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Allometric analysis of sexual dimorphism and morphological variation in two chromosome races of the *Sceloporus grammicus* complex (Squamata: Phrynosomatidae) from Mexico

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Abstract

Sexual dimorphism is a widespread feature in the Animal Kingdom. In lizards of the *Sceloporus grammicus* complex, studies of sexual dimorphism that analyze the allometric trajectories of body traits remain unexplored. Here we investigate sexual dimorphism in key phenotypic traits, including body size (snout-vent length, SVL) as well as head length (HL), head width (HW), and forearm length (FL). We use an allometric approach to detect differences in scale relationships among body parts in the *S. grammicus* complex in Mexico. We focus on two chromosomal races within this complex, F5 (2n = 34) and FM2 (2n = 46). In the complex, we found that males are larger than females in all morphological variables, and this pattern was confirmed in both races. We determined negative allometric trajectories (SVL *vs.* HL and HW), isometry (SVL *vs.* FL) and intersexual differences in the slopes of the SVL *vs.* HL and HW; the males showed steeper slopes. Thus, the growth of the head is more pronounced in males than females. Additionally, we found between-race differences in these trajectories (SVL *vs.* FL) and in all morphological variables (F5 lizards are larger than those of the FM2 race), which correlate with their chromosomal divergence. We discuss biological implications of our findings in relation to sexual selection and natural selection.

Keywords

Introduction

Lizards of the genus *Sceloporus* are one of the most species-rich reptiles in North America and are often utilized as focal species in integrative biological research. The genus contains 110+ morphologically and ecologically distinct species (Uetz et al. 2022), many of which occur sympatrically throughout a distribution from the Pacific northwest of the United States and southern Canada to Costa Rica and western Panama (Sites et al. 1992). Despite substantial progress towards elucidating the phylogeographic patterns for many species of *Sceloporus*, phylogenetic relationships and species delimitation amongst some species groups remain limited (Marshall et al. 2006; Leaché and Sites 2009). In this context, evolutionary changes to the chromosome numbers are hypothesized to be the main factor responsible for driving the diversification of *Sceloporus* (Hall 2009; Leaché and Sites 2009).

Within this lizard genus, the mesquite lizard, *Sceloporus grammicus* Wiegmann, 1828 (Fig. 1), has long been a taxon of much scientific interest (Phrynosomatidae; Frost and Etheridge 1989; Sites et al. 1992; Hall 2009). This taxon has extensive chromosomal variation and has been considered a species complex that is characterized by chromosomal races having diploid numbers ranging from 2n = 32 (inferred ancestral) to 2n = 46 (most derived; Arévalo et al. 1991). Eight races have been identified in central Mexico (LS[2n = 32], HS[32], F5[34], F6[34], F5+6[36], FM1[42], FM2[46], and FM3[38]), all but one of which likely evolved via a linear process of centric fissions in the six pairs of macrochromosomes (Porter and Sites 1986; Arévalo et al. 1994; Marshall et al. 2006). The

most derived race (2n = 46) at the end of this "chain" originated via a second fission in the long arm of chromosome 2 (Reed et al. 1995a, b). Substantial morphological variation also occurs among several chromosomal races, these differences have been reported in meristic and morphometric characters; for instance, dorsal, throat and abdominal patches, as well as head structures and limbs (e.g., Sites 1992; Bastiaans et al. 2013, 2014; Lozano et al. 2020). Two of these races have also been described as distinct species: *S. anahuacus* (HS) and *S. palaciosi* (high-elevation F6; Lara-Góngora 1983). However, species boundaries within the complex are nebulous and still not well defined (Marshall et al. 2006). This extensive variation in chromosome number, molecular markers, and morphology may reflect a complex in the process of speciation (Leyte-Manrique et al. 2006; Hall 2009). The *S. grammicus* complex may serve as an important system in the study of speciation like so many other groups of reptiles and amphibians (Marshall et al. 2018; Wollenberg-Vallero et al. 2019).

All members of the *S. grammicus* complex are viviparous, and distributed across a diversity of environments, from dry tropical, semi-arid, arid, and humid temperate montane habitats that range from sea level to above 3000 m (Sites et al. 1992). Populations show sexual dimorphism in body size (Jiménez-Cruz et al. 2005; Ramírez-Bautista et al. 2005, 2012) and shape (Lozano et al. 2020). Further, lower-elevation populations reproduce throughout the year via synchronized female and male reproductive cycles (Lozano et al. 2014, 2015), whereas high-elevation populations are characterized by asynchronous gonadal maturation (Guillette and Casas-Andreu 1980; Lozano et al. 2014, 2015).

Figure 1. *Sceloporus grammicus* in life. Male, F5 chromosome race. Locality: Zacualtipán, Hidalgo, Mexico. Photo by Abraham Lozano.

Various ecological and evolutionary hypotheses have emerged to explain sexual dimorphism skewed either towards males or females (Ramírez-Bautista and Pavón 2009; Ramírez-Bautista et al. 2014; Lozano et al. 2020). Size and shape of some morphological structures in many lizard species are correlated with body size (Dashevsky et al. 2012; Pérez-Quintero et al. 2019). These types of relationships are called allometric (Lazarus et al. 2020), and analyses of sexual dimorphism provide insight to the scale of relationships among body parts, either with respect to body size or body parts to each other (Rivero Suárez et al. 2016). For example, in some species of lizards, female abdomen length is correlated with SVL (Braña 1996), which has been suggested to be a result of selection for higher fecundity (Olsson et al. 2002; Scharf and Meiri 2013; Jiménez-Arcos et al. 2017). In males, morphological structures of the head and limbs are frequently correlated with SVL (Molina-Borja 2003; Dashevsky et al. 2012), which is related to success in mating and/or territorial defense (Olsson et al. 2002; Jiménez-Arcos et al. 2017). In addition, body sizes and the shapes of various morphological structures could evolve differently between males and females to minimize competition for resources, such as space and food (Hierlihy et al. 2013).

Currently, in the *S. grammicus* complex there have been no previous studies of intersexual divergence that include analyses of scale relationships among body parts (morphometric variables). In this study, using an allometric approach, we first evaluate sexual dimorphism in the entire *S. grammicus* complex, and second, we compare the patterns of sexual dimorphism between the F5 and FM2 races that coexist in the state of Hidalgo. Based on theoretical considerations and given that these races are likely in the process of speciation (Reed et al. 1995a, b; Reed and Sites 1995; Sites et al. 1995), we hypothesize that the races are morphometrically different and intersexual differences are present, thus, we expect: 1) male morphometric variables to be significantly larger than females in both races, and 2) males to have higher allometrically adjusted values than females in the slopes of the variable relationships (body size *vs.* body parts). Given there are no other comparisons of differences between any chromosomal races in the complex, this analysis of these morphological differences will be the first of its kind.

Materials and methods

Ethics statement

The Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT) approved this research (permit # SGPA/DGVS/02726/10). Lizards were euthanized and fixed in 10% formaldehyde solution according to Lozano et al. (2014, 2015). This study was conducted according to the Guidelines for Use of Live Amphibians and Reptiles in Field and Laboratory Research developed by the American Society of Ichthyologists and Herpetologists (Animal Care Guidelines for Herpetology 2004).

Scientific collections

Specimens are deposited in the following scientific collections: the Bean Life Science Museum Herpetological Collection at Brigham Young University (**BYU**), Provo, UT, USA, Colección Nacional de Anfibios y Reptiles of the Instituto de Biología (**CNAR-IBH**), Laboratorio de Ecología Integrativa, CIIDIR Unidad Durango, Instituto Politécnico Nacional (**LEI-IPN**), Museo de Zoología, Facultad de Ciencias (**MZFC**), at the Universidad Nacional Autónoma de México, and Colección Herpetológica of Laboratorio de Ecología de Poblaciones, Universidad Autónoma del Estado de Hidalgo (**UAEH**) (see Supplementary File S1).

Data acquisition

We collected morphological data from 1,722 adult lizards, 54% of which were females. We collected four linear measurements from all specimens (from the left side of the body): snout-vent length (**SVL**), head length (**HL**), head width (**HW**), and forearm length (**FL**) (Butler and Losos 2002; Ramírez-Bautista et al. 2012; Lozano et al. 2020). Morphological measurements were taken to the nearest 0.01 mm using a digital caliper. All lizards were assigned to one of the eight chromosomal races (HS, LS, F5, F5+6, F6, FM1, FM2, FM3) following published distribution maps (Sites 1982, 1983; Porter and Sites 1986; Arévalo et al. 1994; Marshall et al. 2006; Hall 2009). A separate category was designated for lizards from the FM2 X F5 hybrid zone in the state of Hidalgo (Sites et al. 1993). Representatives from another member of the *S. grammicus* complex, *S. grammicus grammicus* (SGG) from the state of Oaxaca (Smith 1939; Arévalo et al. 1994), and potential but unverified F5+6 from the state of Durango (likely but 2n uncertain), were also evaluated (Fig. 2).

Statistical analyses

We first analyzed the entire *S. grammicus* complex, and then we compared the FM2 and F5 races separately; because these are the most chromosomally divergent races (Sites and Davis 1989; Reed et al. 1995a, b), and both are represented by the large numbers of museum vouchers and have overlapping distributions (File S1). Previously, we explored whether morphology was correlated with variables such as altitude, latitude, or sampling year by means of linear regressions, and in no case were the relationships statistically significant ($p > 0.05$; in all cases the determination coefficients r^2 were < 0.07). This result allows us to pool samples into races independent of the ecological conditions of the sampling sites.
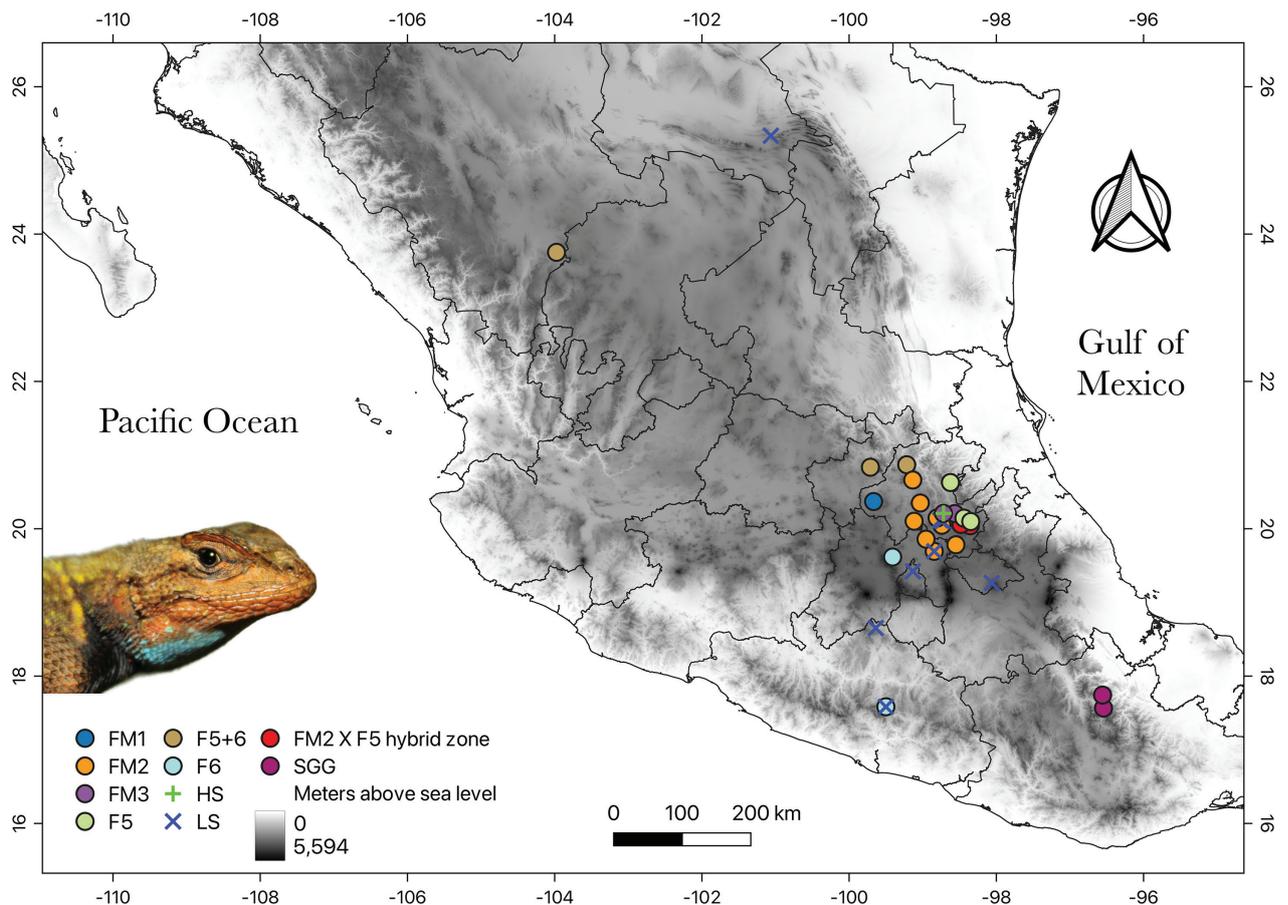
Figure 2. Collection sites for chromosomal races of the *Sceloporus grammicus* complex. Photograph of male, F5 chromosome race from Zacualtipán, Hidalgo, Mexico by Abraham Lozano.

All data were first transformed with logarithm base 10 (log_{10}) and tested for normality (Kolmogorov-Smirnov test, $p > 0.05$) and homogeneity of variances (F-test, $p > 0.05$). Several statistical methods have been proposed and evaluated for the study of morphological data in reptiles (e.g., Chan and Grismer 2021, 2022; Grismer et al. 2022). In this study, between-sex differences for morphological variables were first analyzed for the entire *S. grammicus* complex using Welch's *t*-tests (Welch, 1938). We explored the raw morphological differences by using a two-way analysis of variance (ANOVA) to test for the effect of chromosomal race (FM2 and F5) and sex (male and female) for each morphological variable (SVL, HL, HW, and FL, dependent). In the same way, we explored the size-corrected morphological differences by using a two-way analysis of covariance (ANCOVA) to test for the effect of chromosomal race (FM2 and F5) and sex (male and female) for each morphological variable (HL, HW, and FL, dependent), with SVL as a covariate (independent). Fisher's post hoc comparison tests were used to identify differences between the groups. From the ANCOVAs, we simultaneously performed linear regressions to evaluate the allometric relationships between the SVL (body size) and the other morphological variables (HL, HW and FL), and significance in slope differences were then evaluated using *F*-tests. According to Huxley and Teissier (1936) and Klingenberg (1996, 2016), a regression slope of 1 indicates an isometric relationship between variables; that

is, both variables have the same relative growth. Alternatively, if HL, HW or FL have greater relative growth than SVL, the resulting slope will be greater than 1, indicating positive allometry. In contrast, a slope less than 1 is evidence for less growth of HL, HW or FL relative to the SVL; evidence for negative allometry. All statistical analyses were calculated using Statistica v.7.0 (StatSoft, Inc., Tulsa, OK, USA). Results were considered significant if $p \leq 0.05$ in all the analyses.

Results

Analysis of the eight races of *S. grammicus* complex showed that males were significantly larger than females in all raw morphological variables used (Table 1). Sexual dimorphism was also recorded in the FM2 and F5 races; in both, males were significantly larger than females in all raw characters except SVL in the F5 race (Table 2). Further, the F5 lizards were significantly larger than the FM2 lizards (Table 2, Fig. 3). The results of the ANCOVAs of the eight races of *S. grammicus* complex showed that sexual dimorphism was also recorded for relative HL, relative HW, and relative FL, with males being larger than females (Table 1). There were intersexual differences in the FM2 and F5 races; in both, males were significant-

Table 1. Variation of measurements of morphometric variables of the entire *Sceloporus grammicus* complex. Means ± 1 standard error (SE) are given by sex. Abbreviations: snout-vent length (SVL), head length (HL), head width (HW), and forearm length (FL). Bold values denote statistical significance at the $p < 0.05$ level.

Sexes	SVL (mm)	HL (mm)	HW (mm)	FL (mm)
Males (n = 776)	57.05 ± 0.29	13.50 ± 0.07	11.31 ± 0.06	9.33 ± 0.07
Females (n = 946)	54.63 ± 0.22	12.52 ± 0.05	10.42 ± 0.04	8.71 ± 0.05
Mean differences	$t = 6.53, p <$ **0.0001**	$t = 10.95, p <$ **0.0001**	$t = 11.75, p <$ **0.0001**	$t = 7.19, p <$ **0.0001**
Mean differences, adjusted for covariance (ANCOVA)	---	$F = 76.52, p <$ **0.0001**	$F = 109.90, p <$ **0.0001**	$F = 13.17, p =$ **0.0002**

Table 2. Variation of morphometric variables of FM2 and F5 chromosomal races of the *Sceloporus grammicus* complex. Means ± 1 standard error (SE) are given by sex. Abbreviations: snout-vent length (SVL), head length (HL), head width (HW), and forearm length (FL). Bold values denote statistical significance at the $p < 0.05$ level.

Chromosomal races	Sexes	SVL (mm)	HL (mm)	HW (mm)	FL (mm)
FM2	Males (n = 328)	56.42 ± 0.45	13.20 ± 0.09	10.85 ± 0.09	8.73 ± 0.10
	Females (n = 350)	53.25 ± 0.39	12.13 ± 0.07	9.83 ± 0.07	7.91 ± 0.08
	ANOVA	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**
	ANCOVA	---	**< 0.0001**	**< 0.0001**	**0.0006**
F5	Males (n = 67)	59.68 ± 0.94	13.63 ± 0.15	12.03 ± 0.18	10.44 ± 0.21
	Females (n = 84)	58.13 ± 0.85	12.94 ± 0.11	11.32 ± 0.15	9.69 ± 0.18
	ANOVA	0.2247	**0.0043**	**0.0026**	**0.0076**
	ANCOVA	---	**< 0.0001**	**< 0.0001**	**0.0029**
FM2 *vs.* F5 (ANOVA)	FM2 *vs.* F5	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**
	M *vs.* M	**0.0018**	**0.0292**	**< 0.0001**	**< 0.0001**
	F *vs.* F	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**
FM2 *vs.* F5 (ANCOVA)	FM2 *vs.* F5	---	**< 0.0001**	**< 0.0001**	0.5032
	M *vs.* M	---	$p = 0.9772$	**< 0.0001**	**< 0.0001**
	F *vs.* F	---	$p = 0.0795$	**< 0.0001**	**< 0.0001**

Table 3. Parameters of regressions between the independent (SVL) and the dependent (HL, HW, and FL) variables. Data from the entire *Sceloporus grammicus* complex. Abbreviations: snout-vent length (SVL), head length (HL), head width (HW), forearm length (FL), standard error (SE) of b (slope value). Bold values denote statistical significance at the $p < 0.05$ level.

Regressions	b	SE	r^2	p
LogSVL *vs.* LogHL	0.71	0.019	0.44	**< 0.0001**
LogSVL *vs.* LogHW	0.85	0.016	0.62	**< 0.0001**
LogSVL *vs.* LogFL	1.01	0.025	0.48	**< 0.0001**

ly larger than females in all relative characters (Table 2). Moreover, the F5 lizards were significantly larger than the FM2 lizards in relative HW and FL, but not in HL (Table 2). There were no statistically significant effects of the interactions ($p > 0.1647$ in all cases), which indicates that sexual dimorphism is expressed in the same way in both races.

In general, the SVL was positively and significantly correlated with the other morphological variables (Table 3), but this fit was highest with head width and lowest with head length. In contrast, the relationship between SVL and FL was isometric, while with HL and HW showing negative allometry (Fig. 4).

Analysis of slopes of relationships between SVL and the body variables for the complete data set showed differences in males (ANCOVA: $F = 24.69, p < 0.0001$) and females (ANCOVA: $F = 36.87, p < 0.0001$); in both sexes, the relative HL growth was lower with respect to SVL, compared to the other variables (HW, FL; Fig. 5). The slopes differed significantly for SVL *vs.* HL (ANCOVA: $F = 4.22, p = 0.0401$) between sexes, with males having a greater slope. In contrast, there were no differences between the sexes in SVL *vs.* HW (ANCOVA: $F = 2.36, p = 0.1248$) and SVL *vs.* FL (ANCOVA: $F = 0.03, p = 0.8502$). However, in the latter, the relationship was isometric, while the other variables showed a tendency toward negative allometry (Fig. 5).

We obtained similar results to the complete data set when comparing allometric relationships between the FM2 and F5 races. For the FM2 race, slopes differed significantly in both males (ANCOVA: $F = 26.05, p < 0.0001$) and females (ANCOVA: $F = 23.38, p < 0.0001$). Differences between the sexes were found in the slopes of
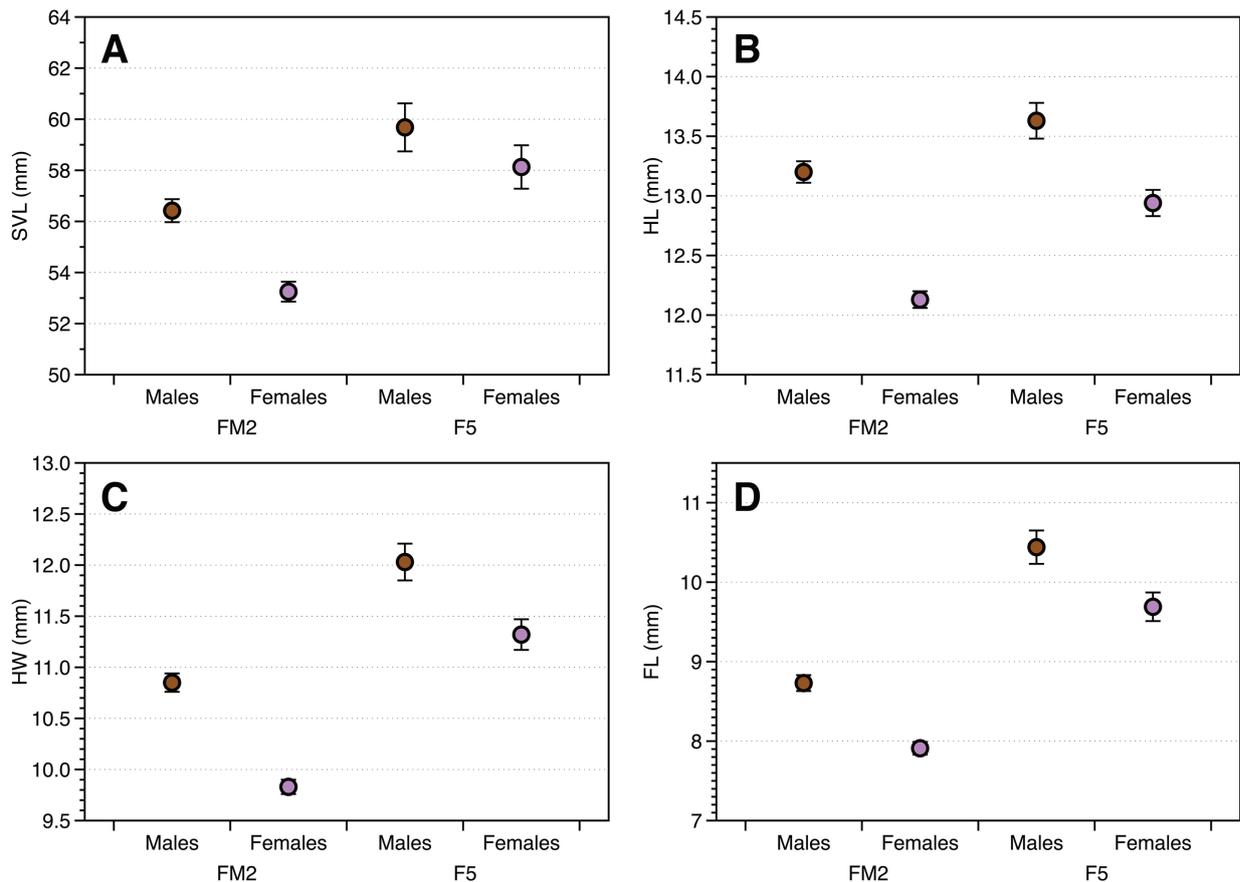
Figure 3. Morphometric variables of the FM2 and F5 chromosomal races of the *Sceloporus grammicus* complex. **A** Snout-vent length (SVL); **B** head length (HL); **C** head width (HW); **D** forearm length (FL). Males (brown circles), females (purple circles). Means ± 1 standard error (SE) are given by sex.
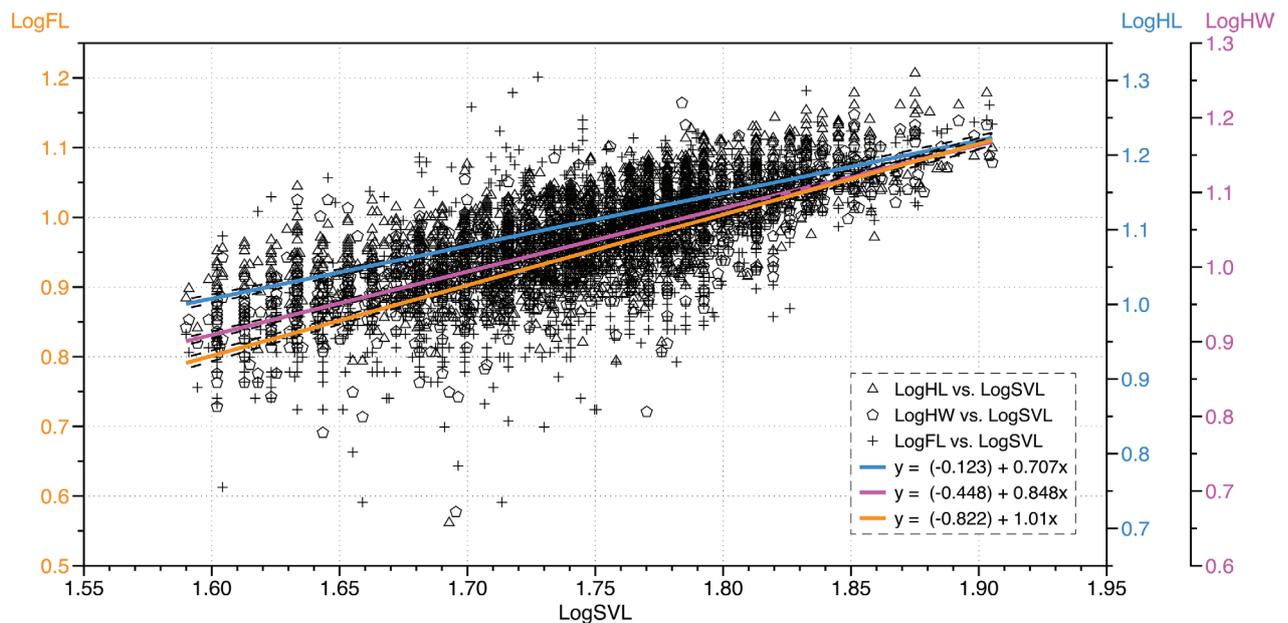
Figure 4. Allometric relationships between the independent (SVL) and the dependent (HL, HW, and FL) variables. Data are from the entire *Sceloporus grammicus* complex. Snout-vent length (SVL), head length (HL), head width (HW), and forearm length (FL). All variables were $\log_{10}$-transformed.

the SVL *vs.* HW relationships (ANCOVA: $F = 7.70$, $p = 0.0057$), but not in the SVL *vs.* HL (ANCOVA: $F = 2.07$, $p = 0.1505$) and SVL *vs.* FL (ANCOVA: $F = 1.11$, $p = 0.2915$) relationships (Fig. 5). In the F5 race, significant differences were also recorded in allometric relationships both in males (ANCOVA: $F = 43.33$, $p < 0.0001$) and fe-
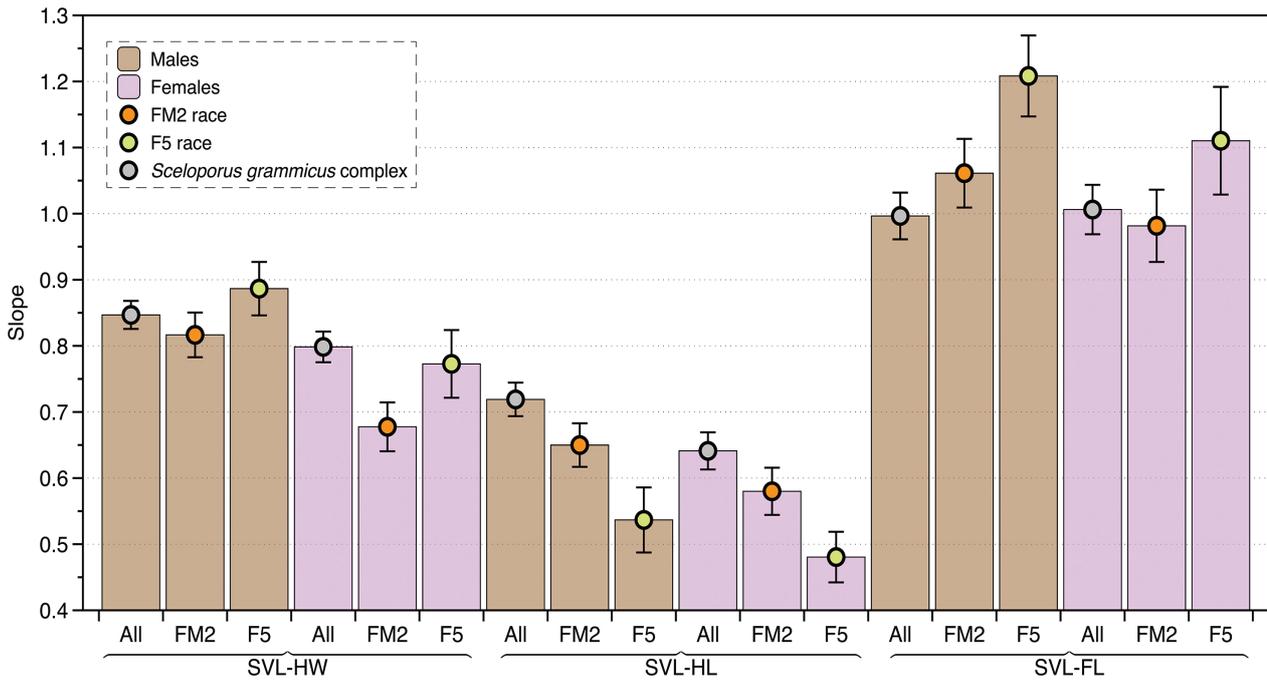
Figure 5. Allometric relationships of lizards of the *Sceloporus grammicus* complex. Slope values (± 1 standard error: SE) of the relationships between the independent (snout-vent length: SVL) and the dependent (head length: HL, head width: HW, and forearm length: FL) variables, separating by sexes (males: brown bars, females: purple bars). *Sceloporus grammicus* complex (grey circles), FM2 race (orange circles), and F5 race (green circles).

Table 4. Summary of results of morphological variables and allometric relationships of the *Sceloporus grammicus* complex. Mean differences of absolute (raw) and relative (size-corrected) morphological variables, and slope differences in the allometric relationships of the entire *Sceloporus grammicus* complex, FM2 race, and F5 race. Green boxes represent $p > 0.05$ (failure to reject the null hypothesis of equal means), while red boxes represent $p \leq 0.05$ (reject the null hypothesis of equal means). Abbreviations: snout-vent length (SVL), head length (HL), head width (HW), forearm length (FL), males (M), females (F), isometry (i), positive allometry (+), and negative allometry (—).

Raw (mean differences)		**SVL**	**HL**	**HW**	**FL**
Sceloporus grammicus complex	M *vs.* F	🟥	🟥	🟥	🟥
FM2	M *vs.* F	🟥	🟥	🟥	🟥
F5	M *vs.* F	🟩	🟥	🟥	🟥
FM2 *vs.* F5	M *vs.* M	🟥	🟥	🟥	🟥
FM2 *vs.* F5	F *vs.* F	🟥	🟥	🟥	🟥
Size-corrected (mean differences)					
Sceloporus grammicus complex	M *vs.* F	—	🟥	🟥	🟥
FM2	M *vs.* F	—	🟥	🟥	🟥
F5	M *vs.* F	—	🟥	🟥	🟥
FM2 *vs.* F5	M *vs.* M	—	🟩	🟥	🟥
FM2 *vs.* F5	F *vs.* F	—	🟩	🟩	🟥
Allometry (slope differences)					
Sceloporus grammicus complex	M *vs.* F	—	– / – 🟥	– / – 🟩	i / i 🟩
FM2	M *vs.* F	—	– / – 🟩	– / – 🟥	+ / i 🟩
F5	M *vs.* F	—	– / – 🟩	– / – 🟩	+ / + 🟩
FM2 *vs.* F5	M *vs.* M	—	– / – 🟩	– / – 🟩	+ / + 🟩
FM2 *vs.* F5	F *vs.* F	—	– / – 🟩	– / – 🟩	i / + 🟩

males (ANCOVA: $F = 27.78$, $p < 0.0001$), but there were no differences between the sexes (ANCOVAs; SVL *vs.* HL: $F = 0.08$, $p = 0.3616$; SVL *vs.* HW: $F = 2.81$, $p = 0.0959$; SVL *vs.* FL: $F = 0.84$, $p = 0.3599$) (Fig. 5). A summary of results of slope differences in the allometric relationships, as well as raw and size-corrected morphological differences are shown in Table 4.

Discussion

Sexual dimorphism is biased towards larger male size in the *S. grammicus* complex, as well as the intersexual divergence of the scale relationships between body size (SVL) and body parts (morphometric variables: HL, HW). These results were expected; males were generally larger than females in both the absolute (raw) and relative (size-corrected) measures of morphological variables. Also, the chromosomal races differed from each other in their morphological attributes. Further, males show higher values of the slopes of the relationships of the morphological variables than the females.

Most species of *Sceloporus* are sexually dimorphic (Fitch 1978; Cox and John-Alder 2007), but some species such as *S. formosus* (Ramírez-Bautista and Pavón 2009) and *S. spinosus* (Ramírez-Bautista et al. 2013) do not exhibit significant differences in body size. In the case of the *S. grammicus* complex, this study corroborates others (Jiménez-Cruz et al. 2005; Ramírez-Bautista et al. 2005, 2012; Jiménez-Arcos et al. 2017), showing that males are larger than females in body morphometric measurements. This pattern holds for the FM2 and F5 chromosomal races, as in other groups of lizard species (Cox et al. 2003, 2007). These morphological differences between-sexes have several potential explanations, including sexual selection. This may occur by intra-sexual interactions in which males fight each other to defend territories, which may give larger males larger territories and provide greater access to females (Cooper 1977; Ruby 1978; Brecko et al. 2008; Herrel et al. 2010), or by inter-sexual selection where females choose males by body size or some other physical attribute (Trivers 1972).

In the *S. grammicus* complex, between-sex differences in morphometric variables seem to be maintained largely by sexual selection (Jiménez-Cruz et al. 2005; Ramírez-Bautista et al. 2005, 2012; Lozano et al. 2020), since male reproductive success is often positively correlated with body, head, and limb length (Ord et al. 2001; Husak et al. 2006; Cox et al. 2007). Further, males are territorial and aggressive (Lozano et al. 2020), and females select males based on throat and ventral patch color patterns, which males display to the female during sexual encounters, again suggesting sexual selection is evident (Bastiaans et al. 2013, 2014).

Herein we quantify differences in morphological attributes between two *S. grammicus* chromosomal races; in the analyses performed both male and female F5 lizards are larger than those of the FM2 race. These results are interesting given that the male size (body and limb lengths) and head shape play a very important role in territorial defense in other lizard species (Herrel et al. 2006; Huyghe et al. 2009; Dollion et al. 2017; Lozano et al. 2020). Larger heads produce greater bite force, which is undoubtedly an advantage in male-male territorial fights to gain greater access to females (Cooper 1977; Ruby 1978; Brecko et al. 2008; Herrel et al. 2006, 2010; Huyghe et al. 2009; Dollion et al. 2017). Moreover, in many lizard species, males have longer distal segments

and faster sprint speeds, improving the defense of their territory (Lailvaux 2007). In the two *S. grammicus* chromosomal races, the variation in head and other morphological attributes (e.g., SVL and limbs) between the F5 and FM2 races would imply, among other things, dominance, or variation in the degree of sexual selection (Butler and Losos 2002). In view of the results obtained, it is possible that the F5 race would be experiencing a higher degree of sexual selection.

Body size (SVL) in other lizard species correlates with aspects of behavior, including escape from predators and intra-specific territorial fights (Huey and Hertz 1982, 1984; Huey et al. 1990; Garland and Losos 1994). Allometric relationships for the complete *S. grammicus* data set show that the relative growth of the head variables (HL and HW) was lower with respect to the growth of body length (SVL) (negative allometry), while the relative growth of body length and forearm length (SVL and FL) were similar (isometry). In addition, we found intersexual differences in the slopes of the relationships SVL *vs.* HL, where males showed a greater slope, thus, the relative growth of head length is more important in males than females, which agrees with our expectation of males to have higher allometrically adjusted values than females. We found a similar pattern, a negative allometric relationship between body and head lengths, *vs.* isometric relationships between body and forearm lengths in the FM2 and F5 races. The single difference with these patterns is a positive allometric relationship in SVL *vs.* FL in the F5 race. We also recorded intersexual differences in the SVL *vs.* HW relationship in the FM2 race; the relative growth of head width is more important in males than females. None of the other allometric relationships differed between the sexes.

These allometric trajectories of body features can be explained by two hypotheses, sexual selection (see above) and/or natural selection. Natural selection could drive ecological divergence if dimorphism in head size or shape due to competition for food or habitat, leads to ecological niche partitioning (Schoener 1977; Shine 1989; Herrel et al. 1996, 2001b). In several lizard species head size and shape are related to resource use, including favored microhabitats and food dimensions (Verwaijen et al. 2002; Herrel et al. 2007). Larger heads provide greater opportunity to occupy various types of microhabitats (Kaliontzopoulou et al. 2015), and access to larger more robust prey (Herrel et al. 1996, 2001b). This pattern of sexual dimorphism in the F5 and FM2 chromosome races is consistent with a recent multivariate study of size and shape in *S. grammicus* populations inhabiting different environments (Lozano et al. 2020). This study showed that males were larger in overall body size and other morphological characteristics (relatively longer fore- and hind limbs), and females had relatively longer head lengths. Thus, the ecological context is a significant component influencing the magnitude and direction of sexual dimorphism (Butler and Losos 2002). The patterns of sexual dimorphism in the F5 and FM2 chromosome races analyzed in this study, as well as other populations of *S. grammicus*, could be explained by geographic differences in selective pressures and local adaptation.

Conclusions

This is the first study to analyze such a large data set for the F5 and FM2 chromosome races of the *S. grammicus* complex. We used an allometric approach to demonstrate significant differences in body size and head shape between the sexes in these two races. Both races are male-biased in body size and size-corrected morphological traits, and we hypothesize that: (1) sexual selection is acting on morphological characteristics associated with behavior, and/or (2) natural selection drives ecological divergence between the sexes via competition for food resources and/or habitat, leading to ecological niche partition. On the basis of these hypotheses, many future research questions can be posed. For instance, are these race morphological differences the result of plastic response to variable environmental factors, or is there a heritable component to the individuals? Is one or several mechanisms operating on sexual dimorphism? In the event that there is more than one, which mechanism is promoting body size and shape dimorphism more strongly, sexual selection, ecological difference between the sexes, or habitat influence? Is there a relationship between morphology and reproductive performance in one or both sexes? If so, what would be the magnitude and direction of this relationship? Such questions could be addressed using a combination of field and laboratory experiments. Therefore, quantification of locomotor performance capacity, behavior, and reproductive characteristics must be performed to shed light on the morphological adaptations of individuals in this widely distributed complex in Mexico.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that support the findings of this study are available upon reasonable request.

Acknowledgments

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Supplementary material 1

File S1

Authors: Lozano A, Sites Jr JW, Ramírez-Bautista A, Marshall JC, Pavón NP, Cruz-Elizalde R (2023)
Data type: .docx
Explanation note: Museum voucher numbers of the *Sceloporus grammicus* complex.
Link: https://doi.org/10.3897/vz.73.e94004.suppl1