Herpetological Conservation and Biology 21(1):53–64.
Submitted: 6 September 2025; Accepted: 3 February 2026; Published: 30 April 2026

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

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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).

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).

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 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-Lopeztello 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×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):

$$SDI = \left[\left(\frac{size\ of\ largest\ sex}{size\ of\ smallest\ sex}\right) - 1\right] x100$$

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, θx represents the mean value of the trait in the larger sex, θy in the smaller sex, and $\sigma x2$ and $\sigma y2$ the variances of θx and θy respectively, and we performed a Two-sample Hypothesis Test to evaluate whether SDI differed significantly between sexes (H0: 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

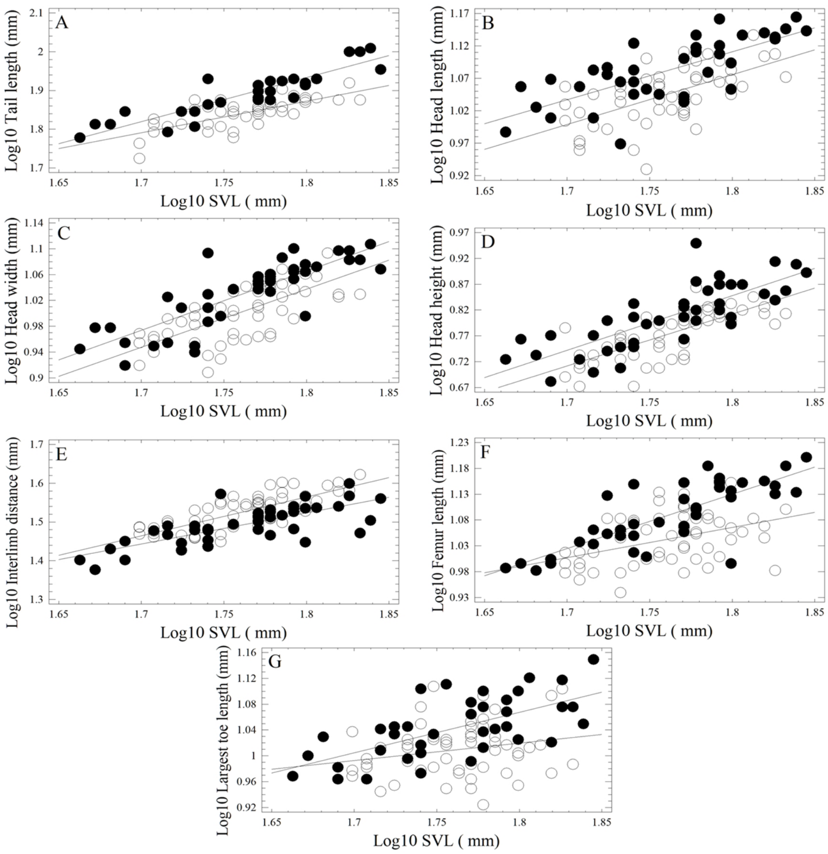

FIGURE 2. $\log_{10}$–$\log_{10}$ regression of (A) tail length, (B) head length, (C) head width, (D) head height, (E) interlimb distance, (F) left femur length, and (G) largest toe of the left hind leg against snout-vent length (SVL) for both adult female (open circles) and adult male (solid circles) 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 (± standard deviation), range (in parentheses), and sexual size dimorphism index (SDI; ± 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.

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

Table 2. Log$_{10}$-log$_{10}$ 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.

		Log$_{10}$–log$_{10}$ regression and allometric analysis							ANCOVA Slopes comparison		
Trait	Sex	r^2	*F*-value	df	Slope	95% CI	Result	Intercept	*F*-value	df	*P*-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).

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.

DISCUSSION

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, Tropiduridae, Varanidae, Teiidae, and Phrynosomatidae, SSD is significantly male-biased

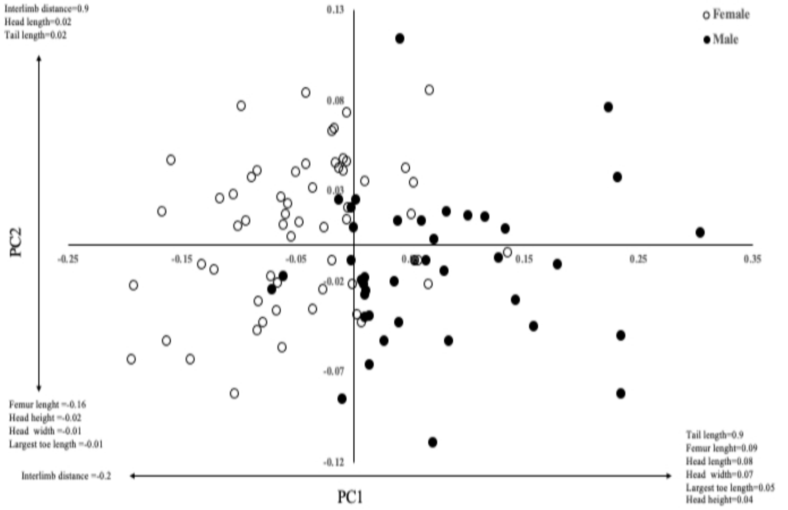

Figure 3. Principal Component Analysis (PCA) showing sexual dimorphism in the Mesquite Lizard (*Sceloporus grammicus*) from El Cerrillo, Piedras Blancas, Toluca, Estado de México, Mexico. Points represent the PCA scores of 100 adult individuals (59 females and 41 males). PC1 explained 75% of the variance 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 posdoctoral scholarship to GS-V (CVU: 693584).

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