
SAME SIZE BUT DIFFERENT BODY PROPORTIONS: SEXUAL DIMORPHISM IN THE MESQUITE LIZARD (*SCELOPORUS GRAMMICUS*)

OSWALDO HERNÁNDEZ-GALLEGOS¹, CAROLINA NAVA-ALMAZÁN¹, GISELA GRANADOS-GONZÁLEZ², GABRIEL SUÁREZ-VARÓN^{2,3,6}, JOSÉ FERNANDO MÉNDEZ-SÁNCHEZ⁴, AND JUSTIN LLOYD RHEUBERT⁵

¹Laboratorio de Herpetología, Facultad de Ciencias, Universidad Autónoma del Estado de México, Instituto Literario No. 100, Código Postal 50000, México

²Laboratorio de Morfofisiología de la Reproducción, Facultad de Ciencias, Universidad Autónoma del Estado México, Instituto Literario No. 100, Código Postal 50000, México

³Red de Investigación y Divulgación de Anfibios y Reptiles MX, Toluca de Lerdo, México

⁴Laboratorio de Ecofisiología Animal, Facultad de Ciencias, Universidad Autónoma del Estado México, Instituto Literario No. 100, Código Postal 50000, México

⁵Department of Biology, University of Findlay, 1000 North Main Street, Findlay, Ohio 45840, USA

⁶Corresponding author: Gabriel Suárez-Varón, email: biogabrielsv@gmail.com

Abstract.—Using linear morphometric measurements and applying the size dimorphism index (SDI), allometric analysis, along with both univariate and multivariate approaches, we evaluated sexual shape dimorphism in adults of the Mesquite Lizard (*Sceloporus grammicus*) from a population in central Mexico. Most SDI values (tail length, head length, head width, head height, femur length, and largest toe length) were biased towards males; the SDI for interlimb distance was biased towards females. In our population, this lizard does not show sexual dimorphism in SVL. Females showed an isometric relationship in five traits, and hypoallometry in femur and largest toe length. Males also showed an isometric relationship in five traits, and hypoallometry in the head length and largest toe length. Body proportions differed between sexes: tail length and femur length increased more rapidly with SVL for males than for females. Additionally, length, width and height of head, and largest toe length were greater in males than in females when accounting for SVL. The interlimb distance was greater for females than for males when accounting for SVL. PCA revealed clear separation between sexes along PC1 (accounting 75%). Tail length showed the highest loading associated with males, while the interlimb distance had the highest loading associated with females. A MANOVA showed significant multivariate sexual dimorphism over all seven morphometric variables. Although this population is not sexually dimorphic in SVL, the observed sexual dimorphism in body proportions was similar to those reported in other lizard species and may be influenced by selective pressures linked to both sexual and fecundity selection.

Key Words.—body shape; fecundity selection; sexual selection; Squamata

Resumen.—Usando mediciones de morfometría lineal y aplicando un índice del tamaño de dimorfismo sexual (SDI), análisis alométrico, junto con enfoques univariados y multivariados, evaluamos el dimorfismo sexual de la forma en adultos de la Lagartija del Mesquite (*Sceloporus grammicus*) de una población del centro de México. La mayoría de los valores de SDI (longitud de la cola, longitud de la cabeza, ancho de la cabeza, alto de la cabeza, longitud del fémur y longitud del dedo más largo) estuvieron sesgados hacia los machos; el SDI para la distancia interaxilar fue sesgado hacia las hembras. En nuestra población, esta lagartija no presenta dimorfismo sexual en la LHC. Las hembras mostraron una relación isométrica en cinco características e hipoalometría en la longitud del fémur y la longitud del dedo más largo. Los machos también mostraron una relación isométrica en cinco características e hipoalometría en la longitud de la cabeza y el dedo más largo. Las proporciones corporales difirieron entre sexos: la longitud de la cola y la longitud del fémur incrementaron más rápidamente con la LHC en machos que en las hembras. Adicionalmente, la longitud, ancho y alto de la cabeza, así como la longitud del dedo más largo, fueron más grandes en machos que en hembras al considerar la LHC. La distancia interaxilar fue mayor en hembras que en machos cuando controlamos con la LHC. PCA reveló clara separación entre sexos a lo largo del PC1 (que explicó el 75%). La longitud de la cola mostró la carga más alta asociada con los machos, mientras que la distancia interaxilar presentó la carga más alta asociada con las hembras. Un MANOVA confirmó un patrón multivariado significativo de dimorfismo sexual en la forma del cuerpo. Aunque esta población no es sexualmente dimórfica en LHC, el dimorfismo sexual observado en sus proporciones corporales fue similar a aquéllos registrados en otras especies de lagartijas y pueden estar influenciados por presiones selectivas ligadas a selección sexual y selección por fecundidad.

Palabras Clave.—forma corporal; selección por fecundidad; selección sexual; Squamata

INTRODUCTION

Sexual dimorphism studies are valuable because dimorphism is a characteristic often related to the fitness of individuals and is broadly distributed across different taxa (Shine 1989; Liang et al. 2025). In lizards, sexual dimorphism can be observed in different traits including body size (e.g., head, trunk and limbs), coloration, behavior, and physiology (Horr et al. 2023; Ali et al. 2024). Sexual dimorphism in lizards has been hypothesized to result from three main ecological and evolutionary processes (Schwarzkopf 2005; Aguilar-Moreno et al. 2010): (1) sexual selection (Shine 1989; Andersson 1994), which may favor larger head dimensions or longer limbs in males, including intrasexual competition among males, and/or mating success selection when males grasp females firmly with their jaws; (2) selection for fecundity, which may favor a greater interlimb distance in females by providing additional abdominal space for developing embryos (Olsson et al. 2002); and (3) ecological divergence with sexual dimorphism in various attributes being the cause of differences in diet to reduce competition (Shine 1989).

Within Phrynosomatid lizards, three hypotheses about patterns of sexual size dimorphism (SSD) have been tested: (1) absence of SSD; (2) female-biased SSD; and most commonly (3) male-biased SSD (Cox et al. 2007). Each of these patterns has evolutionary significance. For instance, absence of SSD may indicate that both sexes experience similar ecological pressures acting to maintain an optimal body size (Shine 1989). Female-biased SSD generally results from fecundity selection because larger females tend to exhibit greater abdominal volume and higher reproductive output (Toyama et al. 2025). In contrast, male-biased SSD is commonly associated with sexual selection, as larger males often have advantages in combat, territory defense, and courtship interactions (Cox et al. 2007).

The Mesquite Lizard (*Sceloporus grammicus*) is a viviparous species widely distributed in Mexico that inhabits different elevations and environments, including temperate forests and shrublands (Leyte-Manrique et al. 2017), and different microhabitats, including rocks, tree branches and trunks, bushes, concrete walls (Lara-Góngora 2004), and aquatic sites (Oviedo-Hernández et al. 2023). Like many lizard species, the adults are sexually dimorphic in body coloration with males displaying blue ventral patches and colored throat patches (Fig. 1), though



FIGURE 1. Ventral side of adult individual (left: female, snout-vent length = 57 mm; right: male, snout-vent length = 56 mm) Mesquite Lizard (*Sceloporus grammicus*) from El Cerrillo, Piedras Blancas, Toluca, Estado de México, Mexico, showing differences in body proportions between sexes. (Photographed by Oswaldo Hernández-Gallegos).

these color traits vary among populations of the species (Bastiaans et al. 2013).

Previous studies have shown that the genus *Sceloporus*, with 75% of extant taxa studied to date, exhibits male-biased SSD. This pattern includes populations of *S. grammicus*, and different morphometric characteristics (Hernández-Salinas et al. 2010; Jiménez-Arcos et al. 2017; Leyte-Manrique et al. 2017; Lozano et al. 2023), where the males are polygynous (Degnan and Arévalo 2004). In the polygynous species, association between mating system and sexual dimorphism have been identified with males significantly larger than females (Sæther et al. 1986). This widespread occurrence suggests that male-biased SSD may represent the ancestral condition within *Sceloporus* (Jiménez-Arcos et al. 2017). There is variance observed in SSD by parity mode, however, as viviparous species typically possess greater abdominal volume resulting from prolonged gestation period versus oviparous species (Jiménez-Arcos et al. 2017).

Dimorphism in body proportions may occur independently of SSD because body size and the morphology of individual structures can evolve under different selective pressures and follow distinct

allometric trajectories (Cox et al. 2007; Valdecantos et al. 2019). Larger heads in males are frequently associated with increased bite force, whereas longer limbs, digits, and tails can enhance sprint, balance, and locomotor performance. Conversely, in females, interlimb distance generally increases fecundity (Jiménez-Arcos et al. 2017; Valdecantos et al. 2019). These morphological traits allow shape dimorphism to arise even when body size does not differ between sexes.

Despite being one of the most widely distributed geographic and morphologically variable species in the genus, *S. grammicus* exhibits geographic variation in life-history traits. Therefore, the intensity of sexual and natural selection may differ in different populations (Jiménez-Arcos et al. 2017; Lozano et al. 2023). Many populations across central Mexico remain unstudied, and published evidence indicates that sexual dimorphism can differ among localities due to environmental, ecological, and genetic factors (Lozano et al. 2023). Therefore, population-level analyses are essential to understand the evolutionary mechanisms shaping sexual dimorphism in this species.

Several studies have been carried out at El Cerrillo, Piedras Blancas, Toluca de Lerdo, Estado de México, Mexico, related to the natural history of *S. grammicus*. The reproductive activity is seasonal (Granados-González et al. 2025), including late pregnancy during winter (Suárez-Varón et al. 2024), with births occurring in spring (Sánchez-Manjarrez 2024). Moreover, preliminary evidence suggests no sexual dimorphism between adults in body size and weight (Sánchez-Manjarrez 2024). Our study provides the first detailed assessment of sexual dimorphism for this population from central Mexico, contributing new data to interpret how both sexual and fecundity selection might influence SSD and body proportions in the species and between different populations. We tested whether males show larger head dimensions, limbs, digits, and tails than females (sexual selection), and if females exhibit greater interlimb distance than males (fecundity selection).

MATERIALS AND METHODS

Study site.—During January, February, March, August, and October of 2024, we conducted fieldwork at El Cerrillo, Piedras Blancas, Toluca de Lerdo, Estado de México, Mexico (located at 19.41181°N, -99.70067°W, datum WGS84, 2,605 m elevation). Mean annual temperature is 8.2° C, and

annual rainfall is 738.6 mm, with most precipitation occurring between June and September; the study site is characterized by an arboreal stratum (willows, *Salix* sp.; cypresses, *Cupressus* sp.; and she-oaks, *Casuarina* sp.), and an herbaceous stratum containing over 118 species of angiosperms (Álvarez-Lopezello et al. 2016). The site is subject to anthropogenic disturbance due to agricultural practices, livestock, and constant human presence (Gómez-Benitez et al. 2023).

Lizard processing.—We captured lizards by hand and marked using a micro-cautery (Bovie Medical Change-A-Tip, Bovie Medical Corporation, Clearwater, Florida, USA) to apply ventral markings following methodology found in Ekner et al. (2011). Only adult individuals were included, determined in males by the minimum snout-vent length (SVL) at which males displayed blue ventral patches and active femoral pores (≥ 46 mm), and in females, the reproductive condition of pregnancy determined by abdominal palpation (≥ 50 mm SVL). After their capture, we determined the sex of individuals and their SVL and tail length (TL) using a transparent plastic ruler (± 1 mm). For TL, we only measured individuals with fully intact tails without evidence of previous caudal autotomy. Additionally, we measured head length (HL), head width (HW), head height (HH), interlimb distance (ILD), femur length (FL), and largest toe length (LTL) with a digital caliper (± 0.01 mm); both FL and LTL were measured from the left side of each lizard to ensure uniformity in the measurements. We used TL, HL, HW, HH, FL, and LTL to evaluate sexual selection in males; the ILD is a common biometric variable used to test the fecundity selection in females. After measurements, we released individuals at their point of capture.

Univariate and SDI analysis.—Before analyses, we evaluated parametric assumptions of normality and homogeneity of variances using both raw and \log_{10} transformed data (Schwarzkopf 2005), which were checked using Shapiro-Wilks and Levene tests, respectively. We compared shapes of males and females using Analysis of Co-Variance (ANCOVA) for each trait, with sex as a fixed factor and SVL as the covariate (Schwarzkopf 2005). For each trait, models included the interaction Sex \times SVL to test for heterogeneity of slopes between sexes.

We also calculated the size dimorphism index (SDI) for each trait using the compressed SDI formula (Lovich and Gibbons 1992):

$$SDI = \left[\left(\frac{\text{size of largest sex}}{\text{size of smallest sex}} \right) - 1 \right] \times 100$$

which makes use of the average values of females and males of the variables to be compared. We multiplied the SDI value by 100 to get the percentage of each trait. We calculated SDIs for SVL, TL, HL, HW, HH, ILD, FL, and LTL (see Zhao and Liu 2014). Following Nemes and Hartel (2010), we applied the SDI adjustment with the Delta method, which estimates a linear function that can be used for statistical inference and as a measure of standard deviation:

$$\sigma_{SDI}^2 = \frac{\theta_y^2 \sigma_x^2 + \theta_x^2 \sigma_y^2}{\theta_y^4}$$

In this case, θ_x represents the mean value of the trait in the larger sex, θ_y in the smaller sex, and σ_x^2 and σ_y^2 the variances of θ_x and θ_y respectively, and we performed a Two-sample Hypothesis Test to evaluate whether SDI differed significantly between sexes (H_0 : SDI = 0).

Allometric analysis.—We evaluated the importance of allometry in the sexual dimorphism of *S. grammicus* through Least Squares Linear Regression. We considered that the growth of a body dimension was isometric with respect to SVL if the 95% confidence interval (CI) for the slope value included the value of 1, while values < 1 or values > 1 were interpreted as hypoallometric or hyperallometric, respectively (Fairbairn 1997; López-González et al. 2025).

Multivariate analysis.—We performed a Principal Component Analysis (PCA) as an exploratory tool to visualize variation in multivariate patterns of sexual dimorphism on seven morphometric variables standardized in proportions of the SVL. To minimize data variance and because the variables were on similar scale, we used a variance-covariance matrix for the PCA. To test for significant multivariate differences in morphometric traits between sexes, we performed a Multivariate Analysis of Variance (MANOVA) using sex as the grouping factor and the standardized morphometric traits (proportions of SVL) as response variables. When the MANOVA indicated significant multivariate differences, we then used One-way Analysis of Variance (ANOVA) to identify which individual traits contributed to the multivariate differences between sexes (Germano

1993). We performed all statistical analyses in Statgraphics Centurion ver. XVI. I, SPSS ver. 25, and in PAST (Paleontological Statistics) ver. 4.15. In all tests, $\alpha = 0.05$.

RESULTS

Normality and homoscedasticity.—Raw data met assumptions of normality for all traits and homoscedasticity for four of the eight variables. \log_{10} transformation improved distributional properties for most variables (Shapiro-Wilk Test, P values = 0.138–0.96 for overall models; Levene’s Test, P values = 0.059–0.605 for seven traits); however, tail length (TL) remained heteroscedastic ($P < 0.001$). Despite this, we retained TL in subsequent analyses because Least Squares Linear Models are robust to moderate heteroscedasticity, particularly when inference focuses on regression slopes rather than mean differences (Quinn and Keough 2002), and results involving TL were corroborated by complementary multivariate analyses (PCA and MANOVA), reducing the likelihood that conclusions were driven by violations of variance homogeneity.

Univariate and SDI analysis.—We captured 100 adult lizards (59 females and 41 males). SVL and measures of body traits were similar between the sexes (Table 1). SDI values we estimated for SVL was 0.63 ± 0.01 (standard deviation) were biased towards males, but the differences were not significant ($Z = 0.34$, $P = 0.730$). In contrast, SDI values estimated for TL, HL, HW, HH, FL, and LTL were significantly biased towards males: adult males were 13.63%, 9.49%, 7.03%, 8.96%, 12.02%, and 8.44% larger than adult females for these traits, respectively. The SDI value we estimated for ILD was biased towards females, which was significantly 7.51% larger than adult males ($P < 0.001$, Table 1).

Tail length and FL increased more rapidly with SVL in males than in females (Fig. 2, Table 2). At the same SVL, males exhibited significantly greater values in four traits (HL, HW, HH, LTL) compared to females; however, no significant differences were found in the regression slopes of these traits with SVL for both sexes (Fig. 2, Table 2), although the intercepts were significantly different ($P < 0.001$ for all cases). Similarly, at the same SVL, ILD was greater in females than in males, without significant differences in regression slopes between sexes (Fig. 2, Table 2), although the intercepts were different ($P < 0.001$). Further supporting these results, for all

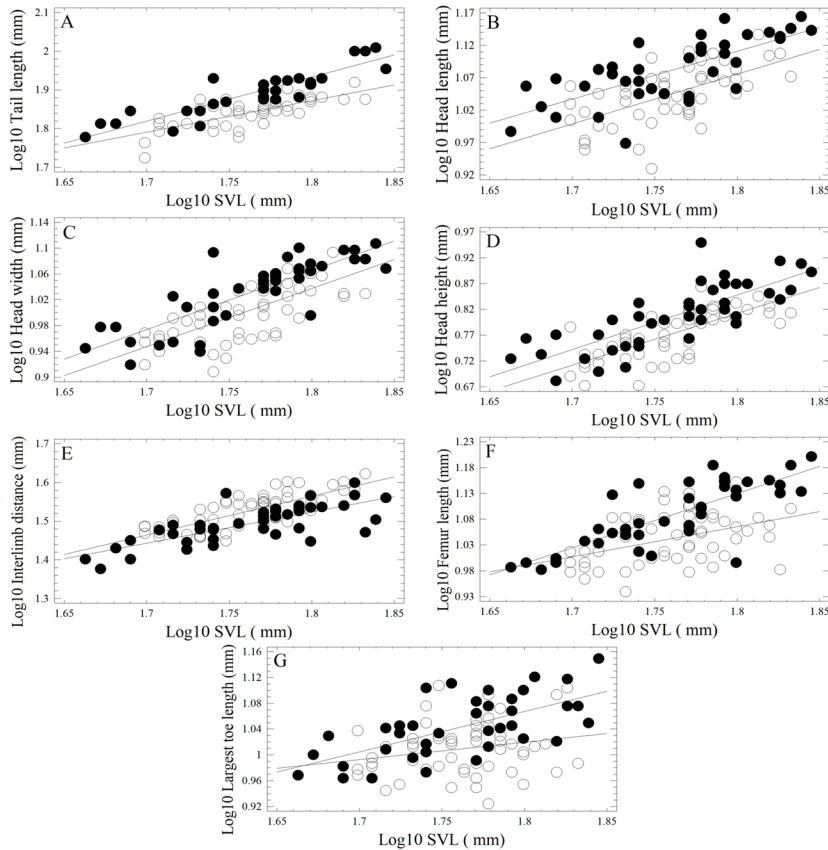


FIGURE 2. Log_{10} - log_{10} regression of (A) tail length, (B) head length, (C) head width, (D) head height, (E) interlimb distance, (F) left femur length, and (G) largest toe of the left hind leg against snout-vent length (SVL) for both adult female (open circles) and adult male (solid circles) Mesquite Lizard (*Sceloporus grammicus*) from El Cerrillo, Piedras Blancas, Toluca, Estado de México, Mexico.

traits except ILD, male regression lines were most parallel to but consistently above those of females, whereas ILD showed the opposite pattern, with the female regression line parallel to and consistently above that of males (Fig. 2).

Allometric analysis.—We observed isometry and hypoallometry in the lizards studied. Females showed an isometric relationship in the TL, HL, HW, HH, ILD, and hypoallometry in the FL, and LTL. Males showed isometry in the TL, HW, HH, ILD, and FL, whereas the remaining traits (HL, and LTL) were

TABLE 1. Sample size (n), mean (\pm standard deviation), range (in parentheses), and sexual size dimorphism index (SDI; \pm standard deviation) of snout-vent length (SVL), tail length (TL), head length (HL), head width (HW), head height (HH), interlimb distance (ILD), femur length (FL), and largest toe length (LTL) of adult female and adult male Mesquite Lizard (*Sceloporus grammicus*) from El Cerrillo, Piedras Blancas, Toluca, Estado de México, Mexico. All morphometric measures are in millimeters.

Trait	Females		Males		Sexual Dimorphism Index		
	n	Mean	n	Mean	SDI	Z	P-value
SVL	59	57.8 \pm 4.5 (50–68)	41	58.2 \pm 6.3 (46–70)	0.63 \pm 0.01	0.34	0.730
TL	48	69.6 \pm 5.7 (53–83)	29	79.1 \pm 11.6 (60–102)	13.63 \pm 0.03	5.41	< 0.001
HL	57	11.1 \pm 1.1 (8.5–13.7)	41	12.2 \pm 1.3 (9.3–14.6)	9.49 \pm 0.02	4.42	< 0.001
HW	59	10.1 \pm 0.99 (8.1–12.4)	41	10.8 \pm 1.3 (8.3–12.8)	7.03 \pm 0.02	3.15	< 0.001
HH	59	6.0 \pm 0.62 (4.7–7.3)	41	6.5 \pm 0.95 (4.8–8.9)	8.96 \pm 0.03	3.44	< 0.001
ILD	59	33.7 \pm 3.5 (28.1–41.9)	41	31.3 \pm 3.6 (23.8–39.7)	7.51 \pm 0.02	3.29	< 0.001
FL	59	11.1 \pm 1.2 (8.7–14.2)	41	12.4 \pm 1.8 (9.6–15.9)	12.02 \pm 0.04	4.43	< 0.001
LTL	59	10.3 \pm 0.98 (8.4–12.8)	41	11.1 \pm 1.2 (9.2–14.1)	8.44 \pm 0.02	3.9	< 0.001

TABLE 2. Log₁₀-log₁₀ regression statistics, allometric relations, and comparison of regression slopes of the relationships by Analysis of Co-Variance (ANCOVA) among tail length (TL), head length (HL), head width (HW), head height (HH), interlimb distance (ILD), femur length (FL), and largest toe length (LTL), against snout-vent length of adult females and adult males of Mesquite Lizard (*Sceloporus grammicus*) from El Cerrillo, Piedras Blancas, Toluca, Estado de México, Mexico. Sexes are F = females and M = males, and df = degrees of freedom.

Trait	Sex	Log ₁₀ -log ₁₀ regression and allometric analysis							ANCOVA Slopes comparison		
		<i>r</i> ²	<i>F</i> -value	df	Slope	95% CI	Result	Intercept	<i>F</i> -value	df	<i>P</i> -value
TL	F	0.53	51.33	1,46	0.81	0.57-1.07	Isometry	0.41	4.23	1,74	0.0433
	M	0.80	111.13	1,27	1.14	0.88-1.34	Isometry	-0.11			
HL	F	0.36	31.18	1,55	0.77	0.50-1.02	Isometry	-0.31	0.02	1,95	0.8780
	M	0.53	44.77	1,39	0.74	0.55-0.91	Hypoallometry	-0.22			
HW	F	0.51	58.25	1,57	0.90	0.68-1.08	Isometry	-0.58	0.01	1,97	0.9057
	M	0.69	87.02	1,39	0.92	0.71-1.09	Isometry	-0.58			
HH	F	0.54	66.82	1,57	1.01	0.77-1.23	Isometry	-1.00	0.09	1,97	0.7638
	M	0.63	65.84	1,39	1.06	0.81-1.26	Isometry	-1.06			
ILD	F	0.59	82.39	1,57	1.00	0.83-1.16	Isometry	-0.24	1.64	1,97	0.2027
	M	0.57	51.23	1,39	0.80	0.58-1.04	Isometry	0.08			
FL	F	0.17	11.73	1,57	0.58	0.28-0.90	Hypoallometry	0.01	4.75	1,97	0.0318
	M	0.62	66.25	1,39	1.05	0.87-1.25	Isometry	-0.76			
LTL	F	0.05	3.05	1,57	0.27	-0.05-0.57	Hypoallometry	0.53	3.27	1,97	0.0739
	M	0.41	27.29	1,39	0.63	0.41-0.84	Hypoallometry	-0.06			

hypoallometric (Table 2).

DISCUSSION

Multivariate analysis.—The first two principal components explained 89% of the total variance among the 100 individuals analyzed (Fig. 3), with PC1 accounting for 75% and PC2 14%. Sexual dimorphism was highly explained in PC1 and PC2 expressed secondary morphological variation within sexes. TL showed the highest loading (0.9) associated with males, and ILD had the highest negative loading (-0.2) associated with females. This indicates that males had longer tails than females, whereas females had larger ILD than males. The other five morphometric traits were larger in males than in females, but their loadings were too small (< 0.1) to be considered sexual dimorphic traits in this analysis. PC2 showed variation within individuals of both sexes, in this case, again a higher loading of ILD (0.9) was associated to females, and the loading of FL (-0.16) to males. The MANOVA showed significant multivariate sexual dimorphism overall the seven morphometric variables (Pillai's trace = 0.46, $F_{7,92} = 11.52$, $P < 0.001$, Wilks Lambda = 0.418, $F_{7,92} = 13.33$, $P < 0.001$). There were significant sex differences in all morphometric traits (P values all < 0.001 for overall models), including the same tendencies as those recorded in SDI values.

We found no evidence for sexual dimorphism in SVL in our population of *S. grammicus*; however, adult males and adult females differed considerably in body proportions. As was hypothesized previously, male morphometric variables (including HL, HW, HH, FL, LTL, and TL) were significantly larger than females, except interlimb distance, which was greater for females. Our results, however, do not simply corroborate previous patterns reported for other lizards. Instead, these results reveal an undocumented combination of traits in this central Mexican population. Males exhibit proportional dimorphism despite the absence of SSD in SVL, and females show an enlarged ILD, patterns consistent with predictions from sexual and fecundity selection, respectively. These findings provide further evidence showing that body size and body shape dimorphism can be decoupled and should be treated independently in analyses (Schwarzkopf 2005; Cruz-Elizalde et al. 2020; Feria-Ortiz et al. 2021; Xiong et al. 2022; Lozano et al. 2023). These differences represent an overall multivariate pattern of sexual dimorphism in body shape, rather than isolated differences among individual traits.

In several families of lizards, such as Iguanidae, Polychrotidae, Tropicuridae, Varanidae, Teiidae, and Phrynosomatidae, SSD is significantly male-biased

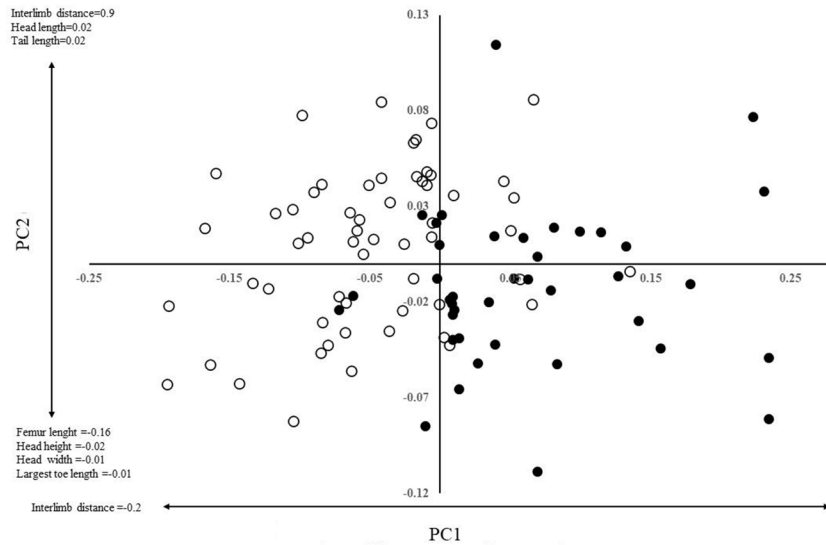


FIGURE 3. Principal Component Analysis (PCA) showing sexual dimorphism in the Mesquite Lizard (*Sceloporus grammicus*) from El Cerrillo, Piedras Blancas, Toluca, Estado de México, Mexico. Points represent the PCA scores of 100 adult individuals (59 females and 41 males). PC1 explained 75% of the variance and PC2 14%. Double pointed arrows indicate the direction in which the morphometric variables and their loadings increase.

(Cox et al. 2007). Our results, and previous studies on the *Sceloporus* genus (Fitch 1978; Jiménez-Arcos et al. 2017), suggest that SSD varies both inter and intra-specifically. In *S. grammicus* from Estado de México, Mexico (this study), *S. poinsettii* from Durango, Mexico (Lemos-Espinal et al. 2014), and *S. spinosus* from Puebla, Mexico (Méndez-de la Cruz et al. 2013), there is an absence of SSD. In *S. bicanthalis* from Estado de México, Mexico (Sánchez-Carpio 2010) and *S. virgatus* from Arizona, USA (Abell 1998), SSD is female-biased, and in *S. grammicus* from Hidalgo, Mexico (Ramírez-Bautista et al. 2012), and *S. poinsettii* from Chihuahua and Coahuila, Mexico, and Texas, USA (Fitch 1978), SSD is male-biased. This variation is likely driven by differences in habitat structure, prey availability, predation, male competition, and fecundity for females across localities, which can modify body size (Herrel et al. 2002; Jiménez-Arcos et al. 2017).

Sexual selection.—In species in which sexual selection is intense, traits that reinforce abilities to acquire territories and/or escape from predators in males are favored (Olsson et al. 2002). Previous studies on variation in SSD in allometry favoring males has provided evidence that males have longer hind limbs (i.e., males of *S. grammicus* have longer FL, and LTL than females of the same size), which facilitate locomotion and allow greater running speed (Aguilar-Moreno et al. 2010). Male *S. grammicus* are territorial (Lozano et al. 2020), which suggests they

may spend a large portion of their time defending territory and searching for females (Schwarzkopf 2005); further studies should test this hypothesis.

Male *S. grammicus* have longer, higher, and wider heads than the females. In lizards, bite force tends to be greater in males due to larger head size, variation in skull shape, and the jaw adductor musculature (Herrel et al. 2007). Mandibular shape and size provide an advantage in holding females and, therefore, greater reproductive success (Scharf and Meiri 2013). Based on previous studies, in territorial species such as *S. grammicus* (Lozano et al. 2020), sexual selection also could favor larger heads in males if differences in fighting ability translate into the ability to maintain a territory and confer an advantage in intrasexual agonistic encounters (Scharf and Meiri 2013). Additionally, some studies have hypothesized that sexual dimorphism in head shape could be the result of differences in diet (Vincent et al. 2004), but no evidence of diet divergence between male and female *S. grammicus* has been found (Leyte-Manrique and Ramírez-Bautista 2010), lending support to sexual selection as a driving force for variation in head shape in this species.

Male *S. grammicus* also have larger TL, which lengthens more quickly with SVL than females. Male lizards of several species have longer tails than similarly sized females (Powell and Russell 1985; Barbadillo and Bauwens 1997; Ansell et al. 2014). A longer tail in males of *S. grammicus* could result from male aggressive behavior through tail-whipping

(Ortiz et al. 2016). Within snakes, however, three hypotheses have been proposed: (1) the morphological constraint hypothesis, which states males have longer tails to accommodate the hemipenes; (2) the female reproductive output hypothesis, which suggests females have shorter tails to increase reproductive output; and (3) the male mating ability hypothesis, which suggests sexual selection favors longer tails in males because longer tails may enhance mating performance and reproductive success (King 1989). Similar mechanisms have also been tested in lizards. For example, the morphological constraint hypothesis is supported by evidence that males possess a proportionally longer proximal tail region where the hemipenes are located; males with longer tails show higher reproductive success, supporting the mating-ability hypothesis (Barbadillo and Bauwens 1997). In females, reproductive output is constrained by abdominal volume rather than tail length (Warne 2008), and these differences may reflect sex-specific ecological pressures. In *S. grammicus*, the tail may serve an intersexual function related to survival and reproduction, as evidenced by interpopulation variation in tail regeneration frequency. For example, in our population, females exhibit a higher percentage of regenerated tails than males (Suárez-Varón et al. 2024), whereas in other populations there is the opposite trend with males showing a greater proportion of regenerated tails than females (Leyte-Manrique et al. 2007). Differences in predation intensity, microhabitat use, or sex-specific activity may alter the probability of tail loss (Suárez-Varón et al. 2024).

Fecundity selection.—There is a strong selection pressure for fecundity on the body of female lizards (Scharf and Meiri 2013). When female and male *S. grammicus* with the same SVL were compared, females have a significantly longer ILD. This character emerged as the main female-biased trait supporting its interpretation as a trait under fecundity selection. Greater ILD is a commonly observed form of sexual dimorphism favoring females of other lizard families including, but not restricted to, Teiidae (Aguilar-Moreno et al. 2010), Lacertidae (Kaliontzopoulou et al. 2010), Scincidae (Feria-Ortiz et al. 2021), Agamidae (Xiong et al. 2022), and Phrynosomatidae (González-Ruiz 2014). Selection for fecundity in females through their larger ILD may provide extra space for developing offspring (Olsson et al. 2002; Schwarzkopf 2005) and/or for maximizing the litter size in each reproductive event

(Aguilar-Moreno et al. 2010). In our population, this pattern may reflect selection for increased abdominal capacity, although we did not record reproductive output. Future studies comparing sexual dimorphism in ILD and reproductive fecundity could help to test hypotheses regarding variation in this dimorphic character.

Linear sexual dimorphism without morphometric sexual dimorphism.—In general, both linear and geometric morphometrics traits often co-occur as in the genera *Phymaturus* and *Podarcis* because neither display sexual dimorphism in heads of these lizards (Kaliontzopoulou et al. 2007; González-Marín et al. 2016). This congruency is not always the pattern. The results of evaluation on the differences between sexes in the head shape of *S. grammicus* showed that there is no sexual dimorphism in this trait (Aldo Gómez-Benitez et al., unpubl. data), indicating that size differences can occur in the absence of shape differences. The sexual dimorphism in body proportions observed in our study contrasts with the results found using only geometric morphometry at the same population (Aldo Gómez-Benitez et al., unpubl. data), emphasizing the importance of deeper investigations of sexual size dimorphism beyond linear and geometric morphometrics. Further research is needed to assess the functional consequences of sexual differences in these morphometrics traits including head size between sexes in *Sceloporus grammicus*.

Acknowledgments.—We thank the students of the Laboratorio de Herpetología of the Facultad de Ciencias for their valuable support in the field, and the Facultad de Ciencias Agrícolas (especially to Aaran Aquilino Morales Pérez) for the facilities provided for the completion of this research. This study was financially supported by Universidad Autónoma del Estado de México, grant number 7037/2024CIB. The Mexican government (Secretaría de Medio Ambiente y Recursos Naturales, SEMARNAT) provided the permit (15/K5-0395/10/21) to capture the lizards. We thank the Secretaría de Ciencia, Humanidades, Tecnología e Innovación (SECIHTI), for postdoctoral scholarship to GS-V (CVU: 693584).

LITERATURE CITED

Abell, A.J. 1998. Phenotypic correlates of male survivorship and reproductive success in the Striped Plateau Lizard, *Sceloporus virgatus*.

- Herpetological Journal 8:173–180.
- Aguilar-Moreno, M., F.J. Rodríguez-Romero, A. Aragón-Martínez, J.A. Muñoz-Manzano, G. Granados-González, and O. Hernández-Gallegos. 2010. Dimorfismo sexual de *Aspidoscelis costata costata* (Squamata: Teiidae) en el sur del Estado de México, México. *Revista Chilena de Historia Natural* 83:585–592.
- Ali, A., S. Spears, P.L. Vaughn, C. Colwell, E.H. Livingston, W. McQueen, A. Schill, D.G. Reichard, E.J. Gangloff, and K.M. Brock. 2024. Physiological phenotypes differ among color morphs in introduced Common Wall Lizards (*Podarcis muralis*). *Integrative Zoology* 19:505–523.
- Álvarez-Lopezello, J., I.V. Rivas-Manzano, L.I. Aguilera-Gómez, and M. González-Ledesma. 2016. Diversidad y estructura de un pastizal en El Cerrillo, Piedras Blancas, Estado de México, México. *Revista Mexicana de Biodiversidad* 87:980–989.
- Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton, New Jersey, USA.
- Ansell, A.K., R. Garcia-Collazo, C.B. Chavez Tapia, and F.F. Mallory. 2014. Sexual dimorphism and thermoregulatory behavior in the Long-Tailed Spiny Lizard, *Sceloporus siniferus* from Mexico. Pp. 121–142 *In* *Lizards: Thermal Ecology, Genetic Diversity and Functional Role in Ecosystems*. Kiernan, M.P. (Ed). Nova Science Publishers, New York, New York, USA.
- Barbadillo, L.J., and D. Bauwens. 1997. Sexual dimorphism of tail length in lacertid lizards: test of a morphological constraint hypothesis. *Journal of Zoology* 242:473–482.
- Bastiaans, E., G. Morinaga, J.G. Castañeda Gaytán, J.C. Marshall, and B. Sinervo. 2013. Male aggression varies with throat color in 2 distinct populations of the Mesquite Lizard. *Behavioral Ecology* 24:968–981.
- Cox, R.M., M.A. Butler, and H.B. John-Alder. 2007. The evolution of sexual size dimorphism in reptiles. Pp. 38–49 *In* *Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism*. Fairbairn, D.J., T. Szekely, and W.U. Blanckenhorn (Eds.). Oxford University Press, Oxford, UK.
- Degnan, P.H., and E. Arévalo. 2004. Isolation of microsatellite loci in *Sceloporus grammicus* (Squamata, Phrynosomatidae). *American Journal of Undergraduate Research* 2:1–11. <https://doi.org/10.33697/ajur.2004.003>.
- Ekner, A., Z. Sajkowska, K. Dudek, and P. Tryjanowski. 2011. Medical cautery units as a permanent and non-invasive method of marking lizards. *Acta Herpetologica* 6:229–236.
- Fairbairn, D.J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology, Evolution, and Systematics* 28:659–687.
- Feria-Ortiz, M., C. Pérez-Malvárez, G. Bribiesca-Escutia, and E.M. Ramírez-Morales. 2021. Dimorfismo sexual en tamaño y forma en una población de escíncidos de cola azul del género *Plestiodon* (Scincidae). *Acta Biológica Colombiana* 26:393–403.
- Fitch, H.S. 1978. Sexual size differences in the genus *Sceloporus*. *University of Kansas Science Bulletin* 51:441–461.
- Germano, D.J. 1993. Shell morphology of North American tortoises. *American Midland Naturalist* 129:319–335.
- Gómez-Benitez, A., E.A. Reyes Velázquez, and O. Hernández-Gallegos. 2023. High ectoparasitic leech load in the Mountain Tree Frog *Hyla eximia* (Hylidae) caused by anthropization. *Revista Latinoamericana de Herpetología* 6:204–208.
- González-Marín, A., A. Morando, and L.J. Avila. 2016. Morfología lineal y geométrica en un grupo de lagartijas patagónicas del género *Phymaturus* (Squamata: Liolaemini). *Revista Mexicana de Biodiversidad* 87:399–408.
- González-Ruiz, M. 2014. Dimorfismo sexual en una población de la lagartija *Sceloporus megalepidorus* (Squamata: Phrynosomatidae) que habita en una comunidad de matorral xerófilo al este de Puebla. M.Sc. Thesis, Universidad Nacional Autónoma de México, México. 48 p.
- Granados-González, G., G. Suárez-Varón, E. Oviedo-Hernández, J.R. Flores-Santín, J.L. Rheubert, and O. Hernández-Gallegos. 2025. Testicular pigmentation in the Mesquite Lizard, *Sceloporus grammicus* in a central Mexico population. *Sonoran Herpetologist* 38:195–197.
- 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.
- Herrel, A., L. McBrayer, and P. Larson. 2007. Functional basis for sexual differences in bite force in the lizard *Anolis lineatopus*. *Biological Journal*

- of the Linnean Society 91:111–119.
- Horr, D.M., A.A. Payne, K.D. McEntire, and M.A. Johnson. 2023. Sexual dimorphism in dynamic body color in the Green Anole lizard. *Behavioral Ecology Sociobiology* 77:1–13.
- Jiménez-Arcos, V.H., S. Sanabria-Urbán, and R. Cueva del Castillo. 2017. The interplay between natural and sexual selection in the evolution of sexual size dimorphism in *Sceloporus* lizards (Squamata: Phrynosomatidae). *Ecology and Evolution* 7:905–917.
- Kaliontzopoulou, A., M.A. Carretero, and G.A. Llorente. 2007. Multivariate and geometric morphometrics in the analysis of sexual dimorphism variation in *Podarcis* lizards. *Journal of Morphology* 268:152–165.
- Kaliontzopoulou, A., M.A. Carretero, and G.A. Llorente. 2010. Sexual dimorphism in traits related to locomotion: ontogenetic patterns of variation in *Podarcis* wall lizards. *Biological Journal of the Linnean Society* 99:530–543.
- King, R.B. 1989. Sexual dimorphism in snake tail length: sexual selection, natural selection, or morphological constraint? *Biological Journal of the Linnean Society* 38:133–154.
- Lara-Góngora, G. 2004. A new species of *Sceloporus* (Reptilia, Sauria: Phrynosomatidae) of the *grammicus* complex from Chihuahua and Sonora, Mexico. *Bulletin of the Maryland Herpetological Society* 40:1–41.
- Lemos-Espinal, J.A., G.R. Smith, J.B. Iverson, and J.M. Morales Sandoval. 2014. Lack of sexual size dimorphism in *Sceloporus poinsettii* from Durango, Mexico. *Bulletin of the Maryland Herpetological Society* 50:8–11.
- Leyte-Manrique, A., and A. Ramírez-Bautista. 2010. Diet of two populations of *Sceloporus grammicus* (Squamata: Phrynosomatidae) from Hidalgo, Mexico. *Southwestern Naturalist* 55:98–103.
- Leyte-Manrique, A., U. Hernández-Salinas, A. Ramírez-Bautista, V. Mata-Silva, and J.C. Marshall. 2017. Habitat use in eight populations of *Sceloporus grammicus* (Squamata: Phrynosomatidae) from the Mexican Plateau. *Integrative Zoology* 12:198–210.
- Leyte-Manrique, A., A. Ramírez-Bautista, and U. Hernández-Salinas. 2007. Contribución a la ecología de *Sceloporus grammicus*: presencia de cola regenerada en dos poblaciones del estado de Hidalgo México. *Boletín de la Sociedad Herpetológica Mexicana* 15:13–15.
- Liang, T., G. Murali, A. Zimin, J. Dembitzer, R. Graboski, U. Roll, and S. Meiri. 2025. Ecology and biogeography of sexual size dimorphism in squamates. *Global Ecology and Biogeography* 34:e70076. <https://doi.org/10.1111/geb.70076>.
- López-González, N.E., M.A. López-Luna, and A.H. Escobedo-Galván. 2025. Sexual size dimorphism and allometric growth of the smallest turtle in the world (Testudines: Kinosternidae). *Salamandra* 61:95–100.
- Lovich, J.E., and J.W. Gibbons. 1992. A review of techniques for quantifying sexual size dimorphism. *Growth, Development and Aging* 56:269–281.
- Lozano, A., A. Ramírez-Bautista, and R. Cruz-Elizalde. 2020. Intraspecific variation in a lizard from the Central Mexican Plateau: intersexual differences in size and shape explored. *Biological Journal of the Linnean Society* 131:656–666.
- Lozano, A., J.W. Sites, Jr., A. Ramírez-Bautista, J.C. Marshall, N.P. Pavón, and R. Cruz-Elizalde. 2023. Allometric analysis of sexual dimorphism and morphological variation in two chromosome races of the *Sceloporus grammicus* complex (Squamata: Phrynosomatidae) from Mexico. *Vertebrate Zoology* 73:23–34.
- Méndez-de la Cruz, F.R., M. Villagrán-Santa Cruz, L. López-Ortiz, and O. Hernández-Gallegos. 2013. Reproductive cycle of a high-altitude oviparous lizard, *Sceloporus spinosus* (Reptilia: Phrynosomatidae). *Southwestern Naturalist* 58:54–63.
- Nemes, S., and T. Harter. 2010. Derivation of variance estimators and statistical inference for indices of sexual size dimorphism: an example. *Belgian Journal of Zoology* 140:241–243.
- Olsson, M., R. Shine, E. Wapstra, B. Ujvari, and T. Masden. 2002. Sexual dimorphism in lizard body shape: the roles of sexual selection and fecundity selection. *Evolution* 56:1538–1542.
- Ortiz, M., J. Boretto, and N. Ibarzüengoytia. 2016. Reproductive biology of the southernmost *Kentropyx* lizard from the Wet Chaco of Corrientes, Argentina. *Herpetological Journal* 26:119–130.
- Oviedo-Hernández, E., K.I. Octaviano-Valencia, O. Hernández-Gallegos, G. Granados-González, and G. Suárez-Varón. 2023. Aquatic escape behavior in the Mesquite Lizard (*Sceloporus grammicus*). *Sonoran Herpetologist* 36:76–77.
- Powell, G.L., and A.P. Russell. 1985. Growth and sexual size dimorphism in Alberta populations of the Eastern Short-Horned Lizard, *Phrynosoma douglassi brevirostre*. *Canadian Journal of Zoology* 63:139–154.

- Ramírez-Bautista, A., B.P. Stephenson, A. Lozano, H. Uribe-Rodríguez, and A. Leyte-Manrique. 2012. Atypical reproductive cycles in a population of *Sceloporus grammicus* (Squamata: Phrynosomatidae) from the Mexican Plateau. *Ecology and Evolution* 2:1903–1913.
- Sæther, B.E., J. Kålås, L. Løfaldli, and R. Andersen. 1986. Sexual size dimorphism and reproductive ecology in relation to mating system in waders. *Biological Journal of the Linnean Society* 28:273–284.
- Sánchez-Carpio, J.M. 2010. Dieta y dimorfismo sexual de *Sceloporus bicanthalis* (Sauria: Phrynosomatidae) en el Nevado de Toluca. Bachelor Thesis, Universidad Autónoma del Estado de México, Toluca, Estado de México, México. 48 p.
- Sánchez-Manjarrez, D. 2024. Perfiles leucocitarios de una comunidad de reptiles: variación estacional, sexual e interespecífica. Doctoral Thesis, Universidad Autónoma del Estado de México, Toluca, Estado de México, México. 120 p.
- Scharf, I., and S. Meiri. 2013. Sexual dimorphism of heads and abdomens: different approaches to ‘being large’ in female and male lizards. *Biological Journal of the Linnean Society* 110:665–673.
- Schwarzkopf, L. 2005. Sexual dimorphism in body shape without sexual dimorphism in body size in Water Skinks (*Eulamprus quoyii*). *Herpetologica* 61:116–123.
- Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quarterly Review of Biology* 64:419–461.
- Suárez-Varón, G., C. Nava-Almazán, K.I. Octaviano-Valencia, E. De la Rosa-Silva, G. Granados-González, and O. Hernández-Gallegos. 2024. Tail bifurcation in a Mesquite Lizard *Sceloporus grammicus* (Squamata: Phrynosomatidae) in a population from Toluca, Mexico. *Revista Latinoamericana de Herpetología* 7:14–17.
- Toyama, K.S. J.B. Losos, A. Herrel, and D.L. Mahler. 2025. Sexual size dimorphism as a determinant of biting performance dimorphism in *Anolis* lizards. *Journal of Evolutionary Biology* 38:251–260.
- Valdecantos, S., F. Lobo, M.G. Perotti, D.L. Moreno Azócar, and F.B. Cruz. 2019. Sexual size dimorphism, allometry and fecundity in a lineage of South American viviparous lizards (Liolaemidae: *Phymaturus*). *Zoologischer Anzeiger* 279:152–163.
- Vincent, S.E., A. Herrel, and D.J. Irschick. 2004. Sexual dimorphism in head shape and diet in the Cottonmouth Snake (*Agkistrodon piscivorus*). *Journal of Zoology* 264:53–59.
- Warne, R.W. 2008. Reproductive allometry and resource allocation in lizards. *Oecologia* 155:567–577.
- Xiong, J., Y. Bai, G. Li, and Z. You. 2022. Sexual dimorphism in the Mountain Dragon, *Diploderma micangshanensis* (Squamata: Lacertilia: Agamidae) from central China. *Animal Biology* 72:325–334.
- Zhao, W., and N-F. Liu. 2014. The proximate causes of sexual size dimorphism in *Phrynocephalus przewalskii*. *PLoS ONE* 9:e85963. <https://doi.org/10.1371/journal.pone.0085963>.



OSWALDO HERNÁNDEZ GALLEGOS is a Professor at the Universidad Autónoma del Estado de México, Toluca City, Mexico, and he earned his Ph.D. at the Universidad Nacional Autónoma de México, Mexico City, Mexico. His research since 1995 has focused on the ecology and evolution of parthenogenesis and reproductive cycles of lizards. Recently, he has been interested in the ecology and conservation of threatened amphibians and reptiles in Mexico. (Photographed by Kevin M. Gribbins).



CAROLINA NAVA-ALMAZÁN is a Biologist trained at the Universidad Autónoma del Estado de México, Toluca City, Mexico. She completed professional training at the Herpetology Laboratory of the same institution. Her academic work included projects on habitat characterization of snakes and the study of sexual dimorphism in lizards. Her main interests focus on ecology, animal behavior, and conservation. (Photographed by Oswaldo Hernández-Gallegos).



GISELA GRANADOS-GONZÁLEZ is a Professor at the Universidad Autónoma del Estado de México, Toluca City, Mexico, and she earned her Ph.D. at the Universidad Nacional Autónoma de México, Cuernavaca City, Mexico. Her research focuses on spermatogenesis and spermiogenesis of lizards. Gisela is interested in the morphology and physiology of sperm, spermatogenesis, and spermiogenesis of invertebrates and vertebrates. (Photographed by Oswaldo Hernández-Gallegos).



GABRIEL SUÁREZ-VARÓN is a Professor at the Universidad Autónoma del Estado de México, Toluca City, Mexico, where he also earned his Ph.D. He is founding member of the Red de Investigación y Divulgación de Anfibios y Reptiles MX. His research interests focus on the evolutionary implications of sex determination systems, morphophysiology, and life-history strategies in reptiles. (Photographed by Luis Macotella).



JOSÉ FERNANDO MÉNDEZ-SÁNCHEZ is a full-time Professor of the Biology Department of Science College at Universidad Autónoma del Estado de México (UAEMéx), Toluca City, Mexico. Fernando earned a B.Sc. in Biology from UAEMéx and a Ph. D. in Biological Science from University of North Texas, Denton, USA. His research interest includes vertebrate ecophysiology with emphasis in high altitude adaptations to breathe in aquatic and terrestrial hypoxic environments. (Photographed by José Fernando Méndez-Sánchez).



JUSTIN LLOYD RHEUBERT is an Assistant Professor of teaching and Co-director of the Honors Program at the University of Findlay, Ohio, USA. Rheubert specializes in anatomy and physiology, microscopy, and herpetology. His research interests include anatomy, electron microscopy, evolution, ecology, pedagogical techniques, and experiential learning. (Photographed by Marisa Prisco).

