



Sexual size dimorphism among populations of the rose-bellied lizard *Sceloporus variabilis* (Squamata: Phrynosomatidae) from high and low elevations in Mexico

Raciel Cruz-Elizalde¹, Aurelio Ramírez-Bautista¹ & Abraham Lozano²

¹Laboratorio de Ecología de Poblaciones, Centro de Investigaciones Biológicas, Instituto de Ciencias Básicas e Ingeniería, Universidad Autónoma del Estado de Hidalgo, Km 4.5 carretera Pachuca-Tulancingo, 42184, Mineral de La Reforma, Hidalgo, México

²Instituto Politécnico Nacional, CIIDIR Unidad Durango, Sigma 119, Fraccionamiento 20 de Noviembre II, Durango, Durango 34220, México

It is well known that geographic variation in morphological traits occurs among populations of lizard species. In this study, we analysed body size and sexual size dimorphism among four populations of the lizard *Sceloporus variabilis* from contrasting elevations. Males from all populations were larger than females in snout-vent length, head length, head width, tibia length, and forearm length. These findings are consistent with the hypothesis that sexual selection acts more strongly on males than on females. Females from higher elevations were larger in size than those found at lower elevations, which could be explained by an increased investment in body size to maximise reproductive success. We suggest that environmental (precipitation, temperature) and ecological (food, competition, predation) factors influence the expression of sexual dimorphism and morphological variation in *S. variabilis*.

Key words: Sexual dimorphism, body size, populations, lizard, morphological characteristics

INTRODUCTION

A range of ecogeographical rules governing the size of males and females have been developed to explain geographic variation among species and populations (Cox et al., 2003; Schauble, 2004). In amphibians and fishes, females are generally the larger sex (Liao et al., 2013; Jonsson & Jonsson, 2015), while in mammals, birds, and reptiles, males tend to be larger (Kratochvíl & Frynta, 2006). Sexual dimorphism can be observed in a wide range of morphological traits, such as body size, head length and limbs length (Darwin, 1871; Polák & Frynta, 2010), and can be related to environmental gradients such as altitude and latitude, and the use and availability of resources such as microhabitats and food (Madsen & Shine, 1993; Roitberg, 2007; Ramírez-Bautista et al., 2014). In general terms, Bergmann's rule predicts that body size increases with latitude (Blackburn et al., 1999), and Rensch's rule establishes that sexual-size dimorphism increases with latitude when males are the larger sex, decreasing when females are larger (Abouheif & Fairbairn, 1997). In reptiles such as lizards, Bergmann's rule has been tested in a large number of taxa, whereas fewer case studies exist for Rensch's rule (Angilletta et al., 2004; Cruz et al., 2005; Kratochvíl & Frynta, 2006; Cox et al., 2007).

Lizards can exhibit high variation in sexual size dimorphism, which has been reported as male-biased (e.g., Tropiduridae, Teiidae: Brandt & Navas, 2013), female-biased (e.g., Pygopodidae, Diplodactylidae: Read, 1999; Cox et al., 2009), and absent (e.g., Anguidae,

Gekkonidae, Scincidae: Cox et al., 2009). Male-biased dimorphism is generally linked to sexual selection, with large males being an advantage during male-male competition for territories and access to females, whereas female-biased dimorphism can be explained by higher fecundity of larger females (Endler & Houde, 1995; Braña, 1996; Cox et al., 2009). Sexual size dimorphism in lizards can further arise from intraspecific niche divergence, enabling each sex to use different resources such as food and microhabitats (Rand, 1967; Schoener, 1967; Cox et al., 2003; Hierlihy et al., 2013). Size dimorphism is also influenced by the environment and is for example evidenced by oviparous species, for which females are generally larger at higher latitudes or altitudes, leading to larger clutches with bigger eggs compared to females at lower latitudes or altitudes (Forsman & Shine, 1995; Du et al., 2005).

Sexual-size dimorphism has been assessed in a range of lizard taxa (e.g. Braña, 1996; Ramírez-Bautista et al., 2006; Cox et al., 2007; Aguilar-Moreno et al., 2010; Hierlihy et al., 2013), including comparisons between populations within species (Hernández-Salinas et al., 2010; Jin et al., 2013; Ramírez-Bautista et al., 2014). The genus *Sceloporus* (Phrynosomatidae) currently comprises almost 100 species, occurring in a wide range of habitats and largely being characterised by a marked male-biased sexual-size dimorphism in line with male-male competition (Fitch, 1978; Ansell et al., 2014; Leaché et al., 2016). Differences in sexual size dimorphism among *Sceloporus* species can be attributed to habitat differences, variation in predation pressure, and lack of

Correspondence: Aurelio Ramirez Bautista (ramibautistaa@gmail.com)

territoriality or interspecific competition (Wiens, 1999; 2001), and can also be reflected in differential head length, head width, forearm length and tibia length between the sexes (Ramírez-Bautista & Pavón, 2009; Ramírez-Bautista et al., 2013).

Sceloporus variabilis shows a wide geographic distribution across tropical and temperate regions (Mendoza-Quijano et al., 1998), but little is presently known about morphological variation between and among populations. Previous evidence from local studies suggests a male-biased sexual-size dimorphism (Benabib, 1994; Ramírez-Bautista et al., 2006), but data from different environments are as yet lacking. Thus, the aim of the present study is to quantify body size and sexual-size dimorphism in four populations *S. variabilis* from different elevations (see also Ramírez-Bautista et al., 2011).

MATERIAL AND METHODS

Specimens were obtained from the Colección Nacional de Anfibios y Reptiles (CNAR) del Instituto de Biología, and Colección del Museo de Zoología, Facultad de Ciencias (MZFC), both at the Universidad Nacional Autónoma de México (UNAM). Additional data were obtained from a database held by the Laboratorio de Ecología de Poblaciones of the Universidad Autónoma del Estado de Hidalgo. The populations at high elevation were located at Cerro Azul, Veracruz (97° 44'N, 21° 11'O; 1, 100 m a.s.l., Table 1, Fig. 1) and Metztitlán, Hidalgo (98° 55'N, 20° 38'O; WGS84; 1, 000 m a.s.l., Table 1, Fig. 1). The low elevation localities were at Atlapexco, Hidalgo (98° 20'N, 21° 01'O; 140 m a.s.l., Table 1, Fig. 1) and Alvarado, Veracruz (95° 46'N, 18° 47'O; 50 m a.s.l., Table 1, Fig. 1; INEGI, 2009).

All specimens were collected between 1986 and 2014. In the absence of statistical variation in morphological characteristics between years within populations ($P > 0.05$ in all cases, detailed data not shown), the samples of all years were pooled for each population. Sample sizes were 55 specimens (Cerro Azul; 20 females and 35 males), 116 (Metztitlán; 23 females and 93 males), 47 (Atlapexco; 25 females and 22 males), and 355 (Alvarado; 131 females and 224 males).

Table 1. Environmental parameters for each of the four localities sampled for sexual-size dimorphism of *S. variabilis*.

Environmental characteristic	Populations			
	Cerro Azul, Veracruz	Metztitlán, Hidalgo	Atlapexco, Hidalgo	Alvarado, Veracruz
Elevation (m)	1100	1000	140	50
Vegetation type	Secondary vegetation/ Coniferous forest	Xeric scrub	Tropical rain forest	Evergreen forest
Average annual precipitation (mm)	1600	700	2000	3435-6435
Mean annual temperature (°C)	22	18.5	20-22	27

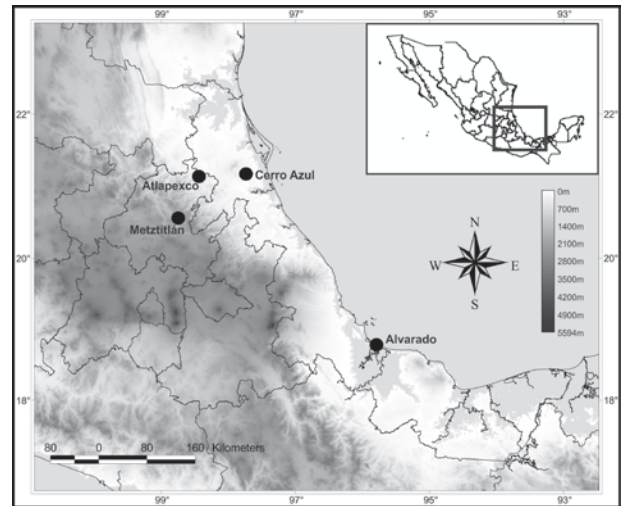


Figure 1. Populations at high (Cerro Azul, Veracruz; Metztitlán, Hidalgo) and low elevations (Atlapexco, Hidalgo; Alvarado, Veracruz) of *S. variabilis* analysed in this study.

Males were considered as adults if they had enlarged testes and convoluted epididymides consistent with sperm production. Adult females were defined by having vitellogenic follicles in ovaries, or eggs in oviducts (following Goldberg & Lowe, 1966). We measured snout-vent length (SVL: measured to the nearest ± 0.01 mm), head length (HL: ± 0.01 mm; distance from the anterior tip of the rostral scale to the posterior margin of the left ear), head width (HW: ± 0.01 mm; maximum width of the head, measured as the distance between the posterior margin of the left and right ears), tibia length (TL: ± 0.01 mm), and forearm length (FL: ± 0.01 mm; measured from the knee (TL) or elbow (FL) to the pad of the foot) in all specimens examined.

For statistical analyses on sexual-size dimorphism, we used a multivariate analysis of variance (MANOVA) to identify differences in body size (SVL) and other morphological characteristics as a function of population origin (Zar, 1999). A Generalized Discriminant Function Analysis (GDFA) was performed at the sex and population level to test for differences between sexes and among populations. Significant variables identified by GDFA were compared between sexes and among populations by univariate Kruskal-Wallis or U Mann-Whitney tests. A correlation analysis was conducted to determine the relationship between morphological traits and elevation. Statistical analyses and post-hoc comparisons were performed when necessary using Statistica version 7.0, and means were presented ± 1 SE (Zar, 1999).

RESULTS

A MANOVA including all traits showed statistically significant differences between sexes (Wilk's $\lambda = 0.704$, $F_{1,565} = 47.15$, $P < 0.001$), among populations (Wilk's $\lambda = 0.582$, $F_{3,565} = 22.37$, $P < 0.001$), and in the interaction of both factors (Wilk's $\lambda = 0.872$, $F_{3,565} = 5.23$, $P < 0.001$). The same pattern occurred in other morphological characteristics, where males were larger than females (Tables 2 and 3). The degree of sexual size dimorphism

Table 2. Mean values (± 1 SE) of morphological characteristics (SVL = snout-vent length, HL = head length, HW = head width, FL = forearm length, and TL = tibia length) of adult males and females of *S. varriabilis* from populations at Veracruz (Alvarado and Cerro Azul), and Hidalgo (Atlapexco and Metztlitlán). Results of Kruskal-Wallis, testing differences by sex among populations.

Trait	Males						Females					
	Alvarado (n=224)	Atlapexco (n=22)	Metztitlán (n=93)	Cerro Azul (n=35)	H	P	Alvarado (n=131)	Atlapexco (n=25)	Metztitlán (n=23)	Cerro Azul (n=20)	H	P
SVL (mm)	59.95 ± 0.37 (44.5-71)	65.6 ± 1.64 (46.49-74.82)	62.20 ± 0.70 (44-77.9)	63.1 ± 1.37 (43-75)	39.86	<0.0001	50.92 ± 0.36 (41.7-68.4)	54.10 ± 0.94 (45-66)	57.89 ± 1.38 (38.5-69.2)	54.35 ± 0.97 (48-62)	35.86	<0.0001
HL (mm)	15.34 ± 0.08 (10.8-18)	16.30 ± 0.34 (12.7-18.39)	15.70 ± 0.15 (11.3-18.72)	16.16 ± 0.43 (8.4-19.5)	25.26	<0.0001	13.07 ± 0.08 (10.5-16.7)	13.81 ± 0.21 (12.2-16.7)	14.77 ± 0.30 (10.79-17.62)	14.23 ± 0.21 (12.8-15.7)	45.84	<0.0001
HW (mm)	10.70 ± 0.08 (7.2-14.5)	11.56 ± 0.48 (7.66-14.95)	11.25 ± 0.15 (7.75-14.7)	12.82 ± 0.34 (8.5-17.7)	41.54	<0.0001	9.05 ± 0.09 (6-13)	9.44 ± 0.31 (6.44-12.5)	8.52 ± 0.30 (6.29-11.8)	10.53 ± 0.20 (9.2-12.5)	33.71	<0.0001
FL (mm)	10.17 ± 0.07 (7-13.5)	11.45 ± 0.27 (8.91-13.05)	10.69 ± 0.11 (7.4-12.59)	10.01 ± 0.26 (6.4-13.5)	42.14	<0.0001	8.51 ± 0.08 (5.8-11.4)	9.44 ± 0.18 (7.8-11.2)	9.37 ± 0.22 (7-11.29)	8.48 ± 0.19 (7.9-9)	30.97	<0.0001
TL (mm)	15.13 ± 0.09 (10.2-18.4)	17.22 ± 0.38 (13.2-20.05)	15.13 ± 0.14 (11-19.41)	16.09 ± 0.44 (7.5-19.2)	37.81	<0.0001	12.84 ± 0.08 (10.6-17.6)	13.82 ± 0.26 (11.8-16.9)	13.90 ± 0.38 (10-17.74)	13.54 ± 0.20 (12.3-16)	30.58	<0.0001

Table 3. Mean values (± 1 SE) of morphological characteristics (SVL = snout-vent length, HL = head length, HW = head width, FL = forearm length, and TL = tibia length) of adult males and females of *S. varriabilis* from populations at Veracruz (Alvarado and Cerro Azul), and Hidalgo (Atlapexco and Metztlitlán), Mexico. * = $P < 0.01$, the rest was $P < 0.001$, by U Mann-Whitney test.

Trait	Alvarado		Atlapexco		Metztlitlán		Cerro Azul	
	Males (n=224)	Females (n=131)	Males (n=22)	Females (n=25)	Males (n=93)	Females (n=23)	Males (n=35)	Females (n=20)
SVL (mm)	59.95 $\pm$ 0.37 (44.5-71)	50.92 $\pm$ 0.36 (41.7-68.4)	65.6 $\pm$ 1.64 (46.49-74.82)	54.10 $\pm$ 0.94 (45-66)	62.20 $\pm$ 0.70 (44-77.9)	57.89 $\pm$ 1.38 (38.5-69.2)*	63.1 $\pm$ 1.37 (43-75)	54.35 $\pm$ 0.97 (48-62)
HL (mm)	15.34 $\pm$ 0.08 (10.8-18)	13.07 $\pm$ 0.08 (10.5-16.7)	16.30 $\pm$ 0.34 (12.7-18.39)	13.81 $\pm$ 0.21 (12.2-16.7)	15.70 $\pm$ 0.15 (11.3-18.72)	14.77 $\pm$ 0.30 (10.79-17.62)	16.16 $\pm$ 0.43 (8.4-19.5)	14.23 $\pm$ 0.21 (12.8-15.7)
HW (mm)	10.70 $\pm$ 0.08 (7.2-14.5)	9.05 $\pm$ 0.09 (6-13)	11.56 $\pm$ 0.48 (7.66-14.95)	9.44 $\pm$ 0.31 (6.44-12.5)*	11.25 $\pm$ 0.15 (7.75-14.7)	8.52 $\pm$ 0.30 (6.29-11.8)	12.82 $\pm$ 0.34 (8.5-17.7)	10.53 $\pm$ 0.20 (9.2-12.5)
FL (mm)	10.17 $\pm$ 0.07 (7-13.5)	8.51 $\pm$ 0.08 (5.8-11.4)	11.45 $\pm$ 0.27 (8.91-13.05)	9.44 $\pm$ 0.18 (7.8-11.2)	10.69 $\pm$ 0.11 (7.4-12.59)	9.37 $\pm$ 0.22 (7-11.29)	10.01 $\pm$ 0.26 (6.4-13.5)	8.48 $\pm$ 0.19 (7-9.9)
TL (mm)	15.13 $\pm$ 0.09 (10.2-18.4)	12.84 $\pm$ 0.08 (10.6-17.6)	17.22 $\pm$ 0.38 (13.2-20.05)	13.82 $\pm$ 0.26 (11.8-16.9)	15.13 $\pm$ 0.14 (11-19.41)	13.90 $\pm$ 0.38 (10-17.74)	16.09 $\pm$ 0.44 (7.5-19.2)	13.54 $\pm$ 0.20 (12.3-16)

varied among populations. Males were 17.53%, 15.06%, 13.87%, and 6.93% larger than females in Atlapexco, Alvarado, Cerro Azul, and Metztitlán, respectively. In females, SVL ($r = 0.39$, $P < 0.001$), HL ($r = 0.45$, $P < 0.001$), HW ($r = 0.14$, $P = 0.05$), and TL increased significantly with altitude ($r = 0.27$, $P < 0.001$), whereas FL did not ($r = 0.12$, $P = 0.08$). Males showed a similar pattern for SVL ($r = 0.15$, $P = 0.002$), HL ($r = 0.13$, $P = 0.009$), and HW ($r = 0.29$, $P < 0.001$), but not for FL ($r = 0.09$, $P = 0.08$) and TL ($r = 0.04$, $P = 0.40$).

The GDFA showed that three out of the five traits were different between sexes, with an eigenvalue of $F_1 = 0.73$ (cumulative percentage 100%): HL (Wilk's $\lambda = 0.982$, $F_{1, 564} = 9.79$, $P < 0.001$), HW (Wilk's $\lambda = 0.974$, $F_{1, 564} = 14.79$, $P < 0.001$), and TL (Wilk's $\lambda = 0.97$, $F_{1, 564} = 17.43$, $P < 0.001$). All traits differed among populations (SVL, Wilk's $\lambda = 0.98$, $F_{3, 564} = 2.78$, $P = 0.040$; HL, Wilk's $\lambda = 0.97$, $F_{3, 564} = 4.26$, $P = 0.005$; HW, Wilk's $\lambda = 0.79$, $F_{3, 564} = 49.30$, $P < 0.001$; FL, Wilk's $\lambda = 0.80$, $F_{3, 564} = 46.27$, $P < 0.001$, and TL, Wilk's $\lambda = 0.92$, $F_{3, 564} = 15.96$, $P < 0.001$), with eigenvalues of $F_1 = 0.46$ and $F_2 = 0.11$ (cumulative percentage 86%).

DISCUSSION

Male-biased sexual-size dimorphism has been recorded in most species of Iguanidae (Fitch, 1978), Tropiduridae (Brandt & Navas, 2013), and Phrynosomatidae (Valdéz-González & Ramírez-Bautista, 2002; Cox et al., 2007; but see also Ramírez-Bautista et al., 2013). The pattern of sexual-size dimorphism found for *S. variabilis* is largely consistent with Fitch's (1978) observations across the genus *Sceloporus*, and similar to that observed in other species (*S. ochoterena*: Smith et al., 2003; *S. grammicus*: Hernández-Salinas et al., 2010; *S. minor*: Ramírez-Bautista et al., 2014; *S. siniferus*: Hierlihy et al., 2013; Ansell et al., 2014), as well as other populations of *S. variabilis* (Ramírez-Bautista et al., 2006; Cruz-Elizalde & Ramírez-Bautista, 2016). The male-biased sexual size dimorphism observed for *S. variabilis* is likely governed by sexual selection which involves male-male aggressive interactions occurs during courtship and mating (see e.g. Ruby, 1978; Ruby & Baird, 1994 for *S. jarrovi*). Larger males with larger relative heads are favoured during male-male combats, resulting in higher reproduction success and the acquisition of more resources (Stamps, 1983; Carothers, 1984; Hierlihy et al., 2013). In addition to sexual size dimorphism, male *S. variabilis* can also show brighter colouration patterns than females (Stephenson & Ramírez-Bautista, 2012; for similar studies on other *Sceloporus* species see Feria-Ortíz et al., 2001; Ramírez-Bautista et al., 2002; Ramírez-Bautista & Pavón, 2009; Lozano, 2013). An analysis of differences in coloration in males from the four studied sites of *S. variabilis* is still outstanding.

The observed effect of altitude on size is consistent with Bergmann's rule, which states that body size increases with higher latitude and elevation and decreasing temperature (e.g., Gaston & Blackburn, 2000). While Bergmann's rule is largely followed by mammals and birds, it is not universally applicable to ectotherm vertebrates such as reptiles (e.g. Ashton

& Feldman, 2003; Cruz et al., 2005). While to present study finds evidence in support of a positive relation between altitude and size traits in males and females, a higher number of populations is required to draw firm conclusions (see also Angilletta et al., 2004). Females from higher elevations were generally larger than those from lower elevations, similar to what has been observed in other oviparous lizards (e.g., Michaud & Echternacht, 1995; Du et al., 2014). In low temperature environments at high elevations and/or high latitude, body size can increase more distinctly with elevation and latitude, because lizards invest more energy in growth and fat storage during the harshest periods of the year (Michaud & Echternacht, 1995; Angilletta et al., 2004), promoting late maturity, larger clutch/litter sizes, bigger eggs, and larger offspring/neonates at birth (Jin & Liu, 2007; Díaz et al., 2012; Du et al., 2014). A recent study about reproduction among populations of *S. variabilis* in Central Mexico indeed revealed differences in clutch size and SVL of females in three populations occurring at different elevations (Cruz-Elizalde & Ramírez-Bautista, 2016). Alternative hypothesis to explain patterns of sexual size dimorphism are related to the differential use of resources, and males and females with larger heads are for example able to ingest larger prey items (Vitt & Pianka, 2007; Ngo et al., 2015). However, difference in prey size, microhabitat, or resource competition between males and females within population do not necessarily constitute promoters of sexual size dimorphism (Cox & Kahl, 2015; see also Schoener, 1967; Butler et al., 2000).

Further studies are needed for a better understanding of geographic patterns of sexual size dimorphism in *S. variabilis*, focusing on the use of resources between sexes, population dynamics, and male coloration. Additionally, differences in body size and sexual-size dimorphism should be assessed between species of the *S. variabilis* group, as traits such as male territoriality, clutch size, and body size in some cases fail to explain geographic variation in morphology within and among species (Cox et al., 2003; Frýdlová & Frynta, 2010; Ramírez-Bautista et al., 2013; Cox & Kahl, 2015).

ACKNOWLEDGEMENTS

The authors would like to thank Víctor Hugo Reynoso for allowing us to analyse specimens at the Colección Nacional de Anfibios y Reptiles (CNAR) at the Universidad Nacional Autónoma de México. We would also like to thank Francisco F. Núñez de Cáceres González, Vicente Mata-Silva and Miguel A. Martínez Morales for reviewing the manuscript and to the three anonymous reviewers for their valuable comments on this report. This study is part of the PhD research of the senior author (RCE) under the Biodiversidad y Conservación programme at the Universidad Autónoma del Estado de Hidalgo, México. A scholarship was granted to the senior author (RCE, Number 360243) by CONACyT and fieldwork was sponsored by CONABIO (project JM001) and Fomix-CONACyT-191908 Biodiversidad del Estado de Hidalgo-3a. The scientific permit No. SGPA DGVS/04989/11 was provided by SEMARNAT to carry out this study.

REFERENCES

- Abouheif, E. & Fairbairn, D. J. (1997). A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. *The American Naturalist* 149, 540–562.
- Aguilar-Moreno, M., Rodríguez-Romero, F. de J., Aragón-Martínez, A., Muñoz-Manzano, J. A., Granados-González, G. & Hernández-Gallegos, O. (2010). Dimorfismo sexual de *Aspidoscelis costata costata* (Squamata: Teiidae) en el sur del Estado de México, México. *Revista Chilena de Historia Natural* 83, 585–592.
- Angilletta, Jr. M. J., Niewiarowski, P. H., Dunham, A. E., Leaché, A. D. & Porter, W. P. (2004). Bergmann's clines in ectotherms: illustrating a life-history perspective with Sceloporine lizards. *The American Naturalist* 164, 168–183.
- Ansell, A. K., García-Collazo, R., Chavez Tapia, C. B. & Mallory, F. F. (2014). Sexual dimorphism and thermoregulatory behaviour in the long-tailed spiny lizard, *Sceloporus siniferus* from Mexico. In *Lizards, Thermal Ecology, Genetic Diversity and Functional Role in Ecosystems*, 121–142. Kiernan, M. P. (ed). Nova Science Publisher, Inc. New York.
- Ashton, K. G. & Feldman, C. R. (2003). Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution* 57, 1151–1163.
- Benabib, M. (1994). Reproduction and lipid utilization of tropical populations of *Sceloporus variabilis*. *Herpetological Monographs* 8, 160–180.
- Blackburn, T. M., Gaston, K. J. & Loder, N. (1999). Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions* 5, 165–174.
- Brandt, R. & Navas, C. A. (2013). Body size variation across climatic gradients and sexual size dimorphism in Tropidurinae lizards. *Journal of Zoology* 290, 192–198.
- Braña, F. (1996). Sexual dimorphism in lacertid lizards: male head increase vs female abdomen increase? *Oikos* 75, 511–523.
- Butler, M. A., Schoener, T. W. & Losos, J. B. (2000). The relationship between sexual size dimorphism and habitat use in Greater Antillean *Anolis* lizards. *Evolution* 54, 259–272.
- Carothers, J. H. (1984). Sexual selection and sexual dimorphism in some herbivorous lizards. *American Naturalist* 124, 244–254.
- Cox, R., Skelly, S. L. & John-Alder, H. B. (2003). A comparative test of adaptation hypotheses for sexual size dimorphism in lizards. *Evolution* 57, 1653–1669.
- Cox, R. M., Butler, M. A. & John-Alder, H. B. (2007). The evolution of sexual size dimorphism in reptiles. In *Sex, Size & Gender Roles: Evolutionary Studies of Sexual Size Dimorphism*, 38–49. Fairbairn, D. J., Blanckenhorn, W. U. & Székely, T. (eds). Oxford University Press, Oxford, UK.
- Cox, R. M., Stenquist, D. S. & Calsbeek, R. (2009). Testosterone, growth, and the evolution of sexual size dimorphism. *Journal of Evolutionary Biology* 22, 1586–1598.
- Cox, R. M. & Kahl, A. F. (2015). Sexual selection and sexual dimorphism. In *Reproductive Biology and Phylogeny of Lizards and Tuatara*, 78–108. Rheubert, J. L., Siegel, D. S. & Trauth, S. E. (eds). CRC Press, Florida, United States.
- Cruz, F. B., Fitzgerald, L. A., Espinoza, R. E. & Schulte, J. A., II. (2005). The importance of phylogenetic scale in tests of Bergmann's and Rapoport's rules: lessons from a clade of South American lizards. *Journal of Evolutionary Biology* 18, 1559–1574.
- Cruz-Elizalde, R. & Ramírez-Bautista, A. (2016). Reproductive cycles and reproductive strategies among populations of the Rose-bellied Lizard *Sceloporus variabilis* (Squamata: Phrynosomatidae) from central Mexico. *Ecology and Evolution* 6, 1753–1768.
- Darwin, C. R. (1871). *The descent of man, and selection in relation to sex*. New York: Appleton.
- Du, W. G., Ji, X., Zhang, Y. P., Xu, X. F. & Shine, R. (2005). Identifying sources of variation in reproductive and life-history traits among five populations of a Chinese lizard (*Takydromus septentrionalis*, Lacertidae). *Biological Journal of the Linnean Society* 85, 443–53.
- Du, W. G., Robbins, T. R., Warner, D. A., Langkilde, T. & Shine, R. (2014). Latitudinal and seasonal variation in reproductive effort of the eastern fence lizard (*Sceloporus undulatus*). *Integrative Zoology* 9, 360–371.
- Díaz, J. A., Iraeta, P., Verdú-Rico, J., Siliceo, I. & Salvador, A. (2012). Intraspecific variation of reproductive traits in a Mediterranean lizard: clutch, population, and lineage effects. *Evolutionary Biology* 39, 106–115.
- Endler, J. A. & Houde, A. E. (1995). Geographic variation in female preferences for male traits in *Poecilia reticulata*. *Evolution* 49, 456–468.
- Feria-Ortiz, M., Nieto-Montes de Oca, A. & Salgado-Ugarte, I. H. (2001). Diet and reproductive biology of the viviparous lizard *Sceloporus torquatus* (Squamata: Phrynosomatidae). *Journal of Herpetology* 35, 104–112.
- Fitch, H. S. (1978). Sexual size differences in the genus *Sceloporus*. University of Kansas Science Bulletin 561, 441–461.
- Forsman, A. & Shine, R. (1995). Parallel geographic variation in body shape and reproductive life history within the Australian scincid lizard *Lampropholis delicata*. *Functional Ecology* 9, 818–828.
- Frydlová, P. & Frynta, D. (2010). A test Rensch's rule in varanid lizards. *Biological Journal of the Linnean Society* 100, 293–306.
- Gaston, K. J. & Blackburn, T. M. (2000). Pattern and Process in Macroecology. Blackwell Science, Malden, MA, United States.
- Goldberg, S. R. & Lowe, C. H. (1966). The reproductive cycle of the western whiptail lizard (*Cnemidophorus tigris*) in southern Arizona. *Journal of Morphology* 118, 543–548.
- Hernández-Salinas, U., Ramírez-Bautista, A., Leyte-Manrique, A. & Smith, G. R. (2010). Reproduction and sexual dimorphism in two populations of *Sceloporus grammicus* (Sauria: Phrynosomatidae) from Hidalgo, Mexico. *Herpetologica* 66, 12–22.
- Hierlihy, C. A., García-Collazo, R., Chavez Tapia, C. B. & Mallory, F. F. (2013). Sexual dimorphism in the lizard *Sceloporus siniferus* support for the intraspecific niche divergence and sexual selection hypotheses. *Salamandra* 49, 1–6.
- INEGI. (2009). Instituto Nacional de Estadística, Geografía e Informática. México. <http://www.inegi.org.mx/inegi/default.aspx> [accessed 7 January 2015].
- Jin, Y. T. & Liu, N. F. (2007). Altitudinal variation in reproductive strategy of the toad-headed lizard, *Phrynocephalus vlangalii* in North Tibet Plateau (Qinghai). *Amphibia-Reptilia* 28, 509–515.
- Jin, Y. T., Li, J. Q. & Liu, N. F. (2013). Elevation-related variation in life history traits among *Phrynocephalus* lineages on the Tibetan Plateau: do they follow typical squamate ecogeographic patterns? *Journal of Zoology* 290, 293–301.
- Jonsson, B. & Jonsson, N. (2015). Sexual size dimorphism in anadromous brown trout *Salmo trutta*. *Journal of Fish Biology* 87, 187–193.
- Kratochvíl, L. & Frynta, D. (2006). Body-size effect on egg size in eublepharid geckos (Squamata: Eublepharidae), lizards

- with invariant clutch size: negative allometry for egg size in ectotherms is not universal. *Biological Journal of the Linnean Society* 88, 527–532.
- Leaché, A. D., Banbury, B. L., Linkem, C. W. & Nieto-Montes de Oca, A. (2016). Phylogenomics of a rapid radiation: Is chromosomal evolution linked to increased diversification in North American spiny lizards (Genus *Sceloporus*)? *BMC Evolutionary Biology* 16, 63.
- Liao, W. B., Zeng, Y., Zhou, C. Q. & Jehle, R. (2013). Sexual size dimorphism in anurans fails to obey Rensch's rule. *Frontiers in Zoology* 10, 10.
- Lozano, A. (2013). *Estudio comparado de la reproducción y cambios histológicos de las gónadas de la lagartija vivípara Sceloporus grammicus (Squamata: Phrynosomatidae) durante un ciclo anual en dos ambientes contrastantes*. Tesis de Maestría, Universidad Autónoma del Estado de Hidalgo, México.
- Madsen, T. & Shine, R. (1993). Temporal variability in sexual selection on reproductive tactics and body size in male snakes. *American Naturalist* 141, 167–171.
- Mendoza-Quijano, F., Flores-Villela, O. & Sites, J. W. (1998). Genetic variation, Species status, and phylogenetic relationships in rose-bellied lizards (*variabilis* group) of the genus *Sceloporus* (Squamata: Phrynosomatidae). *Copeia* 1998, 354–366.
- Michaud, E. J. & Echternacht, A. C. (1995). Geographic variation in the life history of the lizard *Anolis carolinensis* and support for the pelvic constraint model. *Journal of Herpetology* 29, 86–97.
- Ngo, C. D., Ngo, B. V., Hoang, T. T., Nguyen, T. T. T. & Dang, H. P. (2015). Feeding ecology of the common sun skink, *Eutropis multifasciata* (Reptilia: Squamata: Scincidae), in the plains of central Vietnam. *Journal of Natural History* 49, 2417–2436.
- Polák, J. & Frynta, D. (2010). Patterns of sexual size dimorphism in cattle breeds support Rensch's rule. *Evolutionary Ecology* 24, 1255–1266.
- Ramírez-Bautista, A. & Pavón, N. P. (2009). Sexual dimorphism and reproductive cycle in the arboreal spiny lizard *Sceloporus formosus* Wiegmann (Squamata: Phrynosomatidae) from central Oaxaca, Mexico. *Revista Chilena de Historia Natural* 82, 553–563.
- Ramírez-Bautista, A., Ramos-Flores, O. & Sites, Jr. J. W. (2002). Reproductive cycle of the spiny lizard *Sceloporus jarrovi* (Sauria: Phrynosomatidae) from north-central Mexico. *Journal of Herpetology* 36, 225–233.
- Ramírez-Bautista, A., García-Collazo, R. & Guillelte, Jr. L. J. (2006). Reproductive, fat, and liver cycles of male and female rose-bellied lizards, *Sceloporus variabilis*, from coastal areas of southern Veracruz, México. *The Southwestern Naturalist* 51, 163–171.
- Ramírez-Bautista, A., Leyte-Manrique, A., Marshall, J. C. & Smith, G. R. (2011). Effects of elevation on litter-size variation among lizard populations in the *Sceloporus grammicus* complex (Phrynosomatidae) in Mexico. *Western North American Naturalist* 71, 215–221.
- Ramírez-Bautista, A., Stephenson, B. P., Serrano Muñoz, C., Cruz-Elizalde, R. & Hernández-Salinas, U. (2014). Reproduction and sexual dimorphism in two populations of the polymorphic spiny lizard *Sceloporus minor* from Hidalgo, México. *Acta Zoologica* 95, 397–408.
- Ramírez-Bautista, A., Smith, G. R., Leyte-Manrique, A. & Hernández-Salinas, U. (2013). No sexual size-dimorphism in the Eastern spiny lizard, *Sceloporus spinosus*, from Guadalcázar, San Luis Potosí, Mexico. *The Southwestern Naturalist* 58, 510–512.
- Rand, A. S. (1967). Ecology and social organization in *Anolis lineatopus*. *Proceedings of the United States National Museum* 122, 1–79.
- Read, J. L. (1999). Longevity, reproductive effort and movements of three sympatric Australian arid-zone geckos. *Australian Journal of Zoology* 47, 307–316.
- Roitberg, E. S. (2007). Variation in sexual dimorphism within a widespread lizard species. In *Sex, size and gender roles. Evolutionary studies of sexual size dimorphism*, 143–217. Fairbairn, D., Blanckenhorn, W. & Székely, T. (eds). Oxford: Oxford University Press.
- Ruby, D. E. (1978). Seasonal changes in the territorial behaviour of the iguanid lizard *Sceloporus jarrovi*. *Copeia* 1978, 430–438.
- Ruby, D. E. & Baird, D. I. (1994). Intraspecific variation in behaviour: comparison between populations at different altitudes of the lizard *Sceloporus jarrovi*. *Journal of Herpetology* 28, 70–78.
- Schäuble, C. S. (2004). Variation in body size and sexual dimorphism across geographical and environmental space in the grogs *Limnodynastes tasmaniensis* and *L. peronii*. *Biological Journal of the Linnean Society* 82, 39–56.
- Schoener, T. W. (1967). The ecological significance of sexual size dimorphism in the lizard *Anolis conspersus*. *Science* 155, 474–477.
- Sinervo, B. & Lively, C. M. (1996). The rock-paper-scissors game and the evolution of alternative male reproductive strategies. *Nature* 380, 240–243.
- Smith, G. R., Lemos-Espinal, J. A. & Ballinger, R. E. (2003). Body size, sexual dimorphism, and clutch size in two populations of the lizard, *Sceloporus ochoterenae*. *The Southwestern Naturalist* 48, 123–126.
- Stamps, J. A. (1983). Sexual selection, sexual dimorphism, and territoriality. In *Lizard Ecology: Studies of a Model Organism*, 149–160. Huey, R. B. & Pianka, E. R. (eds). Harvard University, Cambridge, MA.
- Stephenson, B. & Ramírez-Bautista, A. (2012). Did sexually dimorphic dorsal coloration evolve by a pre-existing bias in males in the lizard *Sceloporus minor*? *Evolutionary Ecology* 26, 1277–1291.
- Valdéz-González, M. A. & Ramírez-Bautista, A. (2002). Reproductive characteristics of the spiny lizards, *Sceloporus horridus* and *Sceloporus spinosus* (Squamata: Phrynosomatidae) from México. *Journal of Herpetology* 36, 36–43.
- Vitt, L. J. & Pianka, E. R. (2007). Feeding Ecology in the Natural World. In *Lizard Ecology: The Evolutionary Consequences of Foraging Mode*, 141–172. Reilly, S. M., McBrayer, L. D. & Miles, D. B. (eds). Cambridge University Press.
- Wiens, J. J. (1999). Phylogenetic evidence for multiple losses of a sexually selected character in phrynosomatid lizards. *Proceedings of the Royal Society of London, Series B* 266, 1529–1535.
- Wiens, J. J. (2001). Widespread loss of sexually-selected traits: how the peacock lost its spots. *Trends in Ecology and Evolution* 16, 517–523.
- Zar, J. H. (1999). *Biostatistical analysis*. Prentice-Hall New Jersey, United States.

Accepted: 13 December 2016