



# Life history variation in four populations of the Graphic Spiny Lizard, *Sceloporus grammicus* (Squamata: Phrynosomatidae), in central Mexico

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**Abstract.** Widely distributed lizard species that occur in contrasting habitats generally show distinctive morphological and thermal traits that are the results of local adaptations via sexual and natural selection. Here, we assessed the effect of sex and seasonality on morphology, thermal ecology, and perch height of *Sceloporus grammicus* of four populations in central Mexico. In all populations, males had larger body sizes, heads, and limbs than females. Females had larger abdominal volumes than males in two of the four populations. Females and males of the tree–boulder population were smaller than those of the cactus and grassland populations. Females of the tree–boulder population were also lighter in weight, with shorter forearms, than those of the cactus and grassland populations. Assessing thermal ecology, we found sex-specific differences in body temperature and behavioural thermoregulation in the grassland population, and seasonal variation in these thermal traits for lizards in the cactus, tree–boulder, and grassland populations. Lizards in habitats with closed canopy cover had lower body temperatures than lizards in more open habitats. Perch height did not vary between sexes or seasons in three of the four populations. We found that the intensity of fecundity advantage varies between female populations, and that thermal characteristics of lizards show specific relationships with perch height in each population, which is a signal of local adaptation of behavioural thermoregulation.

Key words. Abdominal volume, body temperature, intraspecific variation, *Sceloporus*, sexual dimorphism, widespread lizard.

## Introduction

Populations of widely distributed lizard species use different habitat types and therefore experience diverse environmental regimes and selective pressures (e.g., LATTANZIO et al. 2020). Habitats vary spatially and temporally in their physical structure, providing different gradients of abiotic and biotic conditions (SMITH & BALLINGER 2001, WILLIAMS & MCBRAYER 2015). Additionally, selective pressures, such as sexual and natural selection, may differ also between habitat types, and these may then shape population-specific, contrasting patterns of male and female traits, such as morphology (e.g., HERREL et al. 2001), thermal ecology (KIEFER et al. 2005), and microhabitat use (e.g., WILLIAMS & MCBRAYER 2015, LEYTE-MANRIQUE et al. 2017).

Lizards occupying habitats with dense canopy cover are expected to have small heads, slim and long bodies, long tails, and relatively short limbs (HERREL et al. 2001).

On the other hand, lizards living in habitats with an open canopy can be expected to have flat bodies and longer hindlimbs and toes (e.g., GARLAND & LOSOS 1994; HERREL et al. 2001). Furthermore, selective pressures are likely to affect the anatomy of male and female lizards differently, resulting in sexual size dimorphism (SSD; SHINE 1989, SCHARF & MEIRI 2013). For instance, in females, natural selection can act through a fecundity advantage, favouring a greater body size or abdominal cavity volume, which may enhance the capacity for producing larger clutches or young (e.g., SCHARF & MEIRI 2013).

The thermal ecology of lizards is influenced directly or indirectly by intrinsic and extrinsic factors (HUEY 1991, ANDREWS 1998). Although some males and females lizards do not differ in body temperature or behavioural thermoregulation (e.g., ADOLPH 1990, HUEY & PIANKA 2007), others exhibit intersexual variation in such thermal traits (KIEFER et al. 2005). This latter pattern could arise because of differences in sex-specific social behaviour (ANDREWS

1971) and the degree of SSD, which influences the capacity of heat retention and gain (i.e., thermal inertia) of each sex (CAROTHERS et al. 1998). For instance, territorial male lizards may have access to higher ambient temperatures than females and thus achieve higher body temperatures (CAROTHERS et al. 1998, BEAL et al. 2014). Considering that microhabitat temperatures are generally higher in habitats with an open canopy than in those with closed canopies (VITT et al. 2007), lizards in the former might maintain a higher degree of behavioural thermoregulation than lizards living in the latter because of the greater availability of basking sites. In addition, seasonal variation in body temperature and the behavioural thermoregulation of lizards could arise from their seasonal use of different microhabitat types and biotic interactions (HUEY & PIANKA 1977, ADOLPH 1990, LOSOS 2009).

Lizard microhabitat use frequently differs across and within populations, and this variation has been attributed to ecomorphological associations (LOSOS et al. 1994, LATTANZIO et al. 2020), perch height selection (RAMÍREZ-BAUTISTA & BENABIB 2001, ASBURY & ADOLPH 2007), differences in thermal environment (ORTEGA et al. 2019), or territoriality (ANDREWS 1971, GARCÍA et al. 2010). Intraspecific variation in ecomorphological associations could influence the thermal environment as is experienced by lizards through perch height selection, and consequently their degree of behavioural thermoregulation (ADOLPH 1990, LATTANZIO et al. 2020). For instance, some lizard species that inhabit closed-canopy habitats use lower perches and achieve lower body temperatures than lizards in more open-canopy habitats (HUEY 1974, TERRA et al. 2018).

*Sceloporus grammicus* (WIEGMANN, 1828) is the third most widely distributed lizard species of the genus *Sceloporus*, ranging from southern Texas in the United States to northern Oaxaca in Mexico (SITES 1982). Previous studies have detected variation in morphology and SSD between populations that inhabit different habitat types (HERNÁNDEZ-SALINAS et al. 2010, LOZANO et al. 2020). Despite that, it is as yet unknown whether sexual differences in abdominal volume exist in this species and if that might be the outcome of a stronger fecundity advantage on the females of some populations than in others. Thermal ecology evaluations in this species have been carried out in populations that inhabit high-altitude environments (LEMOS-ESPINAL & BALLINGER 1995, ANDREWS et al. 1997, DÍAZ DE LA VEGA-PÉREZ et al. 2019) and urban areas (WOOLRICH-PIÑA et al. 2006). Despite using contrasting structural and seasonal environments, it has been stated that the genus *Sceloporus* exhibits a conservative pattern in its thermal biology (ANDREWS 1998). Thus, studies comparing multiple populations that inhabit contrasting habitats would permit support for, or the rejection of, this hypothesis. Regarding microhabitat use, a previous study found similarities in these ecological traits between populations using different habitat types (LEYTE-MANRIQUE et al. 2017). Nevertheless, it is unknown whether there is a relationship between morphological and thermal characteristics and the selection of specific perch heights.

Here, we analysed sexual differences in morphology, thermal ecology and perch height use across four populations of *S. grammicus* in central Mexico. The four populations occur in habitats that are clearly structurally different (see Study area, below). For morphology, we predicted that within populations, (1) males would have larger body sizes and heads, and longer limbs than females, while (2) females would have larger abdominal volumes than males. Between populations, we expected that (3) lizards in habitats with more open canopy cover would have shorter bodies, as well as longer heads and limbs than their conspecifics in closed-canopy habitats. Regarding thermal ecology, we expected that (4) males would have higher body temperatures and greater levels of behavioural thermoregulation than females. Within populations, we predicted (5) seasonal variation in body temperature and behavioural thermoregulation as a result of seasonal variation in micro-environmental temperatures. Between populations, we predicted that (6) lizards in open-canopy habitats would reach higher body temperatures and greater levels of behavioural thermoregulation than lizards in closed-canopy habitats. With respect to perch height, we expected (7) that males would use higher perches than females, and (8) seasonal variation in this trait might be associated with the variation in the thermal and hydric environment. Within each population, we predicted that (9) morphological (body size and length of fore and hind limbs) and thermal variables (body, air, and substrate temperatures) would be positively correlated with perch height; between populations, (10) lizards in open habitats would use higher perches than lizards in closed-canopy habitats.

## Materials and methods

### Study area

Fieldwork was carried out in three localities in Hidalgo state, Mexico: Zacualtipán (20°32' N, 98°73' W, 2017 m a.s.l.), Tizayuca (19°51' N, 98°57' W, 2277 m a.s.l.), and Mineral El Chico (20°10' N, 98°43' W, 2362 m a.s.l.); and one in Puebla state, Mexico: Coronango (19°08' N, 98°15' W, 2183 m a.s.l.). In Zacualtipán (hereafter referred to as the 'tree population' [TP], Fig. S1A), the mean annual temperature and total annual precipitation were 14.4°C and 1325.8 mm, respectively (CONAGUA 2010). The climate is humid temperate, with a wet season from June through October and a dry season from November through May (GARCÍA 2004, CONAGUA 2010). The vegetation type here is a cloud forest dominated by *Quercus affinis*, *Pinus patula*, and *Liquidambar macrophylla* (RZEDOWSKI 2006). In Tizayuca (hereafter 'cactus population' [CP], Fig. S1B), the mean annual temperature and total annual precipitation were 15.0°C and 559.1 mm, respectively (CONAGUA 2010). The climate in this locale is semi-arid, with a wet season from May through October and a dry season from November through April (GARCÍA 2004, CONAGUA 2010). The vegetation type is xeric scrubland, with less than 50% tree cover, and the ground between shrubs is exposed for

most of the year (RZEDOWSKI 2006). This location is mainly dominated by species of *Opuntia*, *Yucca*, and *Agave* (RZEDOWSKI 2006). In Mineral El Chico (hereafter 'tree-boulder population' [TBP], Fig. S1C), the mean annual temperature and total annual precipitation were 14.3°C and 1145.6 mm, respectively. The climate at this site is subhumid temperate, with a wet season from May through October and dry one from November through April (GARCÍA 2004, CONAGUA 2010). The vegetation type is pine-oak forest, characterized by *Abies religiosa*, *Pinus rudis*, and *Quercus rugosa* (RZEDOWSKI 2006). In Coronango (hereafter 'grassland population' [GP], Fig. S1D), the mean annual temperature and total annual precipitation were 16.3°C and 845.7 mm, respectively (CONAGUA 2010). The climate is subhumid temperate, with a wet season from May through October and a dry season from November through April (GARCÍA 2004, CONAGUA 2010). The vegetation type is grassland, mainly dominated by *Bothriochloa laguroides*, *Paspalum dilatatum*, and *Setaria parviflora* (FLORES-HUITZIL et al. 2020). All study sites consisted of several zones that covered areas between 1.0 and 1.5 km<sup>2</sup>. In terms of relative openness of canopy, we consider TP and TBP as closed-canopy habitats and CP and GP as open-canopy habitats (Fig. S1).

#### Data collection

We collected data from all populations from March 2018 to December 2019. Visits to the study areas were made on a bimonthly basis. During each visit, we conducted visual encounter surveys (LOVICH 2012) from 09:00 through 18:30 h, ensuring that most of the surveys occurred on sunny days, when the lizards would have higher activity levels. Lizards were captured by hand or after stunning them with rubber bands (LOVICH 2012). This study was conducted according to the ethics and regulations for animal research of the Universidad Autónoma del Estado de Hidalgo and Guidelines for the Use of Animals (2012).

For this study, only adult females and males ( $\geq 40$  mm snout-vent length [SVL]; SITES 1982) were considered. The captured lizards were sexed by the presence of enlarged postcloacal scales in males and their absence in females (SITES 1982). All morphometric measurements were taken in the field using a digital calliper ( $\pm 0.01$  mm; Mitutoyo), and body mass was obtained with a spring scale ( $\pm 0.02$  g; Pesola). We followed LEYTE-MANRIQUE et al. (2017) for the recording of all these measurements. Because body shape differs between groups of lizards, we modified the cylinder formula originally established by SHINE (1992) and GOODMAN et al. (2009) to adjust it to lizards of the genus *Sceloporus*. Therefore, abdominal volume (AV) was obtained through the formula:  $V = \pi r^2 h$ , where 'r' is half of the average of three cross-sectional measures; 1) width at the middle of the body (i.e., the widest region of the abdomen), 2) width of the pectoral girdle (region where the forelimbs are inserted), and 3) width of the pelvic girdle (region where the hindlimbs are inserted); and 'h' is the length of the abdomen (measured from the neck to the anterior

margin of the cloaca). We decided to measure 'h' from the neck region because embryos were found in this region in previous dissections of females of *Sceloporus grammicus* (A. RAMÍREZ-BAUTISTA pers. comm.). These variables were measured with the same digital calliper ( $\pm 0.01$  mm; Mitutoyo) as the other morphometric characters.

Body temperature ( $T_b$ ) was recorded within 15 seconds after the capture of a lizard, using a Miller-Weber rapid registering thermometer ( $\pm 0.2^\circ\text{C}$ ; VITT et al. 2008). To avoid heat gain from the collector's hand, lizards were held by the head while  $T_b$  was measured (VITT et al. 2003). We then recorded the temperature ( $T_s$ ) in the substrate where that lizards had been found and the air temperature ( $T_a$ ) in the shade at 1 m above the ground with the same Miller-Weber thermometer (RAMÍREZ-BAUTISTA & BENABIB 2001, VITT et al. 2008). Additionally, we measured perch height with a tape measure ( $\pm 0.1$  cm) as the vertical distance from the ground to the point where the lizard had first been seen (RAMÍREZ-BAUTISTA & BENABIB 2001).

To avoid pseudoreplication, we marked each lizard in two ways: painting a small temporary mark of nail polish on the dorsum at the hindlimb level, and permanent toe-clipping according to TINKLE (1967). After measuring morphological and thermal characteristics, we released each lizard at the point where it was first observed. We collected data from 336 adult lizards, of which 50 were females and 23 were males from the TP, 45 females and 28 males from the CP, 36 females and 20 males from the TBP, and 69 females and 65 males from the GP. From these samples, all lizards that had required more than 2 minutes from first sighting to capture were excluded from the thermal ecology analyses. Lizards found on the ground were not included in the perch height analyses.

#### Data analyses

To remove the effect of size (SVL), we regressed all morphological variables against SVL and obtained residuals for males and females in each population. Then we used these residuals in subsequent analyses as SVL-adjusted variables. To assess whether there is SSD in each population, we employed the two-tailed Student t-test to compare morphological variables between sexes (ZAR 2010). To detect interpopulational differences in morphological variables in females and males, we applied a one-way multivariate nonparametric analysis (PERMANOVA) using the Gower similarity distance, with 9999 random permutations, and Bonferroni probability adjustment (ANDERSON 2001, QUINN & KEOUGH 2002).

To quantify the degree of behavioural thermoregulation ( $\Delta T$ ), we calculated the absolute values of the difference between  $T_b$  and environmental temperatures ( $T_a$  and  $T_s$ ), where  $\Delta T_a = (T_b - T_a)$  and  $\Delta T_s = (T_b - T_s)$  (VRCIBRADIC & ROCHA 1998, KIEFER et al. 2007, MAIA-CARNEIRO & ROCHA 2013, 2020). Higher absolute values of  $\Delta T_a$  and  $\Delta T_s$  indicate higher degrees of thermoregulation (active thermoregulation) in relation to environmental temperatures

(KIEFER et al. 2007, MAIA-CARNEIRO & ROCHA 2020). Additionally, the degree of behavioural thermoregulation was evaluated by calculating the percentage of negative values of  $\Delta T_a$  and  $\Delta T_s$ , which indicates the frequency at which body temperatures were lower than the environmental temperatures (KIEFER et al. 2007, MAIA-CARNEIRO & ROCHA 2013, 2020). Low percentages of negative values would indicate a lower level of behavioural thermoregulation, whereas higher percentages suggest a higher degree of active thermoregulation (MAIA-CARNEIRO & ROCHA 2013, 2020). The interpretation of the degree of behavioural thermoregulation through  $\Delta T$  and percentage of negative values relies on knowing which are the main behavioural mechanisms for thermoregulation and how they influence the difference between  $T_b$  and environmental temperatures ( $T_a$  and  $T_s$ ) (MAIA-CARNEIRO & ROCHA 2020).

To evaluate the effects of seasonality and sex on  $T_b$ , environmental temperatures ( $T_a$  and  $T_s$ ), and behavioural thermoregulation ( $\Delta T_a$  and  $\Delta T_s$ ) within each population, we performed a two-way PERMANOVA on Gower distances calculated from raw data with 9999 random permutations and a multiple nonlinear regression with season and sex as factors (ANDERSON 2001, QUINN & KEOUGH 2002). To identify the relationships between  $T_b$  and environmental temperatures, and  $T_b$  and SVL, we carried out Spearman correlation analyses between these variables (ZAR 2010). Because thermal variables did not differ between sexes (in three out of four populations) but did differ between seasons in some populations (see Thermal ecology, below), we used a two-way PERMANOVA with similar characteristics and a multiple nonlinear regression with season and population as factors (ANDERSON 2001, QUINN & KEOUGH 2002).

To assess the effects of seasonality and sex on perch height within each population, we used a two-way analysis of variance (ANOVA) with season and sex as independent categorical variables, and perch height as the dependent variable (ZAR 2010). To identify the relationships between morphological and thermal variables and perch height, we carried out Pearson correlation analyses between these variables with Bonferroni probability adjustment (ZAR 2010). Because perch height did not differ between sexes nor seasons in three out of the four populations (see Perch height below), we carried out a one-way ANOVA to establish interpopulational differences in perch height (ZAR 2010). Our results are presented as means  $\pm$  SE unless indicated otherwise. We considered differences with an  $\alpha$  value of 0.05 to be significant. Statistical analyses were computed in Past 4.0 (HAMMER et al. 2001) and Statistica 10.0 (Statsoft, Inc., Tulsa, OK, USA).

## Results

### Morphology

In the TP, males had larger heads and longer femurs (FL) and tibias (TL) than females (Supplementary Table S1). However, females had greater abdominal volumes than

males (Supplementary Table S1). In the CP and TBP, males were larger than females in all traits except body mass and abdominal volume (Supplementary Table S1). In the GP, males had a larger SVL, larger and wider heads, and longer FL and TL than females (Supplementary Table S1); females had greater abdominal volumes than males (Supplementary Table S1). The PERMANOVA showed up differences between female populations ( $F_{3,196} = 4.708$ ,  $P \leq 0.001$ ). Females of the TBP were smaller and had shorter forearm lengths (FOL) than females of the TP (SVL:  $P \leq 0.001$ , FOL:  $P = 0.024$ ), CP (SVL:  $P \leq 0.01$ , FOL:  $P \leq 0.05$ ) and GP (SVL:  $P \leq 0.001$ , FOL:  $P \leq 0.001$ , Supplementary Table S1). Females of the TBP were lighter in weight than those of the TP ( $P \leq 0.01$ ) and GP ( $P \leq 0.001$ ). Females of the CP had narrower heads than females of the TP ( $P \leq 0.001$ ) and GP ( $P \leq 0.01$ ; Supplementary Table S1). The PERMANOVA also revealed differences between male populations ( $F_{3,132} = 2.196$ ,  $P \leq 0.01$ ). Males of the TBP were smaller than those of the CP ( $P \leq 0.01$ ) and GP ( $P \leq 0.001$ ). Males of the CP had narrower heads than those of the TP ( $P \leq 0.05$ ) and GP ( $P \leq 0.01$ , Supplementary Table S1).

### Thermal ecology

In the TP, neither the effect of season ( $F_{2,67} = 0.55$ ,  $P = 0.25$ ) or sex ( $F_{1,67} = 0.71$ ,  $P = 0.18$ ) nor the interaction between them ( $F_{2,67} = -20.75$ ,  $P = 0.98$ ) on the thermal variables (Table 1) turned out to be significant. In both seasons, the percentage of negative values of  $\Delta T_a$  were female-biased (Fig. 1A), whereas those of  $\Delta T_s$  were male-biased (Fig. 2A). The  $T_b$  of both sexes was positively correlated with  $T_a$  ( $r_s = 0.57$ ,  $P \leq 0.001$ ,  $n = 73$ ) and  $T_s$  ( $r_s = 0.65$ ,  $P \leq 0.001$ ,  $n = 73$ ) but not significantly correlated with SVL ( $r_s = 0.02$ ,  $P = 0.89$ ,  $n = 73$ ). Compared to the TP, the CP experienced a significant effect of season ( $F_{2,60} = 3.60$ ,  $P \leq 0.001$ ), but not sex ( $F_{1,60} = 0.39$ ,  $P = 0.48$ ), on thermal variables, and the interaction between them again was not significant ( $F_{2,60} = -14.46$ ,  $P = 0.85$ ). Mean  $T_b$ ,  $T_a$ ,  $T_s$ , and  $\Delta T_a$  varied interseasonally but not intersexually (see Tables 1 and S2); lizards had higher values of  $T_b$ ,  $T_a$ , and  $T_s$  in the dry than in the wet season, whilst they had higher values of  $\Delta T_a$  in the wet than in the dry season (Table 1). However,  $\Delta T_s$  did not differ seasonally or sexually (Tables 1 and S2). Percentages of negative values of  $\Delta T_a$  were male-biased in both seasons (Fig. 1B). On the other hand, those of  $\Delta T_s$  were female-biased and male-biased in the wet season and dry season, respectively (Fig. 2B). The  $T_b$  of both sexes was positively correlated with  $T_a$  ( $r_s = 0.66$ ,  $P \leq 0.001$ ,  $n = 66$ ) and  $T_s$  ( $r_s = 0.73$ ,  $P \leq 0.001$ ,  $n = 66$ ), but not significantly correlated with SVL ( $r_s = -0.08$ ,  $P = 0.53$ ,  $n = 66$ ).

In the TBP, a significant effect of season ( $F_{3,46} = 0.89$ ,  $P \leq 0.05$ ), but not sex ( $F_{1,46} = 1.01$ ,  $P = 0.06$ ) or the interaction between them ( $F_{3,46} = -9.64$ ,  $P = 0.93$ ), on the thermal variables was found (Table 1). The  $T_s$  was higher in females than in males in the dry season, whereas the  $\Delta T_s$  of both sexes was higher in the wet season than in the dry season (Tables 1 and S3). The percentages of negative



Life history variation of *Sceloporus grammicus*

Table 1. Summary of thermal characteristics of female and male *Sceloporus grammicus* of four populations in central Mexico sorted by season. Ranges for each group are shown below mean  $\pm$  SE. All variables are given in °C. Abbreviations: TP, 'tree population'; CP, 'cactus population'; TBP, 'tree-boulder population'; GP, 'grassland population'; n, sample size;  $T_b$ , body temperature;  $T_a$ , air temperature;  $T_s$ , substrate temperature;  $\Delta T_a$ , absolute difference between body and air temperatures;  $\Delta T_s$ , absolute difference between body and substrate temperatures.

	$T_b$	$T_a$	$T_s$	$\Delta T_a$	$\Delta T_s$	n
TP						
Wet season						
Females	28.58 $\pm$ 1.43	24.22 $\pm$ 0.99	24.18 $\pm$ 0.82	4.88 $\pm$ 1.08	4.64 $\pm$ 0.90	10
	21.80–34.40	20.20–28.20	20.20–27.80	0.00–9.40	0.60–9.00	
Males	29.13 $\pm$ 1.59	24.35 $\pm$ 1.21	24.08 $\pm$ 1.05	5.03 $\pm$ 1.06	5.05 $\pm$ 0.80	8
	20.20–33.00	16.80–27.40	17.80–26.80	1.00–9.40	1.00–8.00	
Dry Season						
Females	27.02 $\pm$ 1.02	22.93 $\pm$ 0.82	22.84 $\pm$ 0.81	4.45 $\pm$ 0.49	4.52 $\pm$ 0.58	40
	14.00–33.60	12.60–32.00	13.60–31.60	0.40–13.00	0.00–14.00	
Males	29.55 $\pm$ 1.42	25.95 $\pm$ 1.45	26.21 $\pm$ 1.30	4.53 $\pm$ 0.80	3.95 $\pm$ 0.62	15
	15.40–35.00	12.00–32.00	14.00–34.60	0.60–9.40	1.00–8.20	
CP						
Wet season						
Females	28.27 $\pm$ 0.92	24.57 $\pm$ 0.61	25.13 $\pm$ 0.66	4.53 $\pm$ 0.60	3.98 $\pm$ 0.47	26
	18.80–34.80	19.80–32.80	18.60–31.80	0.00–11.20	0.20–9.80	
Males	29.72 $\pm$ 1.10	24.85 $\pm$ 0.90	25.31 $\pm$ 0.90	5.54 $\pm$ 0.70	5.09 $\pm$ 0.58	21
	19.20–38.00	17.20–36.00	16.80–34.60	0.00–11.40	0.80–10.80	
Dry Season						
Females	32.90 $\pm$ 0.50	30.47 $\pm$ 0.95	30.21 $\pm$ 0.79	3.26 $\pm$ 0.56	3.31 $\pm$ 0.56	14
	29.80–36.40	23.80–36.00	25.00–35.60	0.80–8.60	0.00–7.40	
Males	31.08 $\pm$ 2.05	30.68 $\pm$ 1.62	29.16 $\pm$ 1.69	2.00 $\pm$ 0.74	2.96 $\pm$ 0.77	5
	26.40–36.00	26.80–34.00	25.00–33.00	0.20–3.60	1.40–5.60	
TBP						
Wet season						
Females	29.39 $\pm$ 0.64	24.24 $\pm$ 0.65	25.24 $\pm$ 0.85	5.86 $\pm$ 0.67	5.52 $\pm$ 0.61	17
	24.00–34.00	20.00–30.00	18.80–31.20	0.00–10.20	1.20–11.40	
Males	30.13 $\pm$ 0.98	24.50 $\pm$ 0.84	25.10 $\pm$ 0.82	5.63 $\pm$ 1.12	5.03 $\pm$ 1.32	6
	26.20–33.20	21.60–27.20	22.80–28.00	2.20–8.80	1.00–8.60	
Dry Season						
Females	30.55 $\pm$ 0.92	26.39 $\pm$ 0.98	27.48 $\pm$ 0.78	4.56 $\pm$ 0.95	3.45 $\pm$ 0.57	17
	21.00–34.80	20.00–32.40	21.00–32.20	0.20–13.00	0.80–8.40	
Males	27.43 $\pm$ 1.22	23.41 $\pm$ 0.90	23.47 $\pm$ 1.20	4.01 $\pm$ 0.98	4.24 $\pm$ 0.96	14
	21.00–34.80	19.00–29.40	18.40–32.20	1.00–14.40	0.20–14.00	
GP						
Wet season						
Females	32.34 $\pm$ 0.42	26.05 $\pm$ 0.51	26.81 $\pm$ 0.49	6.34 $\pm$ 0.56	5.68 $\pm$ 0.52	37
	25.80–35.60	20.40–31.00	22.40–34.00	0.00–13.20	0.40–11.60	
Males	33.48 $\pm$ 0.35	26.21 $\pm$ 0.66	27.78 $\pm$ 0.55	7.29 $\pm$ 0.75	5.87 $\pm$ 0.67	34
	28.80–37.00	20.00–34.60	21.20–34.40	0.00–15.00	0.00–14.40	
Dry Season						
Females	30.19 $\pm$ 0.55	25.34 $\pm$ 0.59	25.53 $\pm$ 0.54	5.23 $\pm$ 0.46	4.76 $\pm$ 0.43	32
	22.00–35.40	19.00–30.40	18.60–30.40	0.60–10.60	0.40–12.00	
Males	31.45 $\pm$ 0.61	25.38 $\pm$ 0.62	25.90 $\pm$ 0.65	6.48 $\pm$ 0.58	5.75 $\pm$ 0.60	31
	23.20–37.40	20.00–31.60	20.20–33.20	1.80–11.80	0.60–12.80	

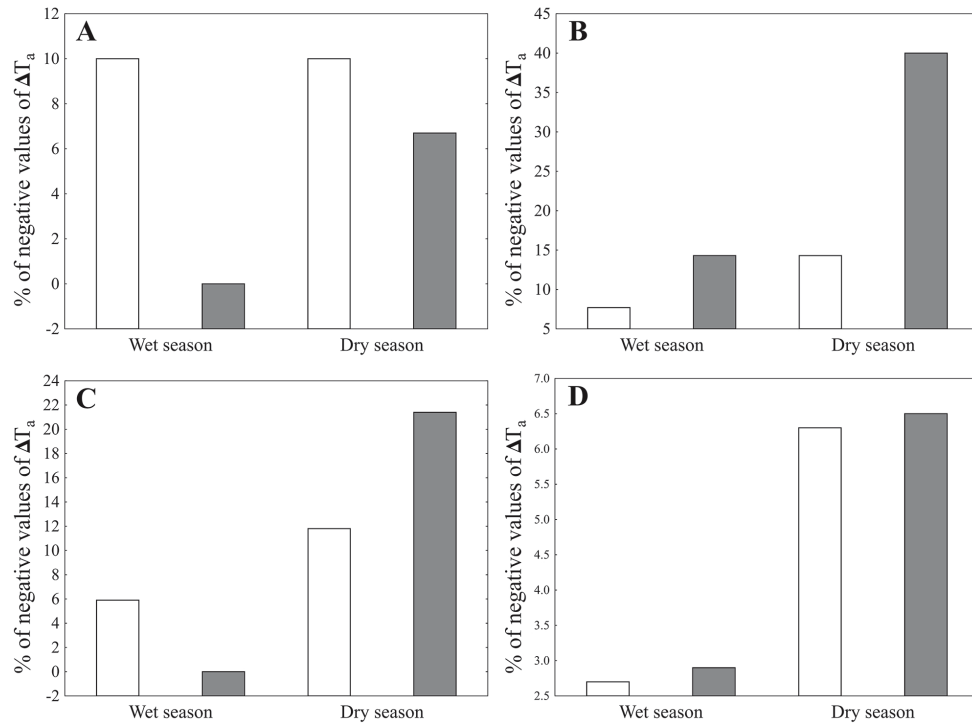


Figure 1. Percentages (%) of negative values of  $\Delta T_a$  for female (white bars) and male (gray bars) *Sceloporus grammicus* of four populations in central Mexico sorted by season. Populations: 'tree population' (TP, A), 'cactus population' (CP, B), 'tree-boulder population' (TBP, C), and 'grassland population' (GL, D).

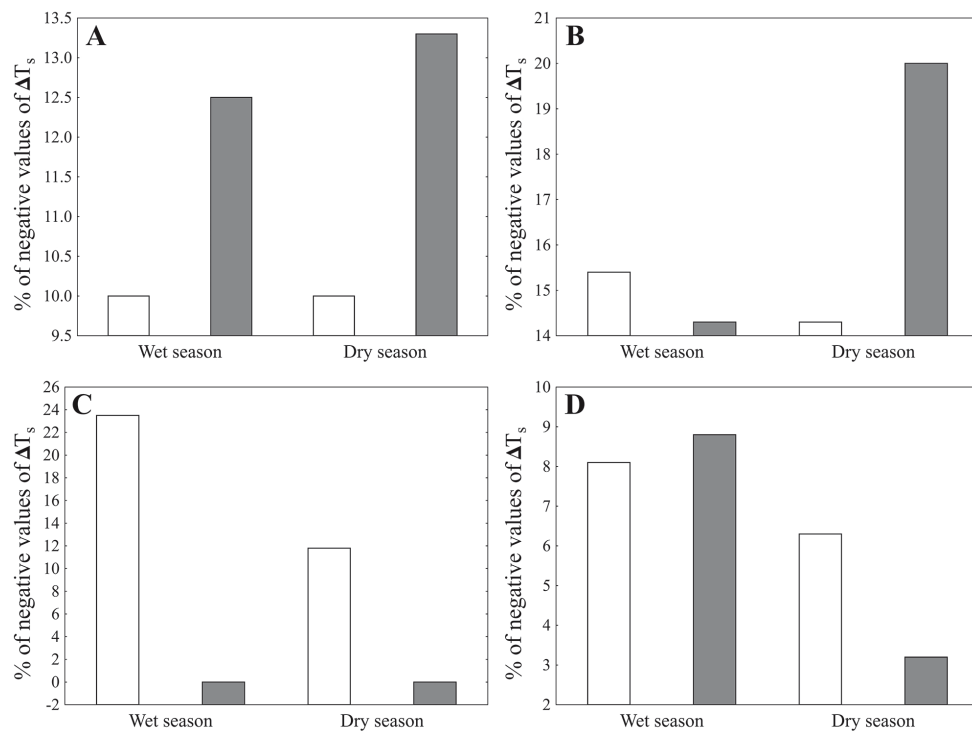


Figure 2. Percentages (%) of negative values of  $\Delta T_s$  for female (white bars) and male (gray bars) *Sceloporus grammicus* of four populations in central Mexico sorted by season. Populations: as in Figure 1.

values of  $\Delta T_a$  were female-biased in the wet season, whilst they were male-biased in the dry season (Fig. 1C). Conversely, those of  $\Delta T_s$  were female-biased in both seasons (Fig. 2C). The  $T_b$  of both sexes was positively correlated with  $T_a$  ( $r_s = 0.39$ ,  $P \leq 0.01$ ,  $n = 54$ ) and  $T_s$  ( $r_s = 0.48$ ,  $P \leq 0.001$ ,  $n = 54$ ), but not significantly correlated with SVL ( $r_s = -0.01$ ,  $P = 0.95$ ,  $n = 54$ ). In the GP, the effect of season was significant on thermal variables ( $F_{1,130} = 5.08$ ,  $P \leq 0.01$ ), but neither on sex ( $F_{1,130} = 1.82$ ,  $P = 0.15$ ) nor the interaction between them ( $F_{1,130} = -2.06$ ,  $P = 0.62$ ). However,  $T_b$  and  $T_s$  varied between seasons, but only  $T_b$  differed between sexes (Supplementary Table S4). Mean  $T_b$  and  $T_s$  were higher in the wet season than in the dry season, and in both seasons males had a higher  $T_b$  than females (Table 1). In both seasons, the percentages of negative values of  $\Delta T_a$  were slightly male-biased (Fig. 1D). Those of  $\Delta T_s$  were, however, male-biased in the wet season, but female-biased in the dry season (Fig. 2D). As in the other populations, the  $T_b$  of both sexes was positively correlated with  $T_a$  ( $r_s = 0.23$ ,  $P \leq 0.01$ ,  $n = 134$ ) and  $T_s$  ( $r_s = 0.31$ ,  $P \leq 0.001$ ,  $n = 134$ ), but not significantly correlated with SVL ( $r_s = 0.08$ ,  $P = 0.36$ ,  $n = 134$ ).

Highly significant effects of population ( $F_{3,311} = 3.70$ ,  $P \leq 0.001$ ) and season ( $F_{3,311} = 2.96$ ,  $P \leq 0.001$ ) on thermal variables were detected in all populations, but the interaction between them was not significant ( $F_{9,311} = -18.77$ ,  $P = 0.45$ ). All but one thermal variables varied interpopulationally, with only  $T_a$  indicating a trend towards significance (Supplementary Table S5). Mean  $\Delta T_a$  and  $\Delta T_s$  differed interseasonally as well (Supplementary Table S5). Lizards from the

GP had a higher  $T_b$  than lizards in the other populations (Supplementary Table S6, Fig. 3A). Environmental temperatures ( $T_s$  and  $T_a$ ) were higher in the GP and CP than in the TP (Supplementary Table S6, Figs 3B–C). In both seasons, mean  $\Delta T_a$  was higher in the GP than in the CP (Supplementary Table S6). Across populations, mean  $\Delta T_a$  was higher in the GP than in the other populations (Supplementary Table S6, Fig. 3D). Mean  $\Delta T_s$  was higher in the GP compared with CP (Fig. 3E). Considering all populations, both thermoregulation indices were higher in the wet ( $\Delta T_a$ :  $5.91 \pm 0.28$ ;  $\Delta T_s$ :  $5.23 \pm 0.24$ ; for both variables  $n = 159$ ) than in the dry season ( $\Delta T_a$ :  $4.78 \pm 0.25$ ;  $\Delta T_s$ :  $4.46 \pm 0.23$ ; for both variables  $n = 168$ ;  $P \leq 0.01$  for  $\Delta T_a$  and  $P \leq 0.05$  for  $\Delta T_s$ ). The highest percentages of negative values of  $\Delta T_a$  were found in the TP and the CP during the wet season and dry season, respectively (Supplementary Table S6). Considering both seasons, CP lizards showed the highest percentages of negative values of  $\Delta T_a$  (Supplementary Table S6). The lizards of TBP and CP had the highest percentages of negative values of  $\Delta T_s$  in the wet season and dry season, respectively (Supplementary Table S6). When pooling both seasons, TBP lizards showed the highest percentages of negative values of  $\Delta T_s$  (Supplementary Table S6).

#### Perch height

Mean perch height did not differ between sexes and seasons in the TP (season effect:  $F_{1,56} = 0.41$ ,  $P = 0.11$ ; sex effect:  $F_{1,56} = 2.71$ ,  $P = 0.11$ ; interaction:  $F_{1,56} = 0.96$ ,  $P = 0.33$ ), CP

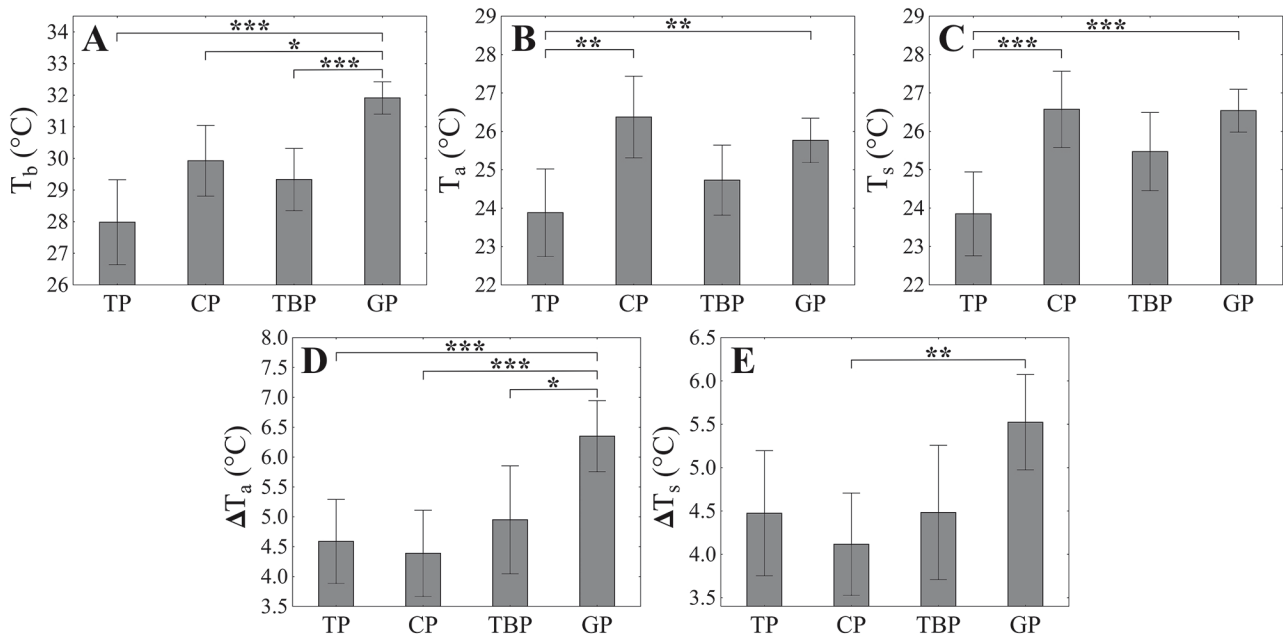


Figure 3. Summary of the variation in body (A), air (B), and substrate (C) temperatures, differences between body temperature and air temperature ( $\Delta T_a$ , D) and differences between body temperature and substrate temperature ( $\Delta T_s$ , E) between populations of *Sceloporus grammicus*. Populations: as in Figure 1. Asterisks between bars indicate significant differences between groups (\* $P \leq 0.05$ , \*\* $P \leq 0.01$ , \*\*\*  $P \leq 0.001$ ). Error bars represent a 95% confidence intervals.

Table 2. Perch height (cm) of female and male *Sceloporus grammicus* of four populations in central Mexico sorted by season in central Mexico. Ranges for each group are shown below mean  $\pm$  SE. Abbreviations are as in Table 1.

	Females	n	Males	n
TP				
Wet season	170.00 $\pm$ 16.81	6	104.16 $\pm$ 26.30	7
	115.00–210.00		37.00–209.00	
Dry season	161.59 $\pm$ 12.88	35	144.83 $\pm$ 27.55	12
	16.00–320.00		19.00–290.00	
CP				
Wet season	87.85 $\pm$ 15.27	17	87.56 $\pm$ 14.88	15
	25.60–204.50		15.50–198.10	
Dry season	115.56 $\pm$ 15.42	10	109.96 $\pm$ 51.68	5
	43.10–190.00		30.00–300.00	
TBP				
Wet season	124.79 $\pm$ 19.33	13	154.67 $\pm$ 13.37	6
	23.60–220.00		110.00–192.00	
Dry season	164.79 $\pm$ 14.60	15	121.41 $\pm$ 17.86	11
	77.00–256.00		40.50–224.00	
GP				
Wet season	90.95 $\pm$ 8.06	36	87.15 $\pm$ 8.58	32
	28.50–209.10		10.00–223.00	
Dry season	128.88 $\pm$ 11.68	30	93.55 $\pm$ 10.55	24
	20.00–323.00		32.00–199.50	

(season effect:  $F_{1,43} = 1.37$ ,  $P = 0.25$ ; sex effect:  $F_{1,43} = 0.02$ ,  $P = 0.89$ ; interaction:  $F_{1,43} = 0.02$ ,  $P = 0.90$ ), and TBP (season effect:  $F_{1,41} = 0.03$ ,  $P = 0.86$ ; sex effect:  $F_{1,41} = 0.13$ ,  $P = 0.72$ ; interaction:  $F_{1,41} = 3.82$ ,  $P = 0.06$ ) (Table 2). In the TP, the snout–vent, forearm, and femur lengths of lizards did not correlate with perch height, but tibia length was negatively correlated with perch height (Table 3). None of the thermal variables were correlated with perch height in lizards of this population (Table 3). Similarly, in the CP and TBP, the morphological variables of the lizards did not correlate with perch height (Table 3). Regarding the relationship with thermal variables in the CP, all of them were positively correlated with perch height (Table 3). On the other hand, the  $T_b$  of lizards in the TBP was positively correlated with perch height, whilst  $T_a$  and  $T_s$  were not (Table 3). In the GP, females used higher perches in the dry than in the wet season ( $F_{1,118} = 5.17$ ,  $P \leq 0.05$ ), and they used marginally higher perches than males ( $F_{1,118} = 4.03$ ,  $P \leq 0.05$ ), but the interaction between both factors was not significant ( $F_{1,118} = 2.61$ ,  $P = 0.11$ ) (Table 2). Morphological variables of the GP lizards did not correlate (Table 3), but all thermal variables were negatively correlated with perch height (Table 3). Additionally, perch height differed between populations ( $F_{3,270} = 13.22$ ,  $P \leq 0.001$ ). Lizards of the TP ( $152.38 \pm 10.04$  cm,  $n = 60$ ) and TBP ( $141.28 \pm 9.01$  cm,  $n = 45$ ) used higher perches than lizards in the CP ( $96.01 \pm 9.42$  cm,  $n = 47$ ) and in the GP ( $99.79 \pm 5.00$  cm,  $n = 122$ ) (see also Fig. 4).

Table 3. Pearson correlation coefficients ( $r$ ) between perch height and morphological and thermal variables in four populations of *Sceloporus grammicus* in central Mexico. Morphological variables are SVL, FOL, FL, and TL; all are in mm. Thermal variables are  $T_b$ ,  $T_a$ ,  $T_s$ ; all are in  $^{\circ}\text{C}$ . Abbreviations for morphological characteristics: SVL, snout–vent length; FOL, forearm length; FL, femur length; TL, tibia length. Abbreviations for populations and thermal characteristics follow Table 1. n, sample size. \* $P \leq 0.05$ , \*\* $P \leq 0.01$ .

	TP	CP	TBP	GP
Trait / n	60	47	45	122
SVL	0.08	0.19	0.22	0.08
FOL	-0.14	-0.24	0.04	-0.09
FL	-0.04	-0.01	-0.19	-0.13
TL	-0.26 *	-0.20	0.01	-0.11
$T_b$	0.03	0.40 **	0.36 *	-0.26 **
$T_a$	-0.07	0.29 *	0.09	-0.19 *
$T_s$	-0.13	0.35 *	0.29	-0.27 **

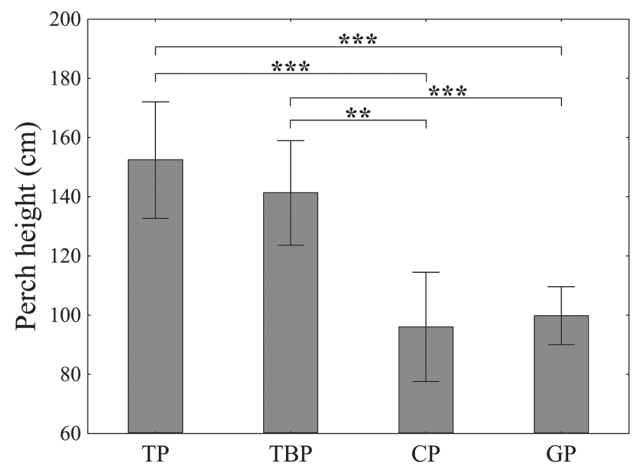


Figure 4. Variation in perch height between four populations of *Sceloporus grammicus*. Abbreviations follow Figure 1. Asterisks between bars indicate significant differences between groups according to Bonferroni post hoc tests (\*\* $P \leq 0.01$ , \*\*\* $P \leq 0.001$ ). Error bars represent a 95% confidence intervals.

## Discussion

### Morphology

Sexual size dimorphism (SSD) was apparent in all lizard populations examined and this result fully supports our first prediction, but the second prediction only partially. Despite differences in habitat use, our analyses indicate that the direction of sexual selection in males is similar in all populations. However, the intensity of the fecundity advantage might be greater in females of the TP and GP than those in the CP and TBP. In the Asian lacertid lizard *Takydromus septentrionalis*, female populations differ



in abdominal length, i.e., those that have shorter abdomens produce eggs with lower egg masses (DU et al. 2005). In addition, body size and reproductive traits in the Asian agamid *Phrynocephalus przewalskii* are related to food availability in that larger females produce more and larger eggs in localities with higher food availability than those where less food is available (ZENG et al. 2013). Hence, our results might be indirect evidence of a greater food availability in the TP and the GP, which potentially promotes female reproductive trait variation in *S. grammicus*; however, this assumption still remains to be tested. Despite that, our results about intersexual variation in abdominal volume should be taken with certain caution, given that, in some cases, we could not clearly identify (by abdominal palpation) the reproductive status of females with greater abdominal volumes.

Males and females of the TBP were smaller, had shorter forearm lengths and were lighter in weight than those from the other populations. These results partially support our third prediction and are consistent with the findings of previous studies of *S. grammicus* (LOZANO et al. 2020) and other lizard species (HERREL et al. 2002, HOPKINS & TOLLEY 2011, LATTANZIO et al. 2020), i.e., that lizards in open habitats have longer forearms, which enhances their performance in climbing on irregular and three-dimensional substrates (MELVILLE & SWAIN 2000) and moving about in sparsely vegetated areas (HOPKINS & TOLLEY 2011). Large-bodied and long-limbed females of the TP, CP, and GP would be able to have improved sprint speeds, enhancing their predation success on specific prey types or escaping from potential predators (MELVILLE & SWAIN 2000, LOSOS et al. 2006). Conversely, short-limbed females of the TBP probably would not run faster, but could be expected to leap farther than their counterparts in the other populations. The larger body sizes of males in the open-canopy habitats (CP and GP) might be the outcome of the dryness and seasonality of these environments, which promotes a high intensity of competition for resources (e.g., females, shelters, and basking sites) among males, as occurs in *Anolis* lizards (LOSOS 2009).

### Thermal ecology

The results of sexual variation in  $T_b$  of the GP partially support our fourth and fifth predictions. Two contrasting sexual patterns were found in  $T_b$  of *S. grammicus*: one in which males attain higher  $T_b$  than females (ANDREWS et al. 1997, WOOLRICH-PIÑA et al. 2006) and another in which there is no substantial intersexual variation in  $T_b$  (LEMOs-ESPINAL & BALLINGER 1995, ANDREWS et al. 1997, DÍAZ DE LA VEGA-PÉREZ et al. 2019). Our results from the GP fit the first pattern, whereas those of the TP, CP, and TBP fit the second pattern. Although lizards within the same population are generally exposed to similar thermal environments, they will often select specific microclimatic conditions. For example, territorial males of *S. jarrovi* have better or more access than females to microhabitats

with higher thermal quality for thermoregulation, thus this circumstance contributes to intersexual differences in  $T_b$  (BEAL et al. 2014). The similarity in  $T_b$  between the sexes in the other three populations concurs with the fact that females had higher percentages of negative values of  $\Delta T_s$  and  $\Delta T_a$  than males, suggesting that they actively thermoregulate in a manner similar to males (VRCIBRADIC & ROCHA 1998, KIEFER et al. 2007, MAIA-CARNEIRO & ROCHA 2013).

In all populations, the  $T_b$  of lizards was positively correlated with  $T_a$  and  $T_s$ , but the relationship was always stronger with  $T_s$ . Additionally, the correlation coefficients of both relationships were higher in the TP and CP than in the TBP and GP. Our results confirm that the heat gain strategy of *S. grammicus* consists of both thigmothermy and heliothermy, as occurs in populations of urban areas (WOOLRICH-PIÑA et al. 2006) and of high-altitude habitats (DÍAZ DE LA VEGA-PÉREZ et al. 2019). During the coolest periods of the day, many lizard species assume body postures that maximize heat gain (either from thigmothermy or heliothermy), whereas in the hottest periods, they adopt postures that favour heat loss (GILLIS 1991, McCONNACHIE et al. 2009). Although we did not directly evaluate body posture and sun exposure of lizards, our study may support the idea that the thigmothermic strategy of *S. grammicus* may vary between populations inhabiting contrasting habitats, as has been noted in other lizard species (GILLIS 1991, McCONNACHIE et al. 2009).

The results of interpopulational variation in  $T_b$ , environmental temperatures ( $T_a$  and  $T_s$ ) and behavioural thermoregulation ( $\Delta T_a$  and  $\Delta T_s$ ) partially support our sixth expectation and are consistent with previous studies of different lizard genera, which have found that lizards from open-canopy habitats are generally exposed to higher environmental temperatures and thus achieve higher body temperatures than conspecifics in closed-canopy habitats (HUEY 1974, WILLIAMS & McBRAYER 2015, TERRA et al. 2018). On the other hand, this intraspecific variation contrasts with the conservative pattern of thermal ecology found in studies of *Sceloporus* and other lizard genera, probably reflecting an ancestral condition (GILLIS 1991, ANDREWS 1998). This conservative pattern in thermal ecology across populations of the same species has been observed even though they are found in differently structured habitats and experience contrasting thermal environments (ANDREWS 1998, SALES & FREIRE 2019). In sum, we demonstrated that *S. grammicus* is relatively plastic in its thermal traits, and the way it behaviourally thermoregulates will depend on the structure of the habitat it uses.

Throughout our comparative approach, we found that most of the morphological and thermal characteristics are subject to conspicuous intraspecific variation in *S. grammicus*. Previous studies in *Anolis* and *Sceloporus* lizards have uncovered different patterns across species and populations: 1) thermal biology exhibits more divergence than does morphology, 2) diversification of thermal biology often follows diversification in morphology, and 3) thermal biology is similar but morphology diverges conspicuously

(GUNDERSON et al. 2018, MUÑOZ & LOSOS 2018, LATTANZIO et al. 2020). In this manner, multiple contrasting selective pressures (natural and sexual) can operate simultaneously, promoting patterns of both similarity and divergence, and behaviour may be the bridge that links these outcomes (MUÑOZ & LOSOS 2018). Despite being larger in many morphological characteristics, males did not necessarily attain a higher  $T_b$  than females, except in the GP. In fact, percentages of negative values of  $\Delta T_s$  and  $\Delta T_a$  indicated that the behavioural thermoregulation of females is sometimes similar to, or even as precise as, the behavioural thermoregulation of males (SALES & FREIRE 2019). This is particularly relevant considering that the  $T_b$  of females will enhance offspring fitness by accelerating embryogenesis and thus parturition (SHINE & DOWNES 1999). Thereby, the ability of *S. grammicus* to take advantage of its available thermal environments depends on the way it behaviourally makes the most of its morphology, which in turn affects the preferred type and height of its perch.

### Perch height

The results of the effects of sex and season on perch height did not confirm our seventh prediction, but weakly supported our eighth prediction. Both patterns are consistent with those found in *S. melanorhinus*, in which females use higher perches than males and there is no seasonal variation in perch height (GARCÍA et al. 2010). Hence, the females and males of *S. grammicus* in our study used the same perch height throughout the year for foraging, social interactions, and in some instances for thermoregulation (see next paragraph). The seasonal variation in perch height by females of the GP could be linked to the seasonal foraging rate, avoidance of certain social interactions or potential predators, or even to remain close to specific refuges, as occurs in other lizard species (GARCÍA et al. 2010). Considering the unique relationship between perch height and  $T_b$  found in each studied population, it is possible that each of these aspects is enhanced in females and males if they attain or maintain a higher and/or stable  $T_b$ .

In all populations, the morphological variables of our studied lizards were not correlated with perch height. Thus, our ninth expectation is not fulfilled. On the other hand, each population exhibited a unique pattern of relationship between thermal variables and perch height. These patterns are similar to those found in *S. occidentalis*, in which the body and environmental temperatures of some populations were independent of perch height (ADOLPH 1990), whereas in others, thermal characteristics were a primary factor modulating perch use (ASBURY & ADOLPH 2007). Our studied lizards of the GP used higher perches (up to two metres above ground) to behaviourally lower their  $T_b$  (especially around midday when the ambient temperature is higher on the ground), whereas lizards in the CP and TBP used higher perches (two metres above ground) to attain a higher  $T_b$  (during the

morning when the environment is cooler on the ground; STEVENSON 1985).

Results of interpopulational variation in perch height failed to confirm our tenth expectation and match a pattern found in *Anolis aeneus*, which was found to perch higher in a closed forest than it would in more open habitats, because of better access to insolation in the former that is not available at lower heights in that habitat (HARRIS et al. 2004). As mentioned previously, each population selects a specific perch height according to their thermal environment (except in the TP), which directly affects their  $T_b$ . Comparative and experimental studies in other *Anolis* species have found that lizard perch height also changes with the habitat in the presence of conspecifics and potential predators, triggering changes in behaviour and morphology, both of which improve its chances of survival (Losos et al. 1993, 2004). *Sceloporus grammicus* shares its habitat with three lizard species and one snake species in the TP, whereas six lizards and two snakes co-occur in the TBP, just one lizard and two snakes in the CP, and two lizards and three snakes in the GP (Supplementary Table S7). Thus, it is likely that the intensity of competition and predation on *S. grammicus* would vary between the studied populations, and as a result, the lizards respond by perching at a height that allows them to avoid or diminish these biotic interactions as to enhance their chances of survival. Nonetheless, other behaviours such as scanning for specific prey, searching for mates, and territoriality, could be determinants of the height at which *S. grammicus* perch in each population, as occurs in other lizard species (ANDREWS 1971).

In conclusion, throughout its wide distribution range, *S. grammicus* encounters a great variety of combinations of environmental factors, suggesting that not all populations experience the same degree of selective pressures. Therefore, we could not expect that different types of traits will diverge in the same trajectory. Our morphological comparisons demonstrated that the direction of sexual selection in males is similar in all populations, while the intensity of fecundity advantage is greater in females of the TP and GP than those in the CP and TBP. This latter selective pressure is of remarkable importance to population dynamics, which finally determines its own persistence over time and space. Our thermal ecology analyses demonstrate that intersexual variation is the exception rather than the rule and, despite marked interpopulational differences in morphology, seasonality and habitat type play a more relevant role in the thermoregulation of this lizard species. In this regard, the plasticity of thermal traits in *S. grammicus* is complex and could be beneficial in the face of the current events of climate change and global warming. Perch height usage is not influenced by sex or by season, but exceptions do occur even if they are rare, as our results indicate. Overall, these results improve our knowledge of the ecology of a widely distributed lizard species, especially of the genus *Sceloporus*, of which many species continue to be little known to herpetologists despite their being quite diverse and abundant in North America.

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- Supplementary Figure S1. Structural differences between habitats used by the central Mexican *Sceloporus grammicus* populations analysed.

### Supplementary data

The following data are available online:

Supplementary Table S1. Sexual dimorphism in morphological characteristics of four populations of *Sceloporus grammicus* in central Mexico.

Supplementary Table S2. Multiple nonlinear regression between seasons and sexes of the thermal characteristics of the cactus population.

Supplementary Table S3. Multiple nonlinear regression between seasons and sexes of the thermal characteristics of the tree–boulder population.

Supplementary Table S4. Multiple nonlinear regression between seasons and sexes of the thermal characteristics of the grassland population.

Supplementary Table S5. Multiple nonlinear regression across populations and between seasons of the thermal characteristics of *Sceloporus grammicus*.

Supplementary Table S6. Thermal characteristics of four populations of *Sceloporus grammicus* by season in central Mexico.

Supplementary Table S7. Field records of the lizard and snake species that occur in sympatry with *Sceloporus grammicus* in the analysed populations.