramírez-Bautista *et al.* 2004, 2005). For example, sexually mature males showed brighter dorsal and ventral color. In addition, they had enlarged testes and highly convoluted epididymides, which are typically associated with sperm production (Lozano *et al.* 2015), while the smallest adult female (sexually mature) containing enlarged vitellogenic follicles (in ovary) or oviductal/uterus embryos (in oviduct/uterus) was used as an estimate of minimum SVL at maturity (Lozano *et al.* 2014). The sample size for each population was as follows: PAC population with a sample size of 18 females and 18 males; LMJ: 21 females and 18 males; EZA: 25 females and 20 males; LMZ: 19 females and 16 males; HUI: 12 females and 11 males; SMR: 16 females and 15 males; CER: 10 females and 13 males; and CAH: 6 females and 6 males. All specimens were caught directly by hand under the scientific permit SGPA-DGVS/04989/10 issued by SEMARNAT (Dirección General de Vida Silvestre).

After lizards were collected, we obtained the following linear measurements: SVL (from the tip of snout to the cloacal region; measured to nearest 1.0 mm); tibia length (TIL: ± 0.1 mm, distance from knee to center of the ankle); femur length (FEL: ± 0.1 mm; distance from the angle of the groin to the knee); forearm length (FOL: ± 0.1; the apex of the elbow to the wrist center); head length (HDL: ± 0.1 mm; distance from the back of the skull to the tip of the snout); and head width (HDW: ± 0.1 mm; the widest point of the head, located mainly on the region of the tympanum). These variables were measured using a Mitutoyo caliper with an accuracy of 0.01 mm. After measurements were taken, the lizards

were humanely euthanized (Sedalphorte: 0.1 ml) and fixed with 10% formalin in the laboratory. Specimens were deposited in the collection of amphibians and reptiles of the Centro de Investigaciones Biológicas at the Universidad Autónoma del Estado de Hidalgo located in the city of Pachuca, Hidalgo, Mexico.

We log₁₀-transformed all morphological variables to normalize and reduce heteroscedasticity. In addition, using a regression analysis, we eliminated the effect of SVL (independent) on all morphological variables (TIL, FEL, FOL, HDL and HDW: dependent) of males and females, and at the same time we obtained residuals. Through the residuals, and using a one-way ANOVA, we conducted morphological comparisons considering sex as a factor. In addition, we developed an analysis of covariance (ANCOVA) to analyze sexual dimorphism. The function of the ANCOVA is to eliminate, through linear regression, the effect of SVL (covariate) on dependent variables (TIL, FEL, FOL, HDL and HDW), and to check whether the regression slopes are different between sexes (factor).

RESULTS

Microhabitat and perch use

The relationship among female populations of *S. grammicus* with all variables that characterize microhabitat and perch height use was significantly different for the two canonical correlation axes ($F = 103.035$, $P = 0.0010$; Fig. 1). The correlation of the environmental variables along with the eight populations of females for the two first axes was 0.93 and 0.94, respectively; this explained the 37 and 31% of variation, respectively, for each axis of this analysis (Fig. 1, Table 2). Therefore, variables that showed a higher correlation in axis 1 were VC, RC and BSC, and for axis two it was BSC (Table 3). The four quadrants in Figure 1 show that females from

PAC, EZA, LMZ, HUI, SMR and CAH populations use similar microhabitats characterized mostly by bare soil, while females from LMJ and CER use microhabitats characterized mostly by vegetation and rocks. Females were observed on 12 different types of perches (Fig. 2), but most frequently on rocks, walls and *Agave* plants. With respect to perch height use, the CCA showed that females from PAC, LMJ, LMZ, SMR, CER and CAH populations were correlated with HNP, which revealed similarities in the females on the use of this characteristic (Fig. 1).

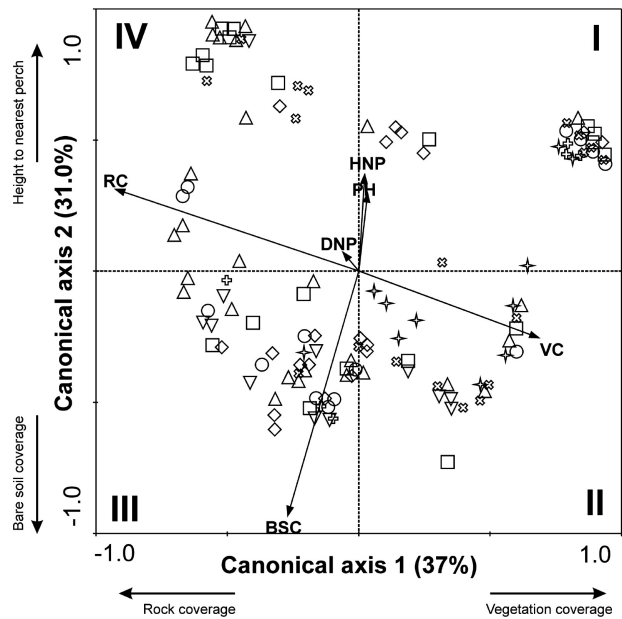


Figure 1 Canonical correspondence analysis of females from eight populations of *Sceloporus grammicus*. +, PAC; □, LMJ; ○, EZA; △, LMZ; ◇, HUI; ☆, SMR; ■, CER; ×, CAH. The arrows correspond to correlations of each variable.

Table 2 Results of the canonical correspondence analysis of the variables of microhabitat and perch height use by males and females from eight populations of *Sceloporus grammicus*

| | Males | | Females | |
|---|--------|--------|---------|--------|
| | Axis 1 | Axis 2 | Axis 1 | Axis 2 |
| Eigenvalues | 0.82 | 0.66 | 0.73 | 0.61 |
| Environmental variables correlation of populations | 0.94 | 0.91 | 0.93 | 0.94 |
| Percentage of accumulated variation by environmental variables of the populations | 37.3 | 67.1 | 36.9 | 67.9 |

Table 3 Correlations between canonical axes and variables that represent the microhabitat and perch height use for males and females from eight populations of *Sceloporus grammicus* from Mexico

| Variables | Males | | Females | |
|-----------|---------|---------|---------|---------|
| | Axis 1 | Axis 2 | Axis 1 | Axis 2 |
| PH | -0.0014 | 0.1904 | 0.0312 | 0.2791 |
| DNP | 0.2235 | 0.0454 | -0.0559 | 0.0681 |
| HNP | 0.3523 | -0.0313 | 0.0206 | 0.3455 |
| VC | -0.7535 | 0.1955 | 0.6406 | -0.2378 |
| RC | 0.8697 | -0.2288 | -0.8649 | 0.292 |
| BSC | -0.388 | -0.8206 | -0.2528 | -0.8728 |

Variables that showed correlation in the ordination axes were significant when the value was ≥ 0.3 . BSC, bare soil coverage; DNP, distance to nearest perch; HNP, height to nearest perch; PH, perch height; RC, rocks coverage; VC, vegetation coverage.

With regard to males, the relationship among populations along with all the variables that characterize the microhabitat and perch height use was significant for the canonical correlation axes ($F = 82.702$, $P = 0.0010$; Fig. 3). The correlation of environmental variables and the eight populations for the first 2 axes was 0.94 and 0.91. Thus, both axes explained 37.3 and 30% of the total variation of this analysis, respectively (Table 2). The variables with greater correlation to axis 1 were VC and RC, and for axis 2 were HNP and BSC (Table 3).

The CCA showed that males from PAC, LMJ and CAH were characterized by microhabitats with vegetation coverage (Fig. 3), while males from LMZ and CER used microhabitats composed of bare soil; males from HUI and SMR populations used microhabitats composed primarily of bare soil and rocks (Fig. 3). Males were observed using nine perch types (Fig. 2) and most frequently observed on rocks, walls and *Agave* plants, similar to females. Regarding perch height use, the CCA showed that males from PAC, LMJ, EZA and LMZ were correlated with DNP.

Morphology and sexual dimorphism

In general, a one-way ANOVA showed that males were larger than females in all morphological variables analyzed (SVL: $F_{1,243} = 10.78$, $P = 0.0012$; TIL: $F_{1,243} = 24.57$, $P = 0.0001$, FEL: $F_{1,243} = 16.46$, $P = 0.0001$, FOL: $F_{1,243} = 10.82$, $P = 0.0012$, HDL: $F_{1,243} = 9.56$, $P = 0.0022$, HDW: $F_{1,243} = 17.42$, $P = 0.0001$; Table 4).

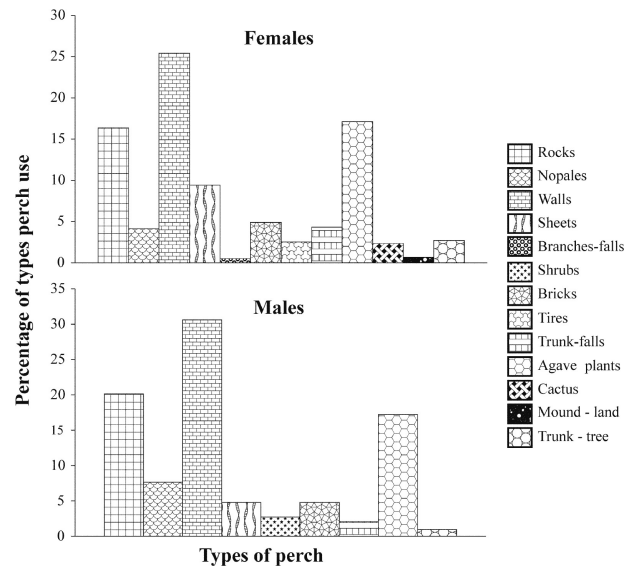


Figure 2 Frequency of occurrence of females and males of *Sceloporus grammicus* in 13 types of perch, based on haphazard sampling over a 1-year sampling.

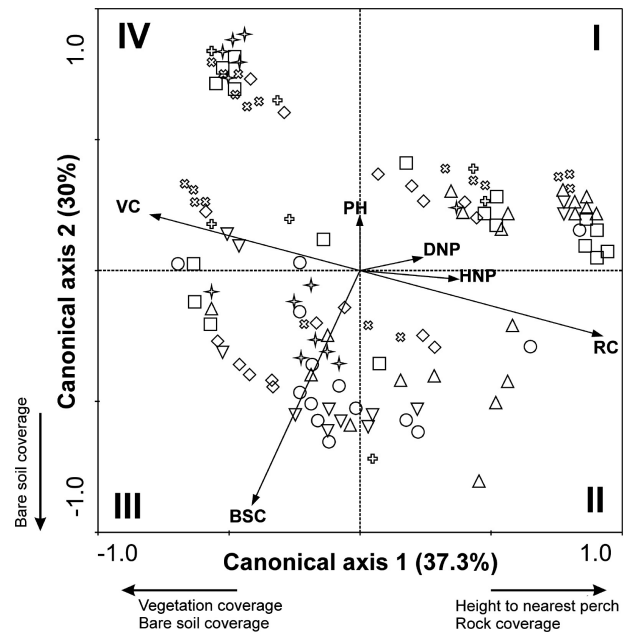


Figure 3 Canonical correspondence analysis of males from eight populations of *Sceloporus grammicus*. +, PAC; □, LMJ; ○, EZA; △, LMZ; ◇, HUI; ✦, SMR; ■, CER; ×, CAH. The arrows correspond to correlations each variable.

Table 4 Mean values (\pm SE) of the morphological variables for males and females from the eight populations of the *Sceloporus grammicus* complex of Mexico

| Variables (mm) | Populations | | | | | | | |
|----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| | CER | PAC | HUI | EZA | SMR | LMJ | LMZ | CAH |
| Females | | | | | | | | |
| SVL | 46.2 \pm 2.18 | 51.3 \pm 1.2 | 54.7 \pm 1.0 | 56.74 \pm 1.8 | 52.5 \pm 1.37 | 55.0 \pm 1.7 | 53.5 \pm 0.9 | 45.3 \pm 1.48 |
| Tibia length | 9.1 \pm 0.45 | 8.9 \pm 0.26 | 10.0 \pm 0.20 | 11.1 \pm 0.38 | 9.5 \pm 0.32 | 11.1 \pm 0.38 | 10.1 \pm 0.26 | 9.2 \pm 0.25 |
| Femur length | 9.5 \pm 0.66 | 8.6 \pm 0.26 | 9.8 \pm 0.37 | 10.8 \pm 0.44 | 9.4 \pm 0.49 | 10.5 \pm 0.32 | 10.3 \pm 0.26 | 10.0 \pm 0.21 |
| Forearm length | 7.8 \pm 0.52 | 7.5 \pm 0.20 | 8.5 \pm 0.26 | 8.9 \pm 0.24 | 8.2 \pm 0.22 | 9.1 \pm 0.26 | 8.6 \pm 0.16 | 9.5 \pm 0.21 |
| Head length | 11.0 \pm 0.35 | 10.9 \pm 0.19 | 12.4 \pm 0.15 | 12.9 \pm 0.34 | 11.6 \pm 0.26 | 13.0 \pm 0.29 | 12.3 \pm 0.28 | 10.5 \pm 0.29 |
| Head width | 9.2 \pm 0.42 | 9.5 \pm 0.15 | 10.6 \pm 0.14 | 11.0 \pm 0.29 | 10.6 \pm 0.27 | 10.9 \pm 0.27 | 10.5 \pm 0.22 | 8.3 \pm 1.49 |
| Males | | | | | | | | |
| SVL | 52.3 \pm 1.83 | 56.2 \pm 1.07 | 57.6 \pm 2.1 | 65.4 \pm 1.3 | 54.7 \pm 2.33 | 56.5 \pm 1.9 | 51.4 \pm 1.84 | 53.0 \pm 2.95 |
| Tibia length | 10.3 \pm 0.42 | 10.4 \pm 0.34 | 11.6 \pm 0.49 | 13.3 \pm 0.47 | 10.6 \pm 0.46 | 12.0 \pm 0.56 | 10.4 \pm 0.42 | 11.0 \pm 0.25 |
| Femur length | 10.2 \pm 0.42 | 10.4 \pm 0.41 | 10.9 \pm 0.59 | 12.7 \pm 0.53 | 10.7 \pm 0.57 | 11.0 \pm 0.54 | 10.5 \pm 0.43 | 11.2 \pm 0.27 |
| Forearm length | 8.0 \pm 0.32 | 8.2 \pm 0.21 | 9.3 \pm 0.42 | 10.5 \pm 0.31 | 9.0 \pm 0.46 | 9.7 \pm 0.48 | 8.5 \pm 0.37 | 10.4 \pm 0.35 |
| Head length | 12.2 \pm 0.37 | 12.0 \pm 0.39 | 13.0 \pm 0.42 | 14.8 \pm 0.31 | 11.7 \pm 0.40 | 13.0 \pm 0.54 | 12.5 \pm 0.45 | 11.7 \pm 0.48 |
| Head width | 10.5 \pm 0.33 | 10.6 \pm 0.26 | 11.6 \pm 0.40 | 12.6 \pm 0.31 | 10.6 \pm 0.40 | 11.7 \pm 0.51 | 10.6 \pm 0.41 | 11.1 \pm 0.38 |

SVL, snout–vent length.

Table 5 Statistical regression and comparison of slopes by ANCOVA of relations between morphological variables and snout–vent length for males (M) and females (F) of *Sceloporus grammicus* of the eight populations from Mexico

| Variables | Sex | Regression | | | | | | ANCOVA | | |
|-----------|-----|------------|--------|------|-------|---------|-------|-------------------|-----|------|
| | | R^2 | F | df | Slope | Ordered | P | Comparison slopes | | |
| | | | | | | | | F | df | P |
| TIL | M | 50.52 | 117.41 | 1116 | 0.89 | –0.5 | 0.001 | 1.37 | 1,2 | 0.24 |
| | F | 38.12 | 76.99 | 1126 | 0.75 | –0.29 | 0.05 | | | |
| FEL | M | 32.33 | 54.93 | 1116 | 0.73 | –0.25 | 0.001 | 0.04 | 1,2 | 0.85 |
| | F | 27.76 | 48.04 | 1126 | 0.71 | –0.22 | 0.049 | | | |
| FOL | M | 40.52 | 78.35 | 1116 | 0.78 | –0.41 | 0.003 | 1.55 | 1,2 | 0.21 |
| | F | 34.72 | 66.47 | 1126 | 0.63 | –0.16 | 0.051 | | | |
| HDL | M | 42.69 | 85.65 | 1116 | 0.66 | –0.05 | 0.042 | 0.23 | 1,2 | 0.63 |
| | F | 46.61 | 109.11 | 1126 | 0.62 | 0.02 | 0.036 | | | |
| HDW | M | 50.75 | 118.5 | 1116 | 0.71 | –0.19 | 0.026 | 1.31 | 1,2 | 0.25 |
| | F | 46.64 | 109.28 | 1126 | 0.61 | –0.03 | 0.028 | | | |

df, degrees of freedom.

In both sexes the SVL is positively correlated with TIL, FEL, FOL, HDL and HDW (Table 5).

Although slopes and ordinates of the origin of TIL, HDW and FOL were larger in males than in females,

the ANCOVAs indicated that there is no increase in the morphological variables with increasing SVL between sexes (Table 5).

DISCUSSION

Sceloporus grammicus populations from the Mexican Plateau represent a taxonomic challenge that has been widely discussed over the past few decades (Hall 1973; Sites *et al.* 1988; Arévalo *et al.* 1991; Marshall *et al.* 2006; Leaché 2010). Our study, which used multivariate methods and comparative analysis of eight populations, provides a description of habitat use and morphological information that ultimately will enhance our understanding of the challenging taxonomic issues that exist in this species complex (Marshall *et al.* 2006, Leyte-Manrique 2011).

Microhabitat and perch use

In this study, we found similarities in habitat use among females from eight populations of *S. grammicus*, as well as among males from the analyzed populations. The predictions of biomechanical models suggest that lizard species that inhabit a wide range of microhabitat types (e.g. bare soil, open areas, sandy areas and up to dense vegetation cover) are often cursorial (runners), with shorter anterior legs and longer hind legs (Herrel *et al.* 2001). Large hind limbs act as drivers to maximize acceleration, and such is the case for *S. grammicus* in this study (Herrel *et al.* 2001). Most saxicolous species (inhabiting rocks) have a dorsoventrally flattened body design that favors the use of crevices as refuges with shorter limbs that aid in turning ability (Adolph 1990; Herrel *et al.* 2002). Therefore, populations of *S. grammicus* may be classified as cursorial and moderately saxicolous, a designation that corresponds to the active foraging mode (Vitt & Congdon 1978), and not as a tree-climber as it had been previously classified (Ortega-Rubio & Arriaga 1990; Herrel *et al.* 2002). Based on our results, females from LMJ, LMZ, HUI, SMR, CER and CAH exhibited primarily terrestrial and cursorial behavior because lizards from these populations used open microhabitats composed of bare soil (Herrel *et al.* 2001), while females from PAC and EZA may be considered cursorial and saxicolous because they displayed a stronger correlation with microhabitats composed of greater vegetation cover and rocks, such as was observed in the CCA.

Males from PAC, LMJ, LMZ, CER and CAH can be considered cursorial because they were correlated with microhabitats composed of greater vegetation cover and bare soil, while a group of males from HUI, SMR and EZA may be considered cursorial and saxicolous because they were more related to microhabitats with

greater vegetation and ground and rock cover. The similarities shown in the use of microhabitats between sexes and populations could be a reflection of their evolutionary history, even though lizards of these populations inhabit different environments (Leyte-Manrique 2011). Therefore, our results indicate that these populations could be exhibiting a high degree of phylogenetic conservatism (Eliosa León *et al.* 2010; Perez-Mendoza *et al.* 2014).

High similarities were observed on perch height use between sexes and populations. The CCA showed that perch choice for females from PAC, LMJ, LMZ, SMR, CER and CAH was more correlated to perches based on the height of the nearest potential perch a lizard could occupy, while males from PAC, LMJ, EZA, and LMZ use the distance to the nearest perch as their main criterion. The use of both variables (height and distance) for both sexes could be related to their evolutionary history, and, therefore, these populations have similar behavioral and ecological characteristics (Eliosa León *et al.* 2010; Perez-Mendoza *et al.* 2014). Adolph (1990) did not find differences in perch use or height among manipulated populations in the field and laboratory studies of *Sceloporus occidentalis* Baird & Girard and *S. graciosus* Baird & Girard and concluded that this was probably due to low genetic differences. In addition, these similarities in relation to both perch characteristics in our study could be a strategy to avoid predators by moving to higher perches and places in close proximity to their shelters (Ramírez-Bautista & Benabib 2001).

Several studies have noted that perch height influences behavior and success of escape in both males and females (Herrel *et al.* 2001, 2002; Losos *et al.* 2003). This explanation is also supported by male behavior during the reproductive season when males display their sexual attributes to their rivals at higher perch sites to defend their territory and priority access to proximate females. This also reduces competition for space among different age classes and sexes, especially when resources are limited (Losos *et al.* 2003; Irschick *et al.* 2005a).

Morphology

The morphological traits analyzed in the eight populations showed significant differences among them. These differences could be due to adaptations to their specific environments, mainly influenced by the availability of resources such as microhabitat, food and predation pressures (Ballinger 1977; Irschick *et al.* 2005a,b). The fact that morphological variations were found within and among populations of *S. grammicus* (in

TIL, FEL, FOL, HDL and HDW) suggests an adaptive response to their respective environments. Similar patterns were found in other populations of the same species (Rubio-Pérez 2005).

Larger SVL in males and females from EZA (see Table 4) could be the outcome of low predation intensity, similar to what has been documented for *Urosaurus ornatus* (Dunham 1982) and other lizard species (Niewiarowski & Dunham 1994). This hypothesis is also supported by a tail regeneration study in *S. grammicus* (Leyte-Manrique *et al.* 2007). These authors observed that lizards with larger body size showed lower proportions of regenerated tails. Therefore, larger lizards possibly have a lower likelihood of being attacked or may be able to escape their predators due to their greater agility (Dunham 1982). Another possible explanation for the variation of body sizes among the eight populations could be that lizards with larger body size feed on larger, higher quality prey. Support for this explanation has been shown in other populations of *S. grammicus* (Leyte-Manrique & Ramírez-Bautista 2010) and other lizard species (Hierlihy *et al.* 2013). Morphologically, females from LMJ, LMZ, HUI, SMR, CER and CAH and males from HUI, SMR and EZA had longer limbs than females from PAC and EZA, and males from PAC, LMJ, LMZ, CER and CAH. This has shown that organisms with longer limbs can be more agile on sandy surfaces, bare soil and rocks, while with those with smaller limbs are more agile in branches, tree trunks and often use a lower height perch (Tulli *et al.* 2012). However, habitat use represents many challenges for all biological groups, and we cannot point to a specific morphology as exclusive for a microhabitat, especially in lizards, considering it is a group in which a single species can exploit different environments.

The ecological and morphological attributes of *S. grammicus* populations from this study seem to have a different degree of importance in patterns of predation in comparison to those that occur in other lizard species (Irschick *et al.* 2005b).

Sexual dimorphism

Sexual dimorphism has been observed as a common characteristic between males and females in species of the genus *Sceloporus* (Fitch 1978); however, studies carried out in species of this genus have also shown that males and females are similar in SVL (Butler *et al.* 2000; Ramírez-Bautista & Pavon 2009). Even though the ANOVAs showed that males were larger than females, the ANCOVAs indicated that there is no increase

in the morphological variables with increasing SVL between sexes. These results reveal that males and females can grow at the same rate. Therefore, we consider it is necessary to conduct future research on growth rates of both sexes of these eight populations, using growth models that allow us to know which sex can reach bigger sizes and grow at higher rates, similar to the research developed by Lemos-Espinal and Ballinger (1995) in the southeast of the state of Puebla. In an ecological context, Butler *et al.* (2000) note that sexual dimorphism in lizard species is strongly linked to the habitat use where males use different microhabitats and perches than females; however, there are very few studies that support this idea in the genus *Sceloporus*. Nevertheless, this is not true for species of the genus *Anolis* where multiple examples exist (Ramírez-Bautista & Benabib 2001; Butler & Losos 2002; Losos *et al.* 2006). Species and populations of single species that inhabit contrasting environments experience a wide gamut of conditions, such as differences in food availability, predation intensity and density of competition (Butler & Losos 2002; Losos *et al.* 2006). Therefore, considering all of these pressures collectively, body size, growth rates and high survivorship among age classes and between sexes should reflect an adaptive response to the environments in which species and populations inhabit (Butler *et al.* 2000), which could be taking place within the eight populations of our study.

The observed differences in tibia length and femur length, which were larger in males than in females, are characteristics that help the body to rise off the ground, to move and increase sprint speed, and are also likely associated with courtship and interactions among males (Filogonio *et al.* 2009). In addition, differences observed in head length and head width could be related to different prey items consumed between sexes, as well as aggressive interactions used to defend territory and subdue females for copulation. Such aggressive behavior has been observed in most lizard species of the genera *Sceloporus* (Fitch 1978) and *Anolis* (Ramírez-Bautista & Benabib 2001).

Our results can be compared to other studies engaged in the relationships among morphology, demography, behavior, life history, and microhabitat use (Vanhooydonck *et al.* 2000; Herrel *et al.* 2002; Rubio-Perez 2005). These also indicate that environmental conditions, interactions (e.g. competitive and predator-prey), and phylogeny are principal forces that may modify the morphology of these lizards.

Finally, our results showed that ecological and morphological variation exists among the eight populations sampled, and provide a baseline for a more in depth study focused on the taxonomic status of this species complex with future data including diet, reproductive characteristics, behavior, genetics, and population dynamics. Our study also revealed similarities in microhabitat and perch height use. This supports variations found in studies of *S. grammicus* of populations focused on genetics (Arévalo *et al.* 1991; Marshall *et al.* 2006), morphology (Lara-Góngora 2004; Hernandez-Salinas *et al.* 2010), ecology (Leyte-Manrique 2011; Bastiaans *et al.* 2013a; Bastiaans *et al.* 2014; Pérez-Mendoza & Zuñiga-Vega 2014), reproduction (Hernández-Salinas *et al.* 2010; Bastiaans *et al.* 2013b; Lozano *et al.* 2014, 2015) and life history (Ramírez-Bautista *et al.* 2004, 2005; Pérez-Mendoza *et al.* 2013, 2014). Nonetheless, future studies are needed regarding population ecology and functional ecology to enhance our understanding of how morphological characteristics operate in the different environments that these populations of *S. grammicus* inhabit.

ACKNOWLEDGMENTS

This study is part of the PhD research of the senior author (ALM), in the program of Doctorado en Biodiversidad y Conservación at the Universidad Autónoma del Estado de Hidalgo, Mexico. We thank D. L. DeSantis for significant improvement of the English version of the manuscript, and two anonymous reviewers for improving the quality of this paper. We thank CONACyT for the scholarship granted to the first author (ALM, #16301), and projects PROMEP/103.5/04/2751 and FOMIX-CONACYT-191908.

REFERENCES

- Adolph SC (1990). Perch height selection by juvenile *Sceloporus* lizards: Interspecific differences and relationship to habitat use. *Journal of Herpetology* **24**, 69–75.
- Arévalo E, Porter CA, González A *et al.* (1991). Population cytogenetics and evolution of the *Sceloporus grammicus* complex (Iguanidae) in central Mexico. *Herpetological Monographs* **5**, 79–115.
- Arévalo E, Davis SK, Lara G, Sites JW (1993). Parapatric hybridization between chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae): Structure of the Ajusco Transect. *Copeia* **1993**, 352–72.
- Arévalo E, Davis SK, Sites JW (1994). Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae) in central Mexico. *Systematic Biology* **43**, 387–418.
- Ballinger RE (1977). Reproductive strategies: Food availability as a resource of proximal variation in a lizard. *Ecology* **58**, 628–35.
- Bastiaans E, Méndez de la Cruz F, Rodríguez Hernández K, Flores Aguirre C, Sinervo B (2013a). Female reproductive investment in the mesquite lizard (*Sceloporus grammicus*) species complex (Squamata: Phrynosomatidae). *The Southwestern Naturalist* **58**, 335–43.
- Bastiaans E, Morinaga G, Castañeda Gaytán JG, Marshall JC, Sinervo B (2013b). Male aggression varies with throat color in 2 distinct populations of the mesquite lizard. *Behavioral Ecology* **24**, 968–81.
- Bastiaans E, Bastiaans MJ, Morinaga G *et al.* (2014). Female preference for sympatric vs. allopatric male throat color morphs in the mesquite lizard (*Sceloporus grammicus*) species complex. *PLoS ONE* **9**, e93197.
- Butler MA, Losos JB (2002). Multivariate sexual dimorphism, sexual selection, and adaptation in greater antillean *Anolis* lizards. *Ecological Monographs* **72**, 541–59.
- Butler MA, Schoener TE, Losos JB (2000). The relationship between sexual dimorphism and habitat use in greater Antillean *Anolis* lizards. *Evolution* **54**, 259–72.
- Dunham AE (1982). Demographic and life-history variation among populations of the iguanid lizard *Urosaurus ornatus*: Implications for the study of life-history phenomena in lizards. *Herpetologica* **38**, 208–21.
- Eliosa León HR, Nieto Montes de Oca A, Navarro Carbajal MC (2010). Conservadurismo filogenético de nicho ecológico un enfoque integral de la evolución. *Ciencias* **98**, 64–9.
- Fitch H (1978). Sexual size differences in the genus *Sceloporus*. *University of Kansas Science Bulletin* **51**, 441–61.
- Filogonio R, Galdino CAB, Cabral DPR *et al.* (2009). Sexual dimorphism in *Leposternon microcephalum* and *L. wuchereri* (Squamata: Amphisbaenidae) from Minas Gerais, southeastern Brazil. *Herpetologica* **65**, 353–62.

- Goodman BA, Miles DB, Schwarzkopf I (2008). Life on the rocks: Habitat use drives morphological and performance evolution in lizards. *Ecology* **89**, 3462–71.
- Hall WP (1973). Comparative population cytogenetics, speciation and evolution of the crevice using species of *Sceloporus* (PhD dissertation). Harvard University, Cambridge, Massachusetts.
- Hernández-Salinas U, Ramírez-Bautista A, Leyte-Manrique A, Smith GR (2010). Reproduction and sexual dimorphism in two populations of *Sceloporus grammicus* (Squamata: Phrynosomatidae) from Hidalgo, Mexico. *Herpetologica* **66**, 12–22.
- Herrel A, Meyers JJ, Vanhooydonck B (2001). Correlations between habitat use and body shape in a phrynosomatid lizard (*Urosaurus ornatus*): A population-level analysis. *Biological Journal of the Linnean Society* **74**, 305–14.
- Herrel A, Meyers JJ, Vanhooydonck B (2002). Relations between microhabitat use and limb shape in phrynosomatid lizards. *Biological Journal of the Linnean Society* **77**, 149–63.
- Hertz PE, Arima Y, Harrison A *et al.* (2013). Asynchronous evolution of physiology and morphology in *Anolis* lizards. *Evolution* **677**, 2101–13.
- Hierlihy CA, García-Collazo R, Chavez-Tapia CB, Mallory FF (2013). Sexual dimorphism in the lizard *Sceloporus siniferus*: Support for the intraspecific niche divergence and sexual selection hypotheses. *Salamandra* **49**, 1–6.
- Irschick DJ, Vitt LJ, Zani PA, Losos JB (1997). A comparison of evolutionary radiations in mainland and Caribbean *Anolis* lizards. *Ecology* **78**, 2191–203.
- Irschick DJ, Vanhooydonck B, Herrel A, Meyers J (2005a). Intraspecific correlations among morphology, performance and habitat use within a green anole lizard (*Anolis carolinensis*) population. *Biological Journal of the Linnean Society* **85**, 211–21.
- Irschick DJ, Carlisle E, Elstrott J *et al.* (2005b). A comparison of habitat use, morphology, clinging performance and escape behaviour among two divergent green anole lizard (*Anolis carolinensis*) populations. *Biological Journal of the Linnean Society* **85**, 223–34.
- Johnson MA, Revell LJ, Losos JB (2009). Behavioral convergence and adaptive radiation: effects of habitat use on territorial behavior in *Anolis* lizards. *Evolution* **64**, 1151–9.
- Lara-Góngora G (2004). A new species of *Sceloporus* (Reptilia, Sauria: Phrynosomatidae) of the *grammicus* complex from Chihuahua and Sonora, México. *Bulletin of the Maryland Herpetological Society* **40**, 1–45.
- Leaché AD (2010). Species three for spiny lizards (Genus *Sceloporus*): Identifying points of concordance and conflict between nuclear and mitochondrial data. *Molecular Phylogenetics and Evolution* **54**, 162–71.
- Lemos-Espinal JA, Ballinger RE (1995). Ecology of Growth of the High Altitude Lizard *Sceloporus grammicus* on the eastern slope of Iztaccihuatl Volcano, Puebla, México. *Transactions of the Nebraska Academy of Sciences* **22**, 77–85.
- Leyte-Manrique A (2011). *Especiación en el complejo Sceloporus grammicus: Evidencias morfológicas y ecológicas*. Ph.D. Universidad Autónoma del Estado de Hidalgo, Pachuca, Hidalgo, México.
- Leyte-Manrique A, Ramírez-Bautista A (2010). Diet of two populations of *Sceloporus grammicus* (Squamata: Phrynosomatidae) from Hidalgo, Mexico. *The Southwestern Naturalist* **55**, 98–103.
- Leyte-Manrique A, Hernández-Salinas U, Chávez-Calzada E *et al.* (2006). El complejo *Sceloporus grammicus*, un grupo de lagartijas en especiación. *Boletín de la Sociedad Herpetológica Mexicana* **14**, 10–7.
- Leyte-Manrique A, Ramírez-Bautista A, Hernández-Salinas A (2007). Contribución a la ecología de *Sceloporus grammicus*: presencia de cola regenerada en dos poblaciones del estado de Hidalgo, México. *Boletín de la Sociedad Herpetología Mexicana* **15**, 13–5.
- Losos JB, Leal M, Glor RE *et al.* (2003). Niche lability in the evolution of a caribbean lizard community. *Nature* **424**, 542–5.
- Losos JB, Glor RE, Kolbe JJ, Nicholson K (2006). Adaptation, speciation, and convergence: a hierarchical analysis of adaptive radiation in Caribbean *Anolis* lizards. *Annals of the Missouri Botanical Garden* **93**, 24–33.
- Lozano A, Ramírez-Bautista A, Uribe MC (2014). Oogenesis and ovarian histology in two populations of the viviparous lizard *Sceloporus grammicus* (Squamata: Phrynosomatidae) from the central Mexican Plateau. *Journal of Morphology* **275**, 949–50.
- Lozano A, Uribe MC, Ramírez-Bautista A (2015). Seasonal and continuous spermatogenesis in the viviparous lizard *Sceloporus grammicus*, a study of two populations in contrasting environments from the

- central Mexican Plateau. *Zoologischer Anzeiger* **254**, 72–85.
- Marshall JC, Arévalo E, Benavides E *et al.* (2006). Delimiting species: Comparing methods for mendelian characters using lizards of the *Sceloporus grammicus* (Squamata: Phrynosomatidae) complex. *Evolution* **60**, 1050–65.
- Mesquita DO, Gomes Faria R, Rinaldi Colli G *et al.* (2015). Lizard life-history strategies. *Austral Ecology*, doi:10.1111/aec.12276.
- Michaud JE, Echternacht AC (1995). Geographic variation in the life history of the lizard *Anolis carolinensis* and support for the pelvic constraint model. *Journal of Herpetology* **29**, 86–97.
- Niewiarowski PH, Dunham AE (1994). The evolution of reproductive effort in squamate reptiles: costs, trade-offs, and assumptions reconsidered. *Evolution* **48**, 137–45.
- Ortega-Rubio A, Arriaga L (1990). Seasonal abundance, reproductive tactics and resource partitioning in two sympatric *Sceloporus* lizards (Squamata: Iguanidae) of México. *Revista de Biología Tropical* **38**, 491–5.
- Pérez-Mendoza HA, Zúñiga-Vega JJ, Zurita-Gutiérrez YH *et al.* (2013). Demographic importance of the life-cycles components in *Sceloporus grammicus*. *Herpetologica* **69**, 411–35.
- Pérez-Mendoza HA, Zúñiga-Vega JJ, Martorell C *et al.* (2014). Patterns of spatio-temporal variation in the survival rates of a viviparous lizard: The interacting effects of sex, reproductive trade-offs, aridity, and human-induced disturbance. *Population Ecology* doi:10.1007/s10144-014-0447-0.
- Pérez-Mendoza HA, Zúñiga-Vega JJ (2014). A test of the fast–slow continuum model of life-history variation in the lizard *Sceloporus grammicus*. *Evolutionary Ecology* **16**, 235–48.
- Ramírez-Bautista A, Benabib M (2001). Perch height of the arboreal lizard *Anolis nebulosus* (Sauria: Polychrotidae) from a tropical dry forest of Mexico: Effect of the reproductive season. *Copeia* **2001**, 187–93.
- Ramírez-Bautista A, Pavón NP (2009). Sexual dimorphism and reproductive cycle in the arboreal spiny lizard *Sceloporus formosus* Wiegmann (Squamata: Phrynosomatidae) from central Oaxaca, Mexico. *Revista Chilena de Historia Natural* **82**, 553–63.
- Ramírez-Bautista A, Jiménez-Cruz E, Marshall JC (2004). Comparative life history for populations of the *Sceloporus grammicus* complex (Squamata: Phrynosomatidae). *Western North American Naturalist* **64**, 175–83.
- Ramírez-Bautista A, Maciel-Mata CA, Martínez-Morales MA (2005). Reproductive cycle of the viviparous lizard *Sceloporus grammicus* (Squamata: Phrynosomatidae) from Pachuca, Hidalgo, México. *Acta Zoologica Sinica* **51**, 998–1005.
- Ramírez-Bautista A, Hernández-Salinas U, Cruz-Elizalde R *et al.* (2014). *Los anfibios y reptiles de Hidalgo, México: Diversidad, Biogeografía y Conservación*. Sociedad Herpetológica Mexicana, A. C.
- Rzedowski J (1978). *Vegetación de México*. Limusa. Mexico. D.F.
- Rubio-Pérez I (2005). *Análisis comparativo de la morfología, historia de vida y uso del hábitat de distintas poblaciones del complejo Sceloporus grammicus: Un enfoque filogenético*. M.Sc. Instituto de Ecología. Universidad Nacional Autónoma de México, México. D.F.
- Schulte JA II, Losos JB, Cruz FB, Nuñez H (2004). The relationship between morphology, escape behaviour and microhabitat occupation in the lizard clade *Liolaemus* (Iguanidae: Tropidurinae: *Liolaemini*). *Journal of Evolutionary Biology* **17**, 408–20.
- Shapiro SS, Wilk MB, Chen HJ (1968). A comparative study of various tests of normality. *Journal of American Statist Association* **63**, 1343–72.
- Sites JW Jr, Camarillo JL, González A, Mendoza F *et al.* (1988). Allozyme variation and genetic divergence within and between three cytotypes of the *Sceloporus grammicus* complex (Sauria: Iguanidae) in central Mexico. *Herpetologica* **44**, 297–307.
- Sites JW Jr, Archie JW, Cole CJ, Flores-Villela O (1992). A review of phylogenetic hypotheses for the lizard genus *Sceloporus* (Phrynosomatidae): Implications for ecological and evolutionary studies. *Bulletin of the American Museum of Natural History* **213**, 1–110.
- Sokal RR, Rohlf FJ (1981). *Biometry: The Principles and Practice of Statistics in Biological Research*, 2nd edn. Freeman, San Francisco.
- Ter Braak CJF (1986). Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**, 1167–79.
- Ter Braak VJF, Verdonschot PFM (1995). Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences* **57**, 255–89.
- Tulli MJ, Abdala V, Cruz FB (2012). Effects of different

- substrates on the sprint performance of lizards. *The Journal of Experimental Biology* **215**, 774–84.
- Vanhooydonk B, Van Damme R, Aerts P (2000). Ecomorphological correlates of habitat partitioning in corsican lacertid lizards. *Functional Ecology* **14**, 358–68.
- Vitt LJ, Congdon JD (1978). Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *American Naturalist* **112**, 595–608.
- Zar JH (1999). *Biostatistical analysis*. Prentice-Hall, New Jersey, USA.
- Zúñiga-Vega JJ, Méndez-de la Cruz FR, Cuellar O (2008). Demography of the lizard *Sceloporus grammicus*: Exploring temporal variation in population dynamics. *Canadian Journal of Zoology* **86**, 1397–409.

Cite this article as:

Leyte-Manrique A, Hernández-Salinas U, Ramírez-Bautista A, Mata-Silva V, Marshall J (2017). Habitat use in eight populations of *Sceloporus grammicus* (Squamata: Phrynosomatidae) from the Mexican Plateau. *Integrative Zoology* **12**, 198–210.