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# Variation in size and shape sexual dimorphism in the *Sceloporus scalaris* species group (Squamata: Phrynosomatidae) from the Transvolcanic Belt of Mexico

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We attempted to identify the factors influencing size and shape dimorphism between sexes, as well as among populations and species in the *Sceloporus scalaris* group (*Sceloporus aeneus*, *S. scalaris*, *S. bicanthalis* and *S. subniger*). Our analysis focused on five morphological characteristics: snout–vent length, head length, head width, forearm length and tibia length. The effect of environmental variables (precipitation and temperature) on these variables was also tested. We found differences in morphological traits between sexes, and among populations of the same species. The oviparous species (*S. aeneus* and *S. scalaris*) were larger in overall body size than the viviparous species (*S. bicanthalis* and *S. subniger*). Differences in overall body size among populations were recorded only in *S. aeneus* and *S. scalaris*. Male-biased sexual size dimorphism occurred in oviparous but not viviparous lizards (except for one population of *S. bicanthalis*). An absence of sexual size dimorphism was also recorded in *S. subniger* and some populations of the remaining species. Two different shape patterns were found; the first was female-biased with larger relative body length in almost all populations, which could be explained by fecundity, and the second was male-biased with relatively larger head and limbs in a few populations, which may be explained by sexual selection. The patterns of sexual size and shape dimorphism show that environment, rather than phylogeny, may be determining the extent of sexual dimorphism. These types of studies show the importance of an integrated evaluation of interpopulation and interspecies variation to determine the factors that generate sexual dimorphism.

**ADDITIONAL KEYWORDS:** fecundity – geographical variation – lizards – populations – sexual selection.

## INTRODUCTION

Sexual size dimorphism (SSD) in a taxon is a phenomenon in which one sex is larger than the other, mainly in body size (Andersson, 1994; Cox *et al.*, 2003). SSD has been explored in many vertebrate groups,

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such as amphibians and fishes, in which females are usually larger than males (Liao *et al.*, 2013; Jonsson & Jonsson, 2015), while in others, such as mammals, birds and reptiles, males are usually the larger sex (Kratohvil & Frynta, 2006). Lizards are an ideal model group to study SSD evolution because high variation in the degree of SSD in lizard species has been reported: male-biased in some families (e.g. Tropicuridae, Teiidae: Brandt & Navas, 2013), female-biased in others (e.g. Pygopodidae, Diplodactylidae: Read, 1999; Cox *et al.*, 2009) or no sexual dimorphism (e.g. Anguillidae, Gekkonidae, Scincidae: Cox *et al.*, 2009).

In lizard species of the genus *Sceloporus*, studies have commonly examined only overall size dimorphism. Three patterns of SSD have been reported: male-biased, female-biased and no dimorphism (Fitch, 1978; Jiménez-Arcos *et al.*, 2017). These patterns were described based on a single morphological feature (snout–vent length, SVL) and single-population data, but such patterns can vary among (Ramírez-Bautista *et al.*, 2013; Jiménez-Arcos *et al.*, 2017) and within populations (Ramírez-Bautista *et al.*, 2015; Ramírez-Bautista *et al.*, 2016a, 2016b). Thus, a more detailed analysis of the morphology of a species, such as the shape or relative dimensions of the head and limbs, may provide a more comprehensive understanding of the possible causes of the evolution of sexual dimorphism because these structures have an important function on the ecology (e.g. diet) or behaviour (e.g. escape or defence of the territory) of the individuals (Cruz-Elizalde *et al.*, 2020; Lozano *et al.*, 2020). Analysis of the variation in sexual dimorphism patterns can help to elucidate and identify the causes that promote these variations (Jiménez-Arcos *et al.*, 2017).

Patterns of sexual dimorphism have been explained in different ways, such as growth rate differences between males and females (Ruby & Dunham, 1984; Smith & Ballinger, 1994), fecundity (Olsson *et al.*, 2002; Pincheira-Donoso & Hunt, 2017), sexual selection (Anderson & Vitt, 1990; Verrastro, 2004; Ramírez-Bautista *et al.*, 2008; Ramírez-Bautista & Pavón, 2009) and niche divergence (Camilleri & Shine, 1990; Perry, 1996; Hierlihy *et al.*, 2013). Sexual dimorphism is generally attributed to morphological traits, which affect an individual's ecology and behaviour (Darwin, 1871; Andersson, 1994; Olsson *et al.*, 2002). For instance, the relatively larger heads of males are believed to increase male success in male–male rivalry, so this trait is considered to have arisen through sexual selection (Olsson *et al.*, 2002). As mentioned above, the longer and wider body size of females has been attributed to fecundity selection to increase the space females have to hold the developing eggs/embryos, larger clutch/litter size and/or larger offspring at hatching (Andersson 1994; Olsson *et al.*, 2002; Cox *et al.*, 2003; Jiménez-Arcos *et al.*, 2017;

Pincheira-Donoso & Hunt, 2017). However, only a small number of studies have tested these hypotheses (Perry, 1996; Puga y Colmenares *et al.*, 2019) because a larger SVL in females could have occurred without female-biased SSD (Pincheira-Donoso & Hunt, 2017). To analyse these assumptions, we need to consider other dimensions of morphological traits such as shape (Lozano *et al.*, 2020). In this regard, little is known about variation among populations with respect to body size and shape differences between females and males (Dunham, 1982; Michaud & Echternacht, 1995; Herrel *et al.*, 2001; Ramírez-Bautista *et al.*, 2016a, 2016b; Lozano *et al.*, 2020), among different years of a single species (Ramírez-Bautista *et al.*, 2015, 2016a), and even less in species of a single taxonomic group (Herrel *et al.*, 2002; Jiménez-Arcos *et al.*, 2017).

Geographical variation in body sizes, and therefore correlation with other structures such as the length of the limbs reported in sexual dimorphism, can also be influenced by variation in environmental conditions (Zamora-Camacho *et al.*, 2014; Slavenko *et al.*, 2019). An example of this is Bergmann's rule, which states that at higher elevations and latitudes (and therefore at lower temperatures), body sizes will tend to be larger (Bergmann, 1847). This hypothesis has been widely tested in endotherms, and diverse studies have addressed this rule in ectotherms, registering negative results (Ashton & Feldman, 2003; Adams & Church, 2008; Pincheira-Donoso *et al.*, 2008; Slavenko *et al.*, 2019). However, evidence for consistent climate effects, especially among ectotherms, remains equivocal; for example, the lizard genus *Sceloporus* includes some species that follow Bergmann's rule (e.g. *S. undulatus*, *S. jarrovi*) and others that exhibit the inverse of Bergmann's rule (e.g. *S. merriami*, *S. graciosus*) at the intraspecific level (Angilletta *et al.*, 2004; Sears & Angilletta, 2004). So, despite finding a general pattern where it has been observed that environmental factors do not influence the body size of many groups of lizards (Slavenko *et al.*, 2019), there are groups such as the genus *Sceloporus* where there are species that do present an effect (Angilletta *et al.*, 2004). These effects are influenced by a mix of factors such as variations in temperature, precipitation, elevation or latitude (Bergmann, 1847; Angilletta *et al.*, 2004; Sears & Angilletta, 2004).

Within the genus *Sceloporus*, the *S. scalaris* group inhabits the central Mexican highlands, and is the only *Sceloporus* species group to exhibit both parity modes, oviparous and viviparous (Sites *et al.*, 1992; Creer *et al.*, 1997). According to Grummer *et al.* (2014), Leaché *et al.* (2016) and recently Bryson *et al.* (2021) this group includes 12 species, nine of which are oviparous (*S. aeneus*, *S. aurantius*, *S. brownorum*, *S. chaneyi*, *S. scalaris*, *S. slevini*, *S. unicanthalis*, *S. dixonii* and *S. hesperus*) and three are viviparous

(*S. bicanthalis*, *S. goldmani* and *S. subniger*; Leaché *et al.*, 2016). Previous studies have described the ecology and reproduction of some of these species (Guillette, 1981, 1982; Guillette & Jones, 1985; Guillette & Góngora, 1986; Ortega & Barbault, 1986; Rodríguez-Romero *et al.*, 2004, 2010, 2011; Ramírez-Bautista *et al.*, 2017); however, little has been studied regarding size dimorphism and even less about shape dimorphism in this group (Ramírez-Bautista *et al.*, 2016a; Jiménez-Arcos *et al.*, 2017) or the relationship with environmental factors or influence of reproductive mode (Jiménez-Arcos *et al.*, 2017).

Our goal here is to describe the body size and shape and compare these traits between sexes, among populations of each species and among species of the *S. scalaris* species group. Also, we evaluate whether morphological variation across populations and years in the *S. scalaris* species group is driven by climate conditions. Therefore, we test whether spatio-temporal (i.e. across sites and years) variation in temperature and precipitation explain body size and shape in these species. All these species descend from a common evolutionary ancestor. They are small-bodied and terrestrial but differ with respect to their reproductive mode (Ramírez-Bautista *et al.*, 2017). We would expect, on the one hand, that all species will have a similar pattern of sexual dimorphism (male-biased, size and shape) mainly in body size, with oviparous and viviparous species being more similar within their own populations (phylogenetic effect), and on the other hand, that variations in the size and shape of all morphological variables within a single species (among populations) could be a response to environmental pressures, mainly temperature and precipitation.

## MATERIAL AND METHODS

### STUDY AREA AND DATA COLLECTION

Environmental characteristics and vegetation types for each locality (Fig. 1) (termed ‘populations’ in this study) are detailed in Table 1. Most of the populations are in the Mexican Transvolcanic Belt physiographical region (except for La Michilía; Fig. 1).

We analysed 537 adult lizards (336 females and 201 males) from two scientific collections: Colección Nacional de Anfibios y Reptiles, Instituto de Biología (CNAR-IBH), and the Museo de Zoología, Facultad de Ciencias (MZFC), both at the Universidad Nacional Autónoma de México. The second author verified the identity of specimens in 1999 that had been collected from 1973 to 1993. Because the information comes from scientific collections and morphology may vary over time (Shine, 1992), in statistical tests, we controlled for ‘year’ of collection of lizards. The oviparous species included in this study were *S. aeneus* (Cahuacán,  $N = 150$ , 35

males and 115 females; Citlaltépetl,  $N = 28$ , 11 males and 17 females; Huamantla,  $N = 19$ , nine males and 10 females; Milpa Alta,  $N = 44$ , 16 males and 28 females; Tulancingo,  $N = 19$ , nine males and 10 females, and Uruapan,  $N = 15$ , four males and 11 females; from 1973 to 1993) and *S. scalaris* (Charahuén,  $N = 41$ , 17 males and 24 females; and La Michilía,  $N = 58$ , 16 males and 42 females; from 1973 to 1987). The viviparous species were *S. bicanthalis* [Atepec,  $N = 15$ , nine males and six females; Parque Nacional El Chico (PNCH),  $N = 15$ , seven males and eight females; Zoquiapan,  $N = 66$ , 33 males and 33 females; from 1973 to 1993] and *S. subniger* (Nevado de Toluca,  $N = 67$ , 35 males and 32 females; from 1982 to 1983).

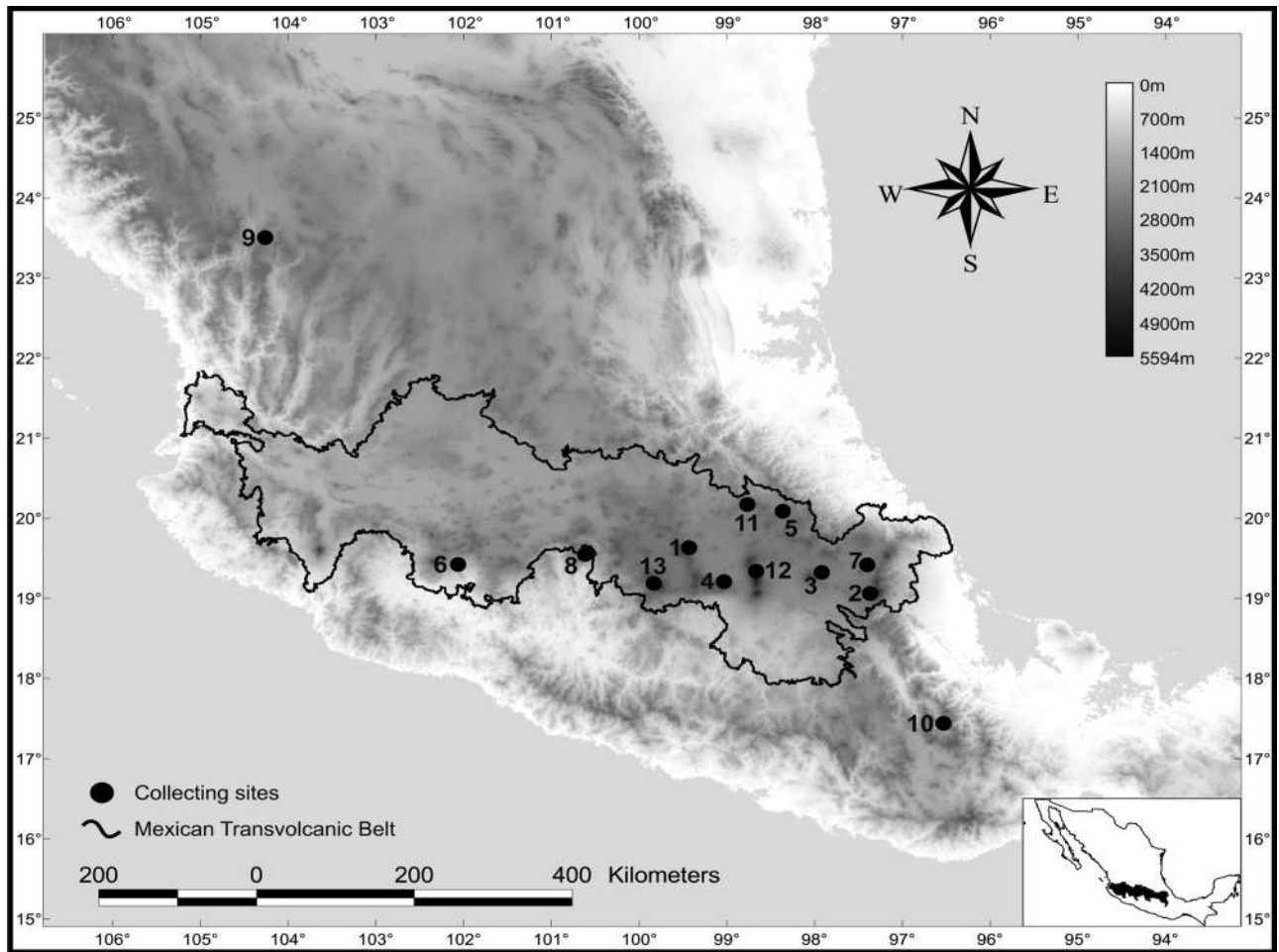
### MORPHOLOGICAL ANALYSIS

We took the following measurements on each adult specimen (from the right side in dorsal view) to the nearest 0.01 mm: snout–vent length (SVL: measured to the nearest 0.01 mm), head length (HL:  $\pm 0.01$  mm; distance from the anterior tip of the rostral scale to the posterior margin of the left ear), head width (HW:  $\pm 0.01$  mm; maximum width of the head, measured as the distance between the posterior margins of the left and right ears), tibia length (TL:  $\pm 0.01$  mm) and forearm length [FL:  $\pm 0.01$  mm; measured from the knee (TL) or elbow (FL) to the pad of the foot] in all specimens examined (Ramírez-Bautista *et al.*, 2014).

We studied sexual size and shape dimorphism in the *S. scalaris* group. Using the method of Mosimann (1970) (which is currently in use due to the broad explanatory power in size and shape analyses of morphological variables; see Cruz-Elizalde *et al.*, 2020; Lozano *et al.*, 2020), we removed the effect of size for each specimen by using an index of individual size (here ‘SIZE’, overall body size), and we then calculated the ratio of each morphological variable to this index (shape variables). SIZE was calculated as the fifth root of the product of the variables SVL, HL, HW, FL and TL. SIZE and shape variables were  $\log_{10}$ -transformed prior to analysis so that they could meet the conditions for parametric tests. Details regarding the estimates of shape variables are available in Lozano *et al.* (2020).

### STATISTICAL ANALYSES

To analyse SSD, we used year as a covariate in a two-way analysis of covariance (ANCOVA) to determine the effect of species–sex and population–sex (and their interactions) on SIZE. To explore for sexual shape dimorphism (SSHD), we carried out multivariate analysis of covariance (MANCOVA) using year as a covariate to test for the effect of species–sex and population–sex (and their interactions) on shape variables. For the ANCOVA and MANCOVA tests, post-hoc tests were



**Figure 1.** Collection sites for populations and species in the *Sceloporus scalaris* group along the Mexican Transvolcanic Belt (1 = Cahuacán, 2 = Citlaltépetl, 3 = Huamantla, 4 = Milpa Alta, 5 = Tulancingo, 6 = Uruapan, 7 = Alchichica, 8 = Charahuén, 9 = La Michilía, 10 = Atepec, 11 = Parque Nacional El Chico, 12 = Zoquiapan, 13 = Nevado de Toluca).

used to identify differences between the effects and the interaction. General discriminant function analyses (GDFAs) were carried out to identify the shape variables that best separated the groups of lizards (sexes, species and populations) (Harris, 2013). Following the procedure of Lozano *et al.* (2020), we selected the variables that best separated the groups by exploring the correlations between the first canonical axis of the GDFa and the shape variables. Species scores were plotted on graphs. Results were considered significant if  $P \leq 0.05$ . Statistical analyses were calculated in the Statistica v.7.0 program, and the measures were represented together with  $\pm 1$  SE (Zar, 2010).

#### MULTILEVEL MODELLING APPROACH

We analysed how morphological variation was related to variation in temperature and precipitation across time and space using a generalized linear mixed model (GLMM). We collected monthly data for maximum and

minimum temperature and total precipitation from the WorldClim database for each locality where individuals of the *S. scalaris* complex were collected and measured. Temperature and precipitation data were averaged for each year in each locality. We fitted GLMMs for each trait across populations from the *S. scalaris* complex using the *lmer* function from the *lme4* R package (Bates *et al.*, 2015). We coded climate variables as fixed effects and sites, sexes and years as random effects. Each trait's marginal effects were computed and contrasted against temperature and precipitation to visualize which features are more affected by climate gradients.

## RESULTS

### COMPARING OVERALL BODY SIZE AMONG SPECIES, POPULATIONS AND SEXES

Variations occurred in body size and morphological traits between sexes, and among populations of the

**Table 1.** Climate characteristics of geographical localities where *Sceloporus scalaris* group populations were collected. Xeric scrub (XS), pine forest (PF), oak forest (OF), pine–oak forest (POF) and prickly pear field (PP). Average annual values of temperature and precipitation are given with minimum and maximum values in parentheses. Populations are ordered by latitude (north to south)

Locality	Geographical location	Elevation (m)	Annual average temperature (°C)	Annual average precipitation (mm)	Vegetation type
La Michilía (Durango)	23°30'10"N, 104°15'46"W	1700–2950	12 (3.3–29.9)	480 (1–129)	PF, POF
Tulancingo (Hidalgo)	20°05'14"N, 98°19'24"W	2181	14.9	552.9	XS
Parque Nacional El Chico (Hidalgo)	20°11'15"N, 98°43'37"W	3035	12	1567.9	PF, POF
Cahuacán (Estado de México)	19°37'48"N, 99°25'54"W	2744	14.5 (2.1–25.5)	998 (8–216)	POF
Charahuén (Michoacán)	19°27'54"N, 100°42'05"W	2480	16.4 (4.5–27.7)	1041.2 (6–253)	PF, OF
Uruapan (Michoacán)	19°25'16"N, 102°03'47"W	1620	19.3	1427	PP
Huamantla (Tlaxcala)	19°19'02"N, 97°55'03"W	2553	14 (3–26)	1000 (9–129)	POF
Milpa Alta (México City)	19°12'20"N, 99°02'03"W	2460	15 (2.1–25.5)	718.7 (8–216)	PF
Nevado de Toluca (Estado de México)	19°11'N, 99°50'W	3200	12	700–1200	PF, POF
Citlaltépetl (Puebla)	19°01'38"N, 97°20'34"W	2600–3200	10 (2.4–25.3)	1600 (7–153)	POF
Zoquiapan (Estado de México)	19°20'N, 98°40'W	3000	11	1169.3	PF
San Juan Atepec (Oaxaca)	17°26'N, 96°32'W	2000	15 (5.5–24.7)	998 (8–216)	PF, OF

same species. Descriptive statistics of morphological variables are shown in Table 2. Results of the species–sex ANCOVA showed differences in overall body size (logSIZE) among species ( $F_{3,528} = 77.9, P < 0.001$ ) and between sexes ( $F_{1,528} = 19.5, P < 0.001$ ), and a significant interaction ( $F_{3,528} = 6.2, P < 0.001$ ). The population–sex ANCOVA showed differences among populations ( $F_{11,512} = 26.2, P < 0.001$ ) and between sexes ( $F_{1,512} = 27.3, P < 0.001$ ), and a significant interaction ( $F_{11,512} = 1.9, P = 0.032$ ). In females, *S. scalaris* was larger than all other species, whereas in males, the oviparous species (*S. aeneus* and *S. scalaris*) were larger than the viviparous species (*S. bicanthalis* and *S. subniger*) (Table 3; Fig. 2). We found differences among populations in *S. aeneus* ( $F_{5,262} = 4.1, P = 0.001$ ) and *S. scalaris* ( $F_{1,94} = 17.7, P < 0.001$ ), but not in *S. bicanthalis* ( $F_{2,89} = 1.5, P = 0.236$ ). When the sexes were separated, females followed the same pattern, but in males we only detected differences among populations in *S. scalaris* (Table 4). The smallest lizards in the *S. scalaris* group were in the Atepec and Nevado de Toluca populations, and Charahuén and La Michilía lizards were the largest (Fig. 3). Post-hoc comparison tests showed male-biased SSD in oviparous (*S. aeneus*:  $P < 0.001$ ; *S. scalaris*:  $P < 0.001$ ) but not in viviparous lizards (*S. bicanthalis*:  $P = 0.185$ ; *S. subniger*:  $P = 0.602$ ) (Fig. 2). At the population level,

males were larger than females in three populations of *S. aeneus* (Cahuacán, Citlaltépetl and Huamantla), and one of *S. scalaris* (Charahuén) and *S. bicanthalis* (PNCH); however, we did not find differences in overall body size between the sexes within *S. subniger* (Table 4; Fig. 3).

#### COMPARING BODY SHAPE AMONG SPECIES, POPULATIONS AND SEXES

The species–sex MANCOVA showed statistically significant differences in body shape among species (Wilks'  $\lambda = 0.768, F = 12.1, P < 0.001$ ) and between sexes (Wilks'  $\lambda = 0.728, F = 49, P < 0.001$ ), and a significant interaction (Wilks'  $\lambda = 0.947, F = 2.3, P = 0.006$ ). The population–sex MANCOVA showed significant differences among populations (Wilks'  $\lambda = 0.598, F = 6.4, P < 0.001$ ) and between sexes (Wilks'  $\lambda = 0.779, F = 36, P < 0.001$ ), but no significant interaction effect (Wilks'  $\lambda = 0.839, F = 1.3, P = 0.074$ ). In both sexes, comparisons among species revealed differences in all shape variables (Table 3). The oviparous species were smaller in relative HW but larger in relative TL than the viviparous species, and *S. aeneus* and *S. subniger* had relatively shorter FL than *S. scalaris* and *S. bicanthalis* (Table 3). In females, the oviparous species were smaller in relative SVL (relative body length) but larger in relative HL than

**Table 2.** Descriptive statistics of morphological characteristics (SVL = snout-vent length; HL = head length; HW = head width; FOL = forearm length; TL = tibia length) by sex of each population and species. Measures are presented as mean  $\pm$  1 SE, with ranges in parentheses

Species/ population	Morphological characteristics											
	SVL (mm)		HL (mm)		HW (mm)		FOL (mm)		TL (mm)			
	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males
<i>Sceloporus aeneus</i>												
Cahuacán	46.89 $\pm$ 0.31 (40.0–58)	47.94 $\pm$ 0.63 (37.0–55.0)	11.51 $\pm$ 0.06 (10.0–13.60)	12.44 $\pm$ 0.16 (9.0–13.9)	8.69 $\pm$ 0.06 (7.20–11.50)	9.50 $\pm$ 0.11 (7.50–10.70)	6.45 $\pm$ 0.06 (5.0–9.30)	6.95 $\pm$ 0.15 (5.50–10.0)	8.66 $\pm$ 0.07 (6.30–10.70)	9.51 $\pm$ 0.15 (6.70–10.90)		
Citlaltépetl	46.47 $\pm$ 0.62 (42.0–51.0)	50.36 $\pm$ 1.34 (41.0–57.0)	11.28 $\pm$ 0.17 (10.0–12.60)	12.64 $\pm$ 0.29 (11.30–14.0)	8.49 $\pm$ 0.09 (7.80–9.20)	9.42 $\pm$ 0.33 (6.80–10.80)	6.84 $\pm$ 0.19 (5.30–8.0)	6.90 $\pm$ 0.26 (5.70–8.20)	8.55 $\pm$ 0.11 (7.90–9.40)	9.73 $\pm$ 0.29 (7.80–11.0)		
Huamantla	50.50 $\pm$ 1.30 (44.0–59.0)	52.33 $\pm$ 1.12 (46.0–58.0)	11.99 $\pm$ 0.21 (11.20–13.50)	12.82 $\pm$ 0.33 (11.30–14.20)	8.93 $\pm$ 0.18 (8.20–10.20)	10.06 $\pm$ 0.33 (8.50–12.0)	6.87 $\pm$ 0.28 (6.0–8.9)	7.19 $\pm$ 0.30 (6.20–8.80)	8.98 $\pm$ 0.28 (7.8–11.20)	10.03 $\pm$ 0.25 (9.0–11.4)		
Milpa Alta	48.36 $\pm$ 0.80 (42.0–60.0)	48.13 $\pm$ 1.26 (41.0–58.0)	11.90 $\pm$ 0.21 (10.4–16.20)	12.75 $\pm$ 0.28 (10.4–14.5)	8.79 $\pm$ 0.19 (7.30–12.50)	9.51 $\pm$ 0.20 (8.30–11.20)	6.96 $\pm$ 0.18 (5.60–10.50)	7.34 $\pm$ 0.25 (5.50–9.50)	9.32 $\pm$ 0.30 (7.50–16.0)	9.69 $\pm$ 0.28 (8.05–12.10)		
Tulancingo	50.30 $\pm$ 1.69 (42.0–58.0)	50.78 $\pm$ 0.64 (48.0–55.0)	12.43 $\pm$ 0.44 (10.60–15.50)	12.71 $\pm$ 0.13 (12.0–13.20)	9.45 $\pm$ 0.34 (8.40–12.0)	9.93 $\pm$ 0.15 (9.0–10.6)	7.16 $\pm$ 0.38 (5.10–9.0)	7.13 $\pm$ 0.18 (6.0–7.6)	9.83 $\pm$ 0.56 (8.20–14.5)	10.10 $\pm$ 0.11 (9.50–10.60)		
Uruapan	47.18 $\pm$ 2.22 (38.0–60.0)	45.85 $\pm$ 0.96 (44.0–48.0)	11.57 $\pm$ 0.37 (10.0–13.50)	12.10 $\pm$ 0.13 (11.80–12.40)	8.55 $\pm$ 0.20 (7.80–9.60)	9.43 $\pm$ 0.06 (9.30–9.60)	6.21 $\pm$ 0.41 (4.60–8.80)	6.85 $\pm$ 0.23 (6.20–7.20)	9.22 $\pm$ 0.52 (7.20–12.70)	9.18 $\pm$ 0.23 (8.50–9.50)		
<i>Sceloporus scalaris</i>												
Charahuén	55.25 $\pm$ 1.36 (44.0–70.0)	58.06 $\pm$ 2.02 (45.0–70.0)	13.18 $\pm$ 0.24 (10.90–16.0)	14.42 $\pm$ 0.44 (11.70–17.8)	9.73 $\pm$ 0.19 (8.40–11.70)	10.65 $\pm$ 0.30 (8.0–12.20)	8.05 $\pm$ 0.22 (5.40–10.50)	8.89 $\pm$ 0.35 (6.70–12.0)	11.31 $\pm$ 0.31 (8.60–14.50)	12.36 $\pm$ 0.45 (9.0–15.60)		
La Michilia	51.95 $\pm$ 0.62 (41.0–62.0)	51.19 $\pm$ 0.70 (46.0–56.0)	12.96 $\pm$ 0.12 (10.60–14.50)	13.24 $\pm$ 0.21 (11.50–14.80)	9.59 $\pm$ 0.11 (7.60–11.0)	9.79 $\pm$ 0.17 (8.80–11.10)	7.40 $\pm$ 0.10 (5.80–8.80)	7.63 $\pm$ 0.15 (6.20–8.50)	9.79 $\pm$ 0.11 (7.90–11.20)	10.44 $\pm$ 0.20 (9.50–12.30)		
<i>Sceloporus bicanthalis</i>												
Atepec	48.67 $\pm$ 1.99 (40.0–54.0)	45.22 $\pm$ 1.01 (40.0–49.0)	11.42 $\pm$ 0.45 (10.0–12.70)	11.71 $\pm$ 0.24 (10.40–12.60)	8.72 $\pm$ 0.40 (7.30–9.70)	8.91 $\pm$ 0.15 (8.30–9.60)	6.28 $\pm$ 0.45 (4.70–7.70)	6.43 $\pm$ 0.20 (5.60–7.30)	8.30 $\pm$ 0.38 (7.0–9.50)	8.62 $\pm$ 0.24 (7.70–9.80)		
PNCH	46.5 $\pm$ 1.55 (40.0–53.0)	46.71 $\pm$ 1.84 (40.0–55.0)	11.29 $\pm$ 0.29 (10.3–12.5)	12.10 $\pm$ 0.45 (10.60–14.20)	8.65 $\pm$ 0.19 (8.0–9.40)	9.57 $\pm$ 0.30 (8.60–11.0)	6.59 $\pm$ 0.22 (5.80–7.50)	7.16 $\pm$ 0.26 (6.30–8.40)	8.60 $\pm$ 0.27 (7.60–10.0)	9.59 $\pm$ 0.39 (8.50–11.70)		
Zoquiapan	47.42 $\pm$ 0.60 (42.0–55.0)	44.67 $\pm$ 0.48 (40.0–51.0)	11.37 $\pm$ 0.11 (10.20–12.50)	11.74 $\pm$ 0.10 (10.50–13.30)	8.82 $\pm$ 0.11 (7.70–10.60)	9.05 $\pm$ 0.09 (7.8–10.20)	6.71 $\pm$ 0.09 (5.90–8.0)	6.92 $\pm$ 0.10 (5.50–8.00)	8.52 $\pm$ 0.11 (7.50–10.20)	8.93 $\pm$ 0.14 (7.50–11.10)		
<i>Sceloporus subniger</i>												
Nevado de Toluca	48.06 $\pm$ 0.66 (40.00–58.00)	44.91 $\pm$ 0.74 (33.00–52.00)	11.31 $\pm$ 0.12 (9.50–12.60)	11.45 $\pm$ 0.15 (9.40–13.00)	8.73 $\pm$ 0.10 (8.70–10.70)	8.92 $\pm$ 0.13 (7.10–10.50)	6.51 $\pm$ 0.10 (5.30–8.20)	6.34 $\pm$ 0.13 (4.50–8.00)	8.58 $\pm$ 0.12 (7.20–10.20)	8.77 $\pm$ 0.17 (6.80–11.00)		

**Table 3.** Results of ANCOVAs (by sex) comparing means of the log-version of the index of individual size (SIZE) and log-shape variables among four species of the *Sceloporus scalaris* group

Characteristic/species	Females	Males
logSIZE	$F_{3,331} = 46.1, P < 0.001$	$F_{3,196} = 43.3, P < 0.001$
<i>Sceloporus aeneus</i>	1.088	1.119
<i>Sceloporus scalaris</i>	1.142	1.170
<i>Sceloporus bicanthalis</i>	1.084	1.093
<i>Sceloporus subniger</i>	1.084	1.079
logSVL/SIZE	$F_{3,331} = 7.4, P < 0.001$	$F_{3,196} = 2.9, P = 0.036$
<i>Sceloporus aeneus</i>	0.587	0.569
<i>Sceloporus scalaris</i>	0.581	0.565
<i>Sceloporus bicanthalis</i>	0.591	0.559
<i>Sceloporus subniger</i>	0.597	0.571
logHL/SIZE	$F_{3,331} = 4.4, P = 0.005$	$F_{3,196} = 5.1, P = 0.002$
<i>Sceloporus aeneus</i>	-0.023	-0.021
<i>Sceloporus scalaris</i>	-0.028	-0.031
<i>Sceloporus bicanthalis</i>	-0.029	-0.023
<i>Sceloporus subniger</i>	-0.031	-0.022
logHW/SIZE	$F_{3,331} = 11.21, P < 0.001$	$F_{3,196} = 20.7, P < 0.001$
<i>Sceloporus aeneus</i>	-0.148	-0.139
<i>Sceloporus scalaris</i>	-0.160	-0.162
<i>Sceloporus bicanthalis</i>	-0.142	-0.135
<i>Sceloporus subniger</i>	-0.143	-0.131
logFL/SIZE	$F_{3,331} = 3.3, P = 0.021$	$F_{3,196} = 4.8, P = 0.003$
<i>Sceloporus aeneus</i>	-0.273	-0.274
<i>Sceloporus scalaris</i>	-0.262	-0.256
<i>Sceloporus bicanthalis</i>	-0.264	-0.259
<i>Sceloporus subniger</i>	-0.272	-0.280
logTL/SIZE	$F_{3,331} = 14.5, P < 0.001$	$F_{3,196} = 11.3, P < 0.001$
<i>Sceloporus aeneus</i>	-0.143	-0.136
<i>Sceloporus scalaris</i>	-0.131	-0.116
<i>Sceloporus bicanthalis</i>	-0.156	-0.143
<i>Sceloporus subniger</i>	-0.151	-0.139

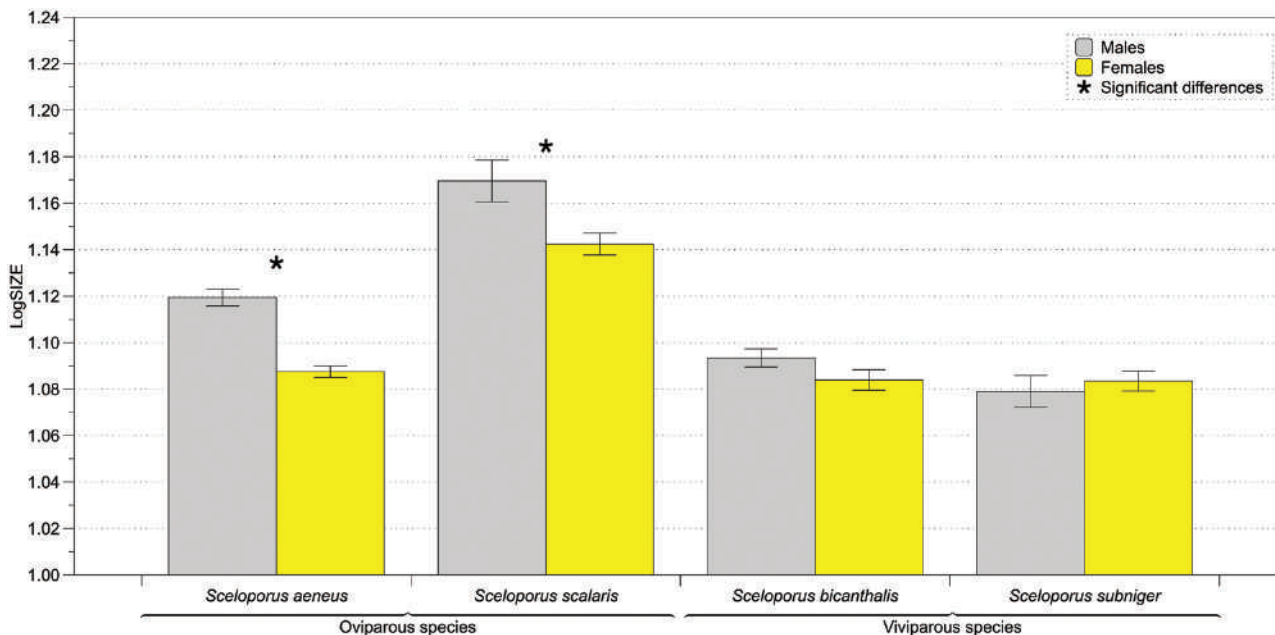
the viviparous lizards. In males, the smallest species in relative SVL and HL were *S. bicanthalis* and *S. scalaris*, respectively (Table 3). Within species, differences in body shape among populations were found in *S. aeneus* (females: relative HW, FL and TL; males: relative SVL), *S. scalaris* (females: relative HL, HW, FL and TL; males: relative HW) and *S. bicanthalis* (females: relative SVL and FL; males: relative SVL) (Table 4). Two patterns of SSHD were found in the *S. scalaris* group. The first, female-biased shape dimorphism in relative SVL, was present in all species and almost all populations (except for the Citlaltépetl and Tulancingo populations, Table 4). The second, male-biased shape dimorphism, was recorded in some other shape variables and very few populations (*S. aeneus*: Uruapan population, relative HW; *S. scalaris*: La Michilía population, relative TL; *S. subniger*: Nevado de Toluca, relative HL, HW and TL) (Table 4). The GDFAs confirmed differences in body shape between sexes (Wilks'  $\lambda = 0.716, P < 0.001$ ; Fig. 4), among species (Wilks'  $\lambda = 0.776, P < 0.001$ ; Fig. 5) and

among populations (Wilks'  $\lambda = 0.594, P < 0.001$ ; Fig. 6) in the *S. scalaris* group. As can be seen in Table 5 and Figures 4–6, there were more noticeable differences in body shape between the sexes than among species or populations. The variable that best separated the sexes was relative SVL, females having relatively longer body length than males (Table 5; Fig. 4). Relative HW and TL separated the species and populations better. The oviparous species were similar to each other and had relatively smaller HW but relatively larger TL than the viviparous species (Table 5; Fig. 5). Among populations, Charahuén was the largest in relative TL and the smallest in relative HW (Table 5; Fig. 6).

#### MULTILEVEL MODELLING APPROACH

We did not find mixed responses in variation in morphological traits to temperature and precipitation in the *S. scalaris* complex (Fig. 7). We did not detect any climate signatures in body size traits (e.g. overall





**Figure 2.** Comparison of means of the log-version of the index of individual size (SIZE) between sexes in oviparous and viviparous lizards of the *Sceloporus scalaris* group. \*Significant differences.

body size and shape or SVL; Fig. 7). Nor did we observe strong climate signatures in limb traits (Fig. 7) or support for any effect of variation across years, localities, sexes or species (Supporting Information, Figs S1–S4). The computation of marginal effects for GLMMs showed that no particular morphological traits exhibited stronger responses across temperature and precipitation gradients than others (Fig. 8). Accordingly, the morphological response to climate variation is complex, and context-dependent on the trait examined; however, no effect of environmental variables was found (Fig. 8).

## DISCUSSION

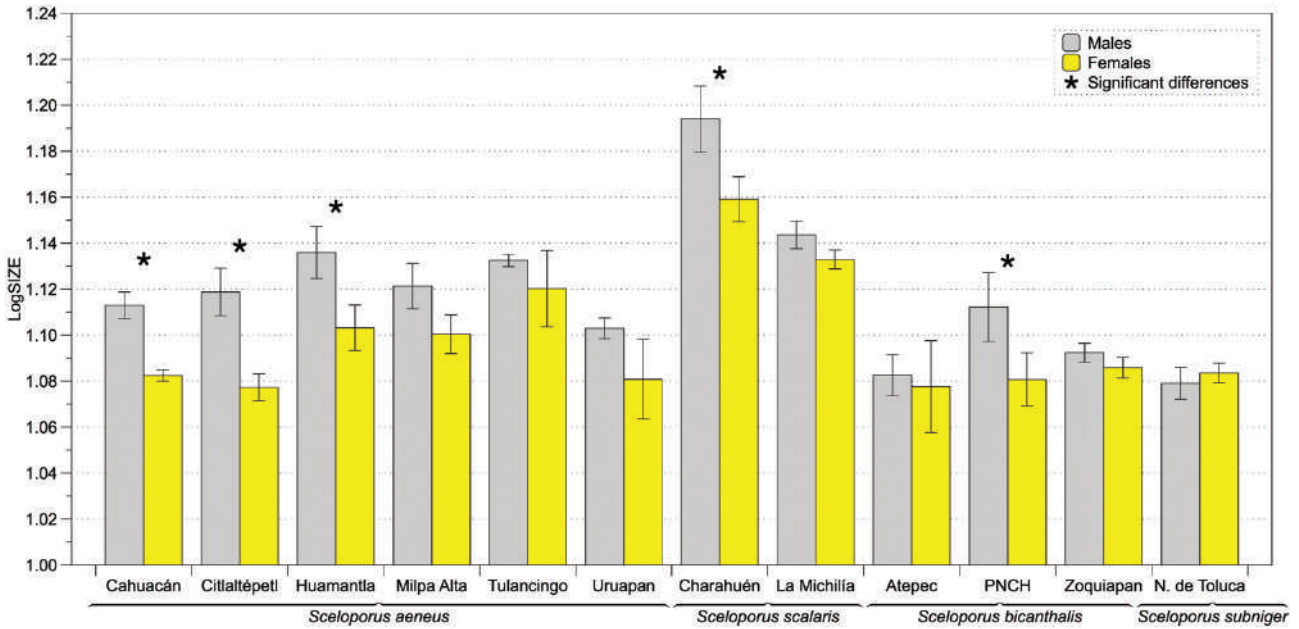
SSD and SSHD have been recognized in several vertebrate species (Andersson, 1994; Vanhooydonck & Van Damme, 1999; Cox *et al.*, 2003, 2009). In lizard species, SSD has been found to be expressed through morphological traits, such as allometry (Kaliontzopoulou *et al.*, 2007, 2008, 2010), SVL (Olsson *et al.*, 2002; Cox *et al.*, 2003; Roitberg & Smirina, 2006; Valencia-Limón *et al.*, 2014; Ramírez-Bautista *et al.*, 2016a), behaviour and colour patterns (Cooper & Vitt, 1989; Andrews & Stamps, 1994; Stephenson, 2010; Stephenson & Ramírez-Bautista, 2012), and niche divergence (Kaliontzopoulou *et al.*, 2007; Hierlihy *et al.*, 2013). In this study, we used two different methods to detect morphological differences among populations and species, and to evaluate sexual dimorphism in the

*S. scalaris* group. First, we used an overall body size comparison approach (applying an index of individual size); second, we determined the shape attributes of the body (shape variables). In addition, we evaluated the relationship between spatial variation in morphological traits and the environmental factors temperature and precipitation.

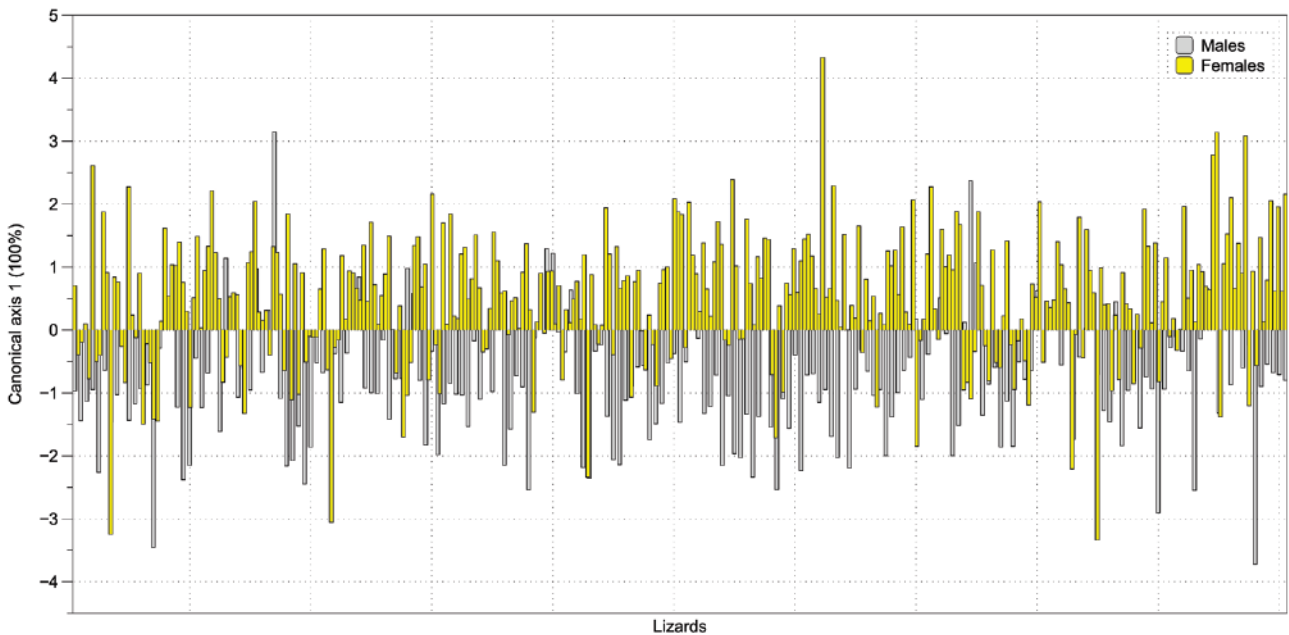
We found that the oviparous lizards (*S. aeneus* and *S. scalaris*) were different and larger in overall body size than the viviparous lizards (*S. bicanthalis* and *S. subniger*; Fig. 2), with each species being more similar among its own populations (Fig. 3). Specifically, the largest lizards in the *S. scalaris* group were in the Charahuén and La Michilía populations (*S. scalaris*), while those of Atepec and Nevado de Toluca were the smallest (*S. bicanthalis* and *S. subniger*, respectively). Differences in overall body size among populations were recorded in *S. aeneus* and *S. scalaris* but not in *S. bicanthalis*. In addition, at the species level, male-biased SSD was recorded in the oviparous but not in the viviparous species (Fig. 2). However, at the population level, some populations of oviparous lizards did not present SSD (*S. aeneus*: Milpa Alta, Tulancingo, Uruapan; *S. scalaris*: La Michilía), but one population of viviparous lizards did (*S. bicanthalis*: PNCH; Fig. 3). These results can be explained by phylogenetic (parity mode, oviparous vs. viviparous species) and environmental effects (within-species and within-population variation) acting on the *S. scalaris* group. For instance, males and females of *S. bicanthalis*

**Table 4.** Means of the log-version of the index of individual size (SIZE) and log-shape variables of male (M) and female (F) lizards of the *Sceloporus scalaris* group from 12 populations from Mexico. Comparisons were among populations within a single species (ANCOVAs), and between males and females within a single population (post-hoc comparison tests in the MANCOVA; \* indicates the larger sex when a significant difference was recorded)

Species/ population	Overall body size																
	logSIZE						Shape variables										
	Females		Males		logSVL/SIZE		logHL/SIZE		logHW/SIZE		logFL/SIZE		logTL/SIZE				
<i>Sceloporus</i> <i>aeneus</i>																	
Cahuacán	1.0824	1.1130*	0.5876*	0.5663	-0.0221	-0.0194	-0.1448	-0.1362	-0.2746	-0.2739	-0.1461	-0.1368					
Citlaltépetl	1.0773	1.1188*	0.5893	0.5817	-0.0257	-0.0182	-0.1489	-0.1477	-0.2688	-0.2830	-0.1460	-0.1328					
Huamantla	1.1032	1.1359*	0.5988*	0.5821	-0.0249	-0.0291	-0.1530	-0.1353	-0.2692	-0.2822	-0.1516	-0.1355					
Milpa Alta	1.1004	1.1213	0.5825*	0.5589	-0.0266	-0.0174	-0.1588	-0.1446	-0.2613	-0.2593	-0.1357	-0.1376					
Tulancingo	1.1202	1.1325	0.5791	0.5729	-0.0280	-0.0285	-0.1470	-0.1358	-0.2711	-0.2803	-0.1329	-0.1284					
Uruapan	1.0808	1.1030	0.5885*	0.5580	-0.0195	-0.0203	-0.1497	-0.1288*	-0.2969	-0.2681	-0.1224	-0.1408					
ANCOVA	$F_{5,184} = 4.0, F_{5,77} = 1.6, P = 0.0016$	$F_{5,77} = 1.7, F_{5,184} = 3.4, P = 0.0073$	$F_{5,184} = 1.0, F_{5,77} = 1.2, P = 0.4130$	$F_{5,184} = 2.2, F_{5,77} = 1.3, P = 0.2932$	$F_{5,184} = 2.5, F_{5,77} = 1.1, P = 0.0295$	$F_{5,184} = 2.9, F_{5,77} = 0.5, P = 0.0016$	$F_{5,184} = 1.1, F_{5,77} = 1.1, P = 0.3507$	$F_{5,184} = 2.9, F_{5,77} = 0.5, P = 0.0162$	$F_{5,184} = 2.9, F_{5,77} = 0.5, P = 0.0162$	$F_{5,184} = 2.9, F_{5,77} = 0.5, P = 0.0162$	$F_{5,184} = 2.9, F_{5,77} = 0.5, P = 0.0162$	$F_{5,184} = 2.9, F_{5,77} = 0.5, P = 0.0162$					
<i>Sceloporus</i> <i>scalaris</i>																	
Charahuén	1.1591	1.1940*	0.5802*	0.5654	-0.0408	-0.0384	-0.1727	-0.1697	-0.2573	-0.2505	-0.1094	-0.1068					
La Michilía	1.1329	1.1436	0.5815*	0.5650	-0.0209	-0.0226	-0.1521	-0.1538	-0.2652	-0.2627	-0.1432	-0.1258*					
ANCOVA	$F_{1,63} = 7.0, F_{1,30} = 9.6, P = 0.0100$	$F_{1,63} = 1.5, F_{1,30} = 0.2, P = 0.2188$	$F_{1,63} = 17.8, F_{1,30} = 0.4, P = 0.0001$	$F_{1,63} = 0.2, F_{1,30} = 0.4, P = 0.5429$	$F_{1,63} = 25.1, F_{1,30} = 7.3, P < 0.0001$	$F_{1,63} = 6.6, F_{1,30} = 1.3, P = 0.0114$	$F_{1,63} = 25.1, F_{1,30} = 7.3, P < 0.0001$	$F_{1,63} = 6.6, F_{1,30} = 1.3, P = 0.0127$	$F_{1,63} = 6.6, F_{1,30} = 1.3, P = 0.0127$	$F_{1,63} = 6.6, F_{1,30} = 1.3, P = 0.0127$	$F_{1,63} = 6.6, F_{1,30} = 1.3, P = 0.0127$	$F_{1,63} = 6.6, F_{1,30} = 1.3, P = 0.0127$					
<i>Sceloporus</i> <i>bicanthalis</i>																	
Atepec	1.0776	1.0826	0.6076*	0.5719	-0.0219	-0.0147	-0.1397	-0.1331	-0.2852	-0.2759	-0.1609	-0.1482					
PNCH	1.0807	1.1122*	0.5850*	0.5553	-0.0291	-0.0311	-0.1444	-0.1324	-0.2638	-0.2591	-0.1477	-0.1326					
Zoquiapan	1.0858	1.0924	0.5891*	0.5568	-0.0308	-0.0233	-0.1413	-0.1365	-0.2602	-0.2538	-0.1568	-0.1432					
ANCOVA	$F_{2,43} = 0.3, F_{2,45} = 1.4, P = 0.7298$	$F_{2,43} = 3.8, F_{2,45} = 4.3, P = 0.0306$	$F_{2,43} = 1.5, F_{2,45} = 1.8, P = 0.2226$	$F_{2,43} = 1.5, F_{2,45} = 1.8, P = 0.1679$	$F_{2,43} = 0.2, F_{2,45} = 0.4, P = 0.8561$	$F_{2,43} = 1.8, F_{2,45} = 1.8, P = 0.1679$	$F_{2,43} = 0.2, F_{2,45} = 0.4, P = 0.8561$	$F_{2,43} = 0.4, F_{2,45} = 0.4, P = 0.6638$	$F_{2,43} = 4.1, F_{2,45} = 2.4, P = 0.0237$	$F_{2,43} = 2.4, F_{2,45} = 2.4, P = 0.1005$	$F_{2,43} = 0.9, F_{2,45} = 0.6, P = 0.4227$	$F_{2,43} = 0.9, F_{2,45} = 0.6, P = 0.5229$					
<i>Sceloporus</i> <i>subniger</i>																	
Nevado de Toluca	1.0835	1.0790	0.5970*	0.5712	-0.0308	-0.0216*	-0.1431	-0.1305*	-0.2717	-0.2802	-0.1514	-0.1389*					



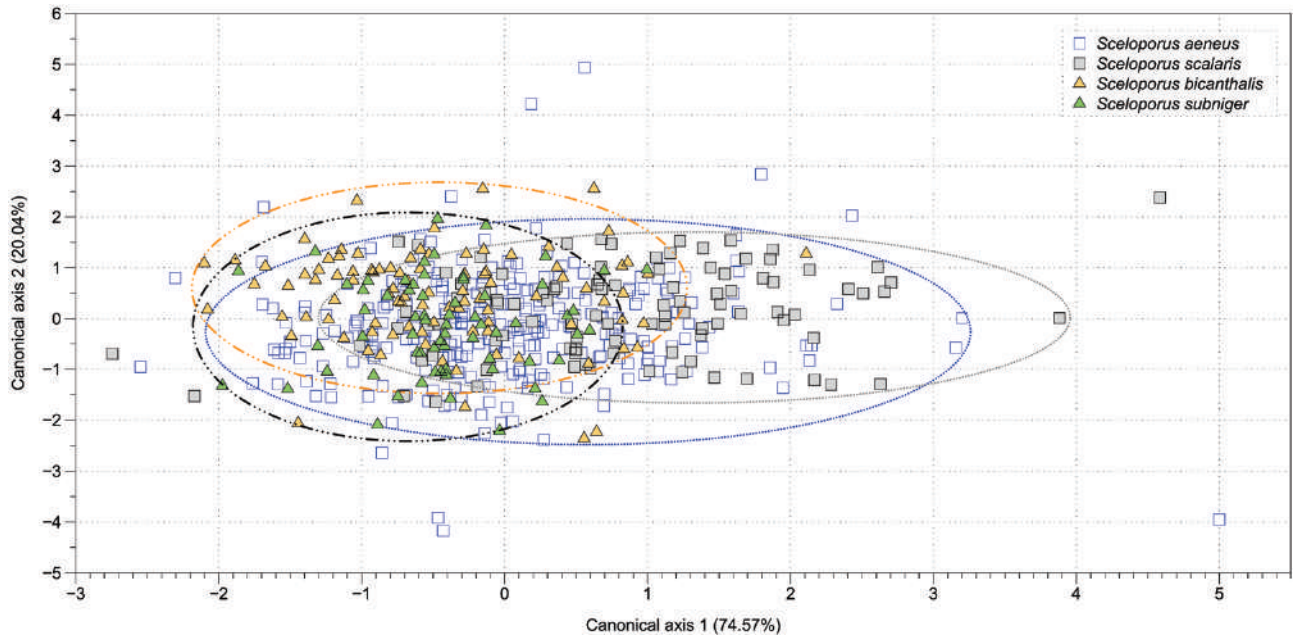
**Figure 3.** Comparison of means of the log-version of the index of individual size (SIZE) between sexes in populations of the *Sceloporus scalaris* group. \*Significant differences.



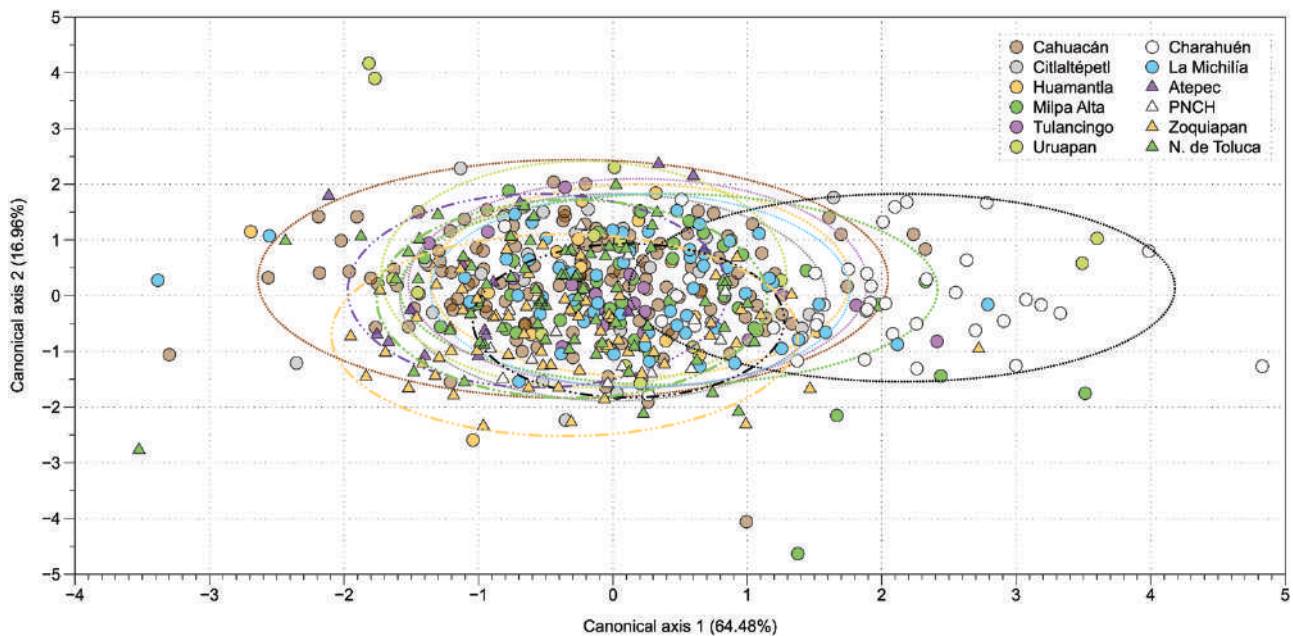
**Figure 4.** Species scores for the first canonical axis of the GDA including five log-shape variables of the *Sceloporus scalaris* group. Comparison between males and females.

and *S. subniger* that inhabit high elevations are smaller in SVL than the oviparous species (*S. aeneus* and *S. scalaris*) from lower elevations; therefore, viviparous species from colder environments cannot attain larger SVL to produce and maintain appropriate energy during the reproductive season

(Roitberg *et al.*, 2015). These lizard species invest more energy in growing to a larger SVL at the beginning of the reproductive season, and then direct all their energy to reproduction and none to growth, as occurs in many lizard species from high mountains (Lemos-Espinal *et al.*, 1998).



**Figure 5.** Species scores for the first two canonical axes of the GDFA including five log-shape variables of the *Sceloporus scalaris* group. Comparison among species.



**Figure 6.** Species scores for the first two canonical axes of the GDFA including five log-shape variables of the *Sceloporus scalaris* group. Comparison among populations.

Male-biased SSD could be explained by the sexual selection hypothesis (Olsson *et al.*, 2002; Cox *et al.*, 2003; Kaliontzopoulou *et al.*, 2007, 2008, 2010; Valencia-Limón *et al.*, 2014; Ramírez-Bautista *et al.*, 2015, 2016a). As in most species of the genus *Sceloporus*,

males are larger than females in many morphological structures, as also occurs in other genera of lizards (Kaliontzopoulou *et al.*, 2007, 2008, 2010; Valencia-Limón *et al.*, 2014). As mentioned, this pattern was found in half of the populations in oviparous species,

**Table 5.** Results of general discriminant function analysis (GDFA) by sex, species and populations of the *Sceloporus scalaris* group. Correlations between the first canonical axis of GDFA and shape variables are shown. Variables that best separated the groups are in bold type

Canonical axes	GDFA (sexes)			GDFA (species)			GDFA (populations)		
	Eigenvalue	Wilk's $\lambda$	P-value	Eigenvalue	Wilk's $\lambda$	P-value	Eigenvalue	Wilk's $\lambda$	P-value
First	0.395	0.717	< 0.001	0.204	0.776	< 0.001	0.377	0.595	< 0.001
Second	–	–	–	0.055	0.934	< 0.001	0.099	0.819	< 0.001
Third	–	–	–	0.015	0.985	0.020	0.088	0.901	< 0.001
Fourth	–	–	–	–	–	–	0.020	0.980	0.230
Shape variables	Canonical axis 1 (correlations)			Canonical axis 1 (correlations)			Canonical axis 1 (correlations)		
logSVL/SIZE	<b>0.91</b>			–0.11			–0.18		
logHL/SIZE	–0.14			–0.17			–0.44		
logHW/SIZE	–0.32			<b>–0.89</b>			<b>–0.77</b>		
logFL/SIZE	–0.03			0.21			0.28		
logTL/SIZE	–0.27			<b>0.69</b>			<b>0.76</b>		

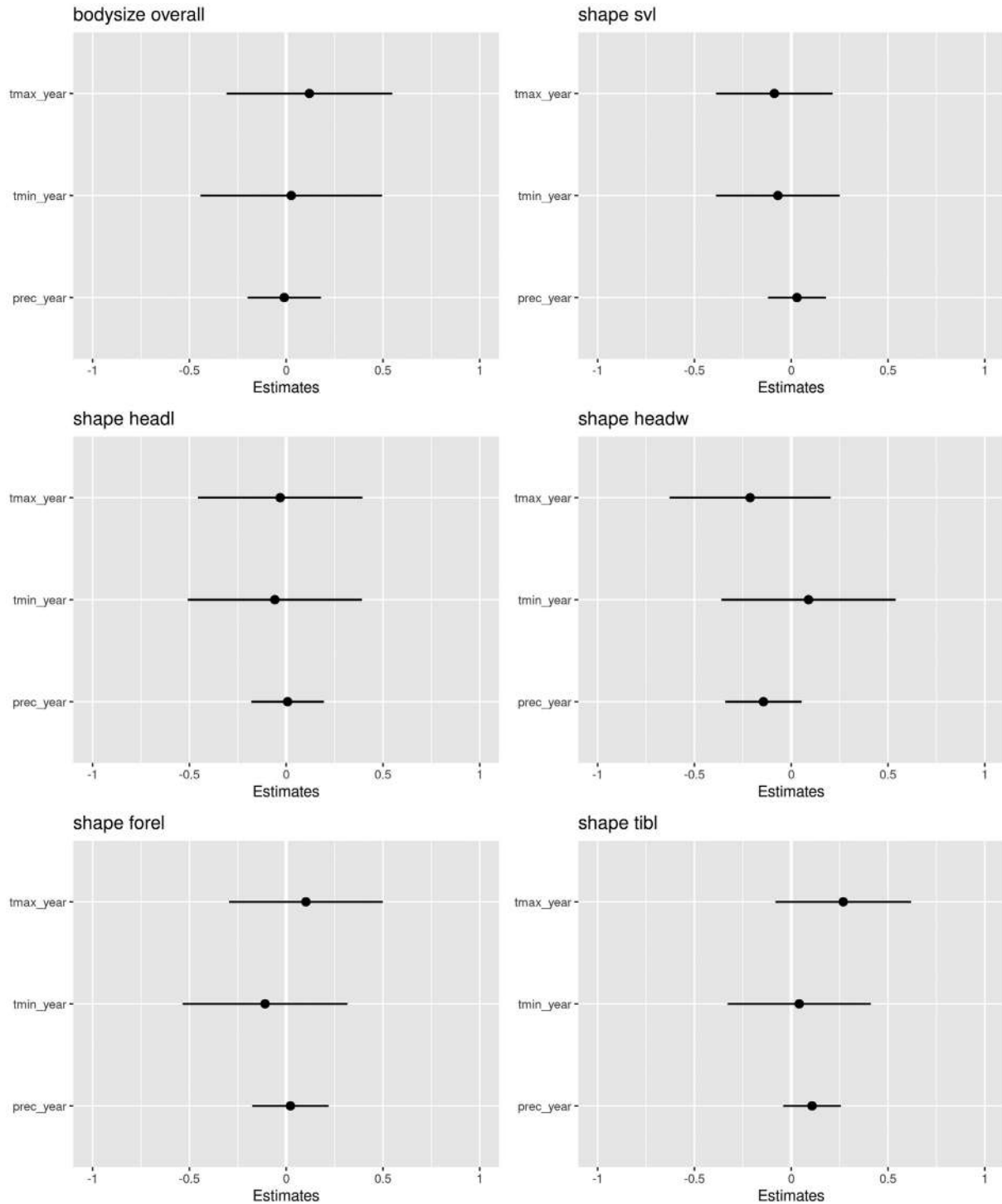
and in only one population of viviparous species (Table 4). For example, the oviparous lizard *S. aeneus* is territorial; therefore, males with larger overall body size could be explained in the following ways: males defend their territory against intruders (aggression), mating success (male–male combat for access to females) and intersexual selection (female choice). These characteristics could explain males being larger in overall body size (and other morphological traits) to benefit male reproduction (Manriquez-Morán *et al.*, 2013; Ramírez-Bautista *et al.*, 2016a, 2016b). Females of *S. aeneus* reproduce from April to September, during which they bear at least two clutches (frequencies; Ramírez-Bautista *et al.*, 2016a, 2016b); therefore, larger males will be more competitive to reach sexual maturity and success in reproduction during the reproductive period to attain a higher number of copulations (Stamps, 1993; Anderson & Vitt, 1990; Haenel *et al.*, 2003; Cox *et al.*, 2003).

The lack of SSD could be related to similarity between males and females in sex ratio, low territoriality for males or feeding niche convergence, as occurs in other lizard species (Zamudio *et al.*, 1998; Kaliontzopoulou *et al.*, 2007; Hierlihy *et al.*, 2013; Ramírez-Bautista *et al.*, 2015, 2016a). As noted above, this pattern could be explained by a low degree of polygyny (e.g. *S. siniferus*, Hierlihy *et al.*, 2013; Ramírez-Bautista *et al.*, 2015; *S. spinosus*, Ramírez-Bautista *et al.*, 2013; *S. aeneus*, Ramírez-Bautista *et al.*, 2016a; this study), or by non-territoriality, as occurs in other lizard species (Cox *et al.*, 2003; Hierlihy *et al.*, 2013). Population densities of the *S. scalaris* group could be high for males and females; therefore, when densities increase, mainly in females, males do not need to look for females or to fight other males to access females during reproduction. Males thus do not need

to increase in body size to maintain the population during the reproductive period (Zamudio *et al.*, 1998; Ramírez-Bautista *et al.*, 2015, 2016a).

Another explanation for a lack of SSD (and other morphological features) could be related to colour patterns. It has been well documented that when males and females are similar in morphological traits, males of the genus *Sceloporus* usually exhibit brighter colours in the dorsal and ventral region (Ossip-Drahos *et al.*, 2016), as has been reported in viviparous species (*S. formosus*, Ramírez-Bautista & Pavón, 2009; *S. dugesii*, Ramírez-Bautista & Dávila-Ulloa, 2009; *S. minor*, Stephenson & Ramírez-Bautista, 2012; García-Rosales *et al.*, 2017). This could be the case in the *S. scalaris* group because the ventral region of males presents dark blue patches and their gular region presents black bars, which become more conspicuous in the reproductive period (Ramírez-Bautista *et al.*, 2017). However, it is important to note that the colour pattern is not a determining factor in SSD, but is a characteristic associated with defence of territory and courtship of females, being more successful in larger males (Stephenson & Ramírez-Bautista, 2012; García-Rosales *et al.*, 2017).

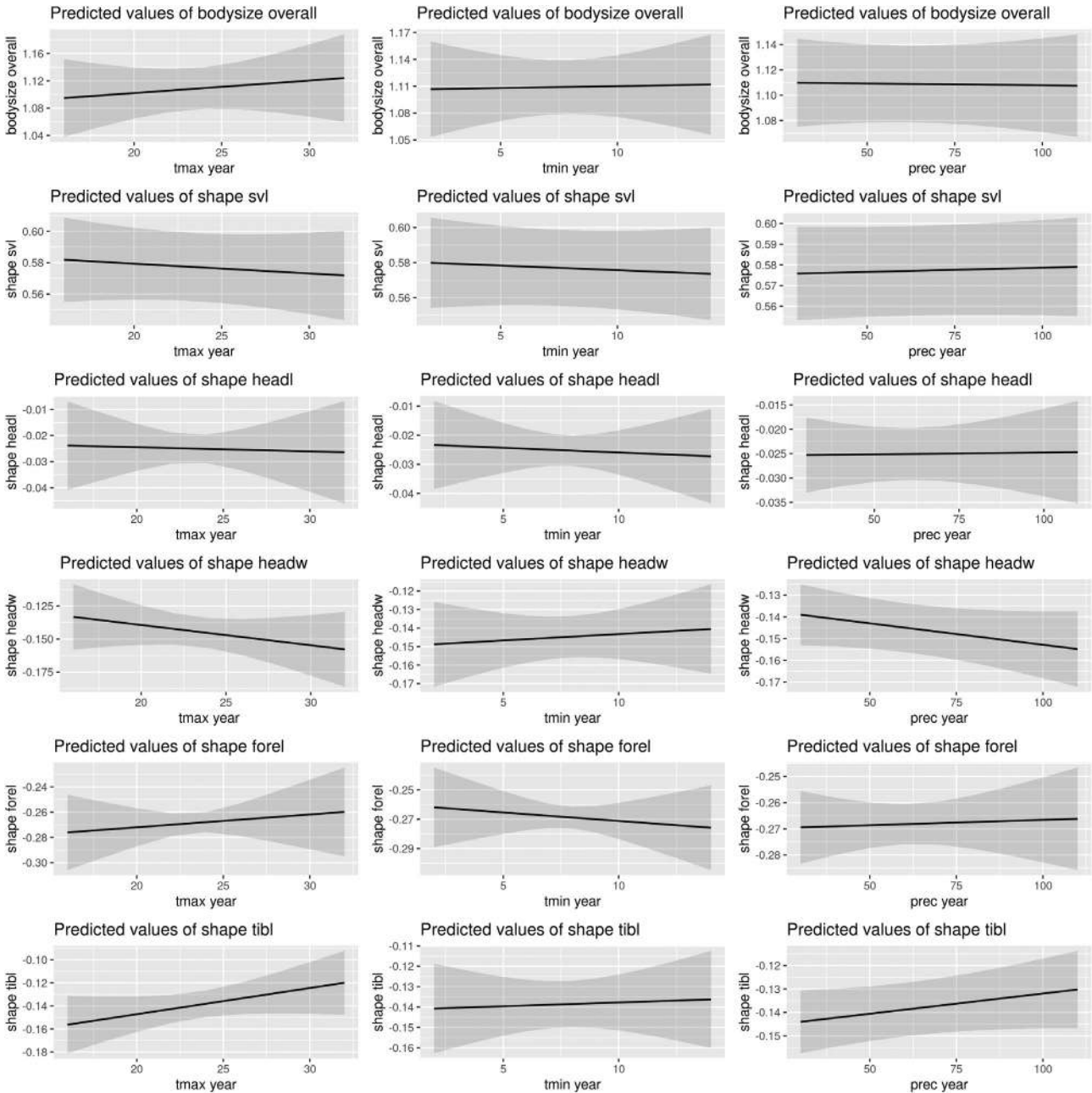
The multivariate analysis carried out in this study revealed that the body shape variable that best separated the sexes was relative SVL (elongation of the body; see below), while relative HW and TL better separated species and populations. The oviparous lizards were similar to each other in some shape variables (smaller in relative HW and larger in relative TL) but different from the viviparous lizards (Table 3; Fig. 5). Also, *S. aeneus* and *S. subniger* had relatively shorter FL than *S. scalaris* and *S. bicanthalis* (Table 3). Our results indicate that a phylogenetic effect could be acting on these species (as suggested for overall



**Figure 7.** Estimates (fixed effects) of generalized linear mixed models for each trait regressed against climate variables. tmax\_year: maximum temperature averaged across a year; tmin\_year: minimum temperature averaged across a year; prec\_year: precipitation averaged across a year.

body size). Additionally, we found variation among populations in several shape variables (within species, Fig. 6), which could be a response to ecological causes

(i.e. mating, defence of territory) or use of resources (i.e. microhabitat, size of prey) in the environment (Vanhooydonck & Van Damme, 1999; Herre *et al.*, 2001).



**Figure 8.** Marginal effects of morphological traits against climatic variables.

For instance, [Lozano \*et al.\* \(2020\)](#) observed strong differences in body shape (head and limbs) between populations of *S. grammicus* that inhabit different environments. These authors suggested that shape divergence may be due to structural features of the habitats, which could also be the case with certain morphological structures analysed in our study (see [Table 4](#)).

We found two patterns of SSHD in the *S. scalaris* group. The first was that females had relatively longer SVL (elongated body) than similarly sized

males in all species and almost all the populations. This kind of pattern has been mentioned (based on body length) in pioneering ([Darwin, 1871](#)), historical ([Fitch, 1970, 1978](#); [Vitt, 1986](#); [Olsson \*et al.\*, 2002](#); [Cox \*et al.\*, 2003, 2009](#)) and current studies. Larger females than males are explained mainly by fecundity ([Horvathova \*et al.\*, 2013](#); [Scharf & Meiri, 2013](#); [Pincheira-Donoso & Hunt, 2017](#)). The fecundity advantage hypothesis focuses on selection to maximize clutch/litter size in a given reproductive episode, and it could be the case for both viviparous

(*S. formosus*, Ramírez-Bautista & Pavón, 2009; *S. grammicus*, Hernández-Salinas *et al.*, 2010; *S. bicanthalis*, Rodríguez-Romero *et al.*, 2004) and oviparous (*S. variabilis*, Benabib, 1994; Ramírez-Bautista *et al.*, 2006; *S. aeneus*, Ramírez-Bautista *et al.*, 2016a, 2016b; this study) lizards in this study, as was recognized in the fecundity hypothesis by Olsson *et al.* (2002) and Cox *et al.* (2003).

The fecundity hypothesis better explains the larger sizes in females; however, a larger size in females due to fecundity does not necessarily result in female-biased sexual dimorphism (Pincheira-Donoso & Hunt, 2017). For example, Olsson *et al.* (2002) showed that a positive directional fecundity selection in *Niveoscincus microlepidotus* targets female trunk length for increased fecundity, but males were significantly larger in body size (i.e. male-biased SSD). This study supports the fecundity prediction, but not the body size (or SSD) prediction of fecundity selection. Also, another possible explanation of SSHD in females is selection favouring small relative SVL in males (elongation of the body). For instance, selection for small-bodied males could be due to early maturation of males, different sex ratios or changes in the skewness of the male body size distribution, as occurs in the species *Phrynosoma douglasi*, *P. ditmarsii* and *P. hernandezi* (Zamudio *et al.*, 1998).

The second pattern was found in very few populations. Male-biased SSHD was recorded in *S. aeneus* (Uruapan: relative HW), *S. scalaris* (La Michilía: relative TL) and *S. subniger* (Nevado de Toluca: relative HL, HW and TL). Previous research in lizards has suggested that the shape of the head and limbs in males are important morphological features linked to territorial defence and mating (Butler & Losos, 2002; Herrel *et al.*, 2006; Huyghe *et al.*, 2009; Lozano *et al.*, 2020); therefore, differences in body shape between sexes in the *S. scalaris* group could also be explained by sexual selection. The same pattern has been observed in other species of the genus *Sceloporus* such as *S. grammicus* (Lozano *et al.*, 2020) and *S. variabilis* (Cruz-Elizalde *et al.*, 2020). However, this result can be applied to any species with male-biased sexual dimorphism, so that a greater number of studies focused on the form–function relationship of the analysed characteristics can give a better explanation of the result found in males.

Considering environmental factors, in general no pattern was observed where the overall body size and the shape variables might increase as the maximum and minimum temperature of the study sites increases. For example, head length did not vary across temperature and precipitation, but head width decreased slightly toward higher maximum temperatures and more precipitation (Fig. 8), and limb traits (fore and hindlimb) exhibited different responses, showing larger dimensions toward higher maximum temperatures and more precipitation

(Fig. 8). These results largely coincide with the inverse of Bergmann's rule (Ashton & Feldman, 2003; Olalla-Tárraga & Rodríguez, 2007; Slavenko *et al.*, 2019; Velasco *et al.*, 2020). This result can be explained by the way temperature is thermoregulated, since heliotherm reptiles occur in cold winter environments, such as the species of the *Scalaris* group (Mathies & Andrews, 1995; Andrews, 1998). A wide number of studies have shown that annual and daily activity and thermoregulatory processes in cold climate lizards may vary substantially in comparison to warm climate lizards (Lara-Reséndiz *et al.*, 2014), but there are no studies that show an effect of these behaviours on body size (Sagonas *et al.*, 2013). For example, Mathies & Andrews (1995) showed that *S. scalaris* has less activity time in high-elevation populations than in low-elevation populations, and has a smaller body size in the high-elevation populations than low-elevation populations.

In conclusion, we have recorded differences in sexual dimorphism between sexes, populations and species of the *S. scalaris* group. The oviparous species (*S. aeneus* and *S. scalaris*) were larger in overall body size than the viviparous species (*S. bicanthalis* and *S. subniger*). The same pattern of differences in size was recorded only for populations of *S. aeneus* and *S. scalaris*. The pattern of female-biased sexual dimorphism was more common than male-biased sexual dimorphism, at both the species and the population levels. This result differs from the general pattern for species of the genus, where male-biased dimorphism is more common. When shape is analysed, two patterns were found: one where the females presented larger relative sizes, which could be explained by fecundity, and the other where males were larger in relative sizes, which may be explained by sexual selection. Temperature and precipitation had no effect on body size or on any of the morphological variables analysed. Based on the results obtained from this study, we identify a need for a more detailed analysis of the morphological variables of the species of the genus *Sceloporus* at the intra- and inter-population level. This, together with conducting further analyses of size and shape, will allow us to explore the factors that promote sexual dimorphism in the genus *Sceloporus* and other highly diverse species groups.

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#### DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author (A.R.B.) upon reasonable request.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Figures S1–S4.** Standardized coefficients for random effects for each trait. Variation across years, localities, sexes and species was fitted as a random effect.