See discussions, stats, and author profiles for this publication at: https://www.researchgate.net/publication/339540004

# Sexual Dimorphism and Reproductive Characteristics of the Cozumel Spiny Lizard, Sceloporus cozumelae (Squamata: Phrynosomatidae) from Mexico

Article in Current Herpetology · February 2020 DOI: 10.5358/hsj.39.19



Project

Evolution of life histories in reptiles View project

ANIDACIÓN DE LA TORTUGA VERDE, Chelonia mydas (CHELONIIDAE) EN PLAYA CHAPARRALES, CAZONES, VERACRUZ View project

# Sexual Dimorphism and Reproductive Characteristics of the Cozumel Spiny Lizard, *Sceloporus cozumelae* (Squamata: Phrynosomatidae) from Mexico

# AURELIO RAMÍREZ-BAUTISTA<sup>1</sup>, RACIEL CRUZ-ELIZALDE<sup>2\*</sup>, DULCE MARÍA GALVÁN-HERNÁNDEZ<sup>3</sup>, URIEL HERNÁNDEZ-SALINAS<sup>4</sup>, AND CHRISTIAN BERRIOZABAL-ISLAS<sup>5</sup>

<sup>1</sup>Laboratorio 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
<sup>2</sup>Museo de Zoología "Alfonso L. Herrera", Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), A.P. 70-399, Ciudad de México CP 04510, MÉXICO
<sup>3</sup>Laboratorio de Micología, 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
<sup>4</sup>Instituto Politécnico Nacional, Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional (CIIDIR) Unidad Durango, Calle Sigma 119 Fraccionamiento 20 de Noviembre II, 34220, Durango, Durango, MÉXICO
<sup>5</sup>Programa Educativo de Ingeniería en Biotecnología. Universidad Politécnica de Quintana Roo. Av. Arco Bicentenario, M 11, Lote 1119-33, Sm 255, 77500 Cancún, Ouintana Roo, MÉXICO

Abstract: We analyzed sexual dimorphism and reproductive characteristics (minimum size at sexual maturity, clutch size, and reproductive period) of females and males of *Sceloporus cozumelae*, a species endemic to the Yucatan Peninsula, Mexico, and which belongs to the *Sceloporus variabilis* group. Sexual dimorphism was recorded, with the males being larger in snout-vent length, head length, head width, forearm length, and tibia length. The average clutch size was 3.4. Females containing eggs and vitellogenic follicles were observed at the same time, indicating that the population produces at least two clutches annually. Minimum size at sexual maturity was similar for both sexes (40 mm), and reproduction, determined according to the months in which gonads were obtained, was synchronous between males and females. The species shows high similarity to populations of *S. variabilis* in sexual dimorphism and reproductive characteristics; however, it has smaller snout-vent length when compared to other populations of *S. variabilis* in Mexico.

Key words: Endemic species; Life history characteristics; Morphological characteristics; *Sceloporus variabilis* group

<sup>\*</sup> Corresponding author.

E-mail address: cruzelizalde@gmail.com

### INTRODUCTION

To date, extensive studies have been published on the natural history of both oviparous and viviparous lizard species (Fitch, 1970; Tinkle et al., 1970; Du et al., 2005; Wang et al., 2011). Classical studies often treated anecdotal data on the natural history of some species (Fitch, 1970). Subsequently, based on these studies, a high number of studies were carried out to test ecological and evolutionary hypotheses regarding life history evolution using lizards as models (Roitberg et al., 2015; Cruz-Elizalde and Ramírez-Bautista, 2016). These studies documented variation in some life history characteristics, such as fecundity (Ramírez-Bautista et al., 2011; Pincheira-Donoso and Hunt, 2017; Roitberg et al., 2015; Schwarz and Meiri, 2017), growth rate (Pérez-Mendoza et al., 2013; Pérez-Mendoza and Zúñiga-Vega, 2014), reproductive cycles (Cruz-Elizalde and Ramírez-Bautista, 2016; Ramírez-Bautista et al., 2017), and sexual size dimorphism (Cox et al., 2003). Nonetheless, these studies have been carried out on common species with wide distributions, and very little is known about uncommon or endemic species (Ramírez-Bautista et al., 2017; Zúñiga-Vega et al., 2017).

Reproduction and sexual size dimorphism of the genus Sceloporus are well documented not only in large populations of small-bodied oviparous species, such as Sceloporus aeneus (Manríquez-Morán et al., 2013; Ramírez-Bautista et al., 2016), S. siniferus (Hierlihy et al., 2013; Ramírez-Bautista et al., 2015), and S. scalaris (Ramírez-Bautista et al., 2017), but also in larger-bodied oviparous (S. spinosus, Valdéz-González and Ramírez-Bautista, 2002; Valencia-Limón et al., 2014; S. variabilis, Cruz-Elizalde and Ramírez-Bautista, 2016) and viviparous species (S. formosus, Ramírez-Bautista and Pavón, 2009; S. grammicus, Hernández-Salinas et al., 2010). Nothing is known about the natural history of endemic Sceloporus species with restricted distribution (microendemics). An example of these species is *S. cozumelae*, which is endemic to southeastern Mexico, and it has poorly studied with respect to its reproduction, sexual dimorphism, and general ecology (Lee, 1996).

Sceloporus cozumelae exhibits one of the smallest snout-vent length (SVL) of any species in the Sceloporus variabilis group (Leaché et al., 2016). This terrestrial lizard is oviparous and swift-moving, and inhabits beaches and coastal strands (Lee, 1996). We present information about the morphology and reproduction of a population from Puerto Morelos, Quintana Roo, Mexico. Our goal is to provide information on sexual size dimorphism and reproduction of males and females of S. cozumelae and to compare these data to those from populations of S. variabilis. Because this species belongs to the Sceloporus variabilis group, we expected some of its morphological and reproductive characteristics to be similar to those observed in populations of S. variabilis.

## MATERIALS AND METHODS

#### Study site

The data were obtained from April 1980 to September 1992 at Puerto Morelos, Ouintana Roo (20°51'13" N, 86°52'31" W; datum WGS84) at elevations 3-5 m. The topography of this locality is uniform, with scarce relief; the climate is warm and subhumid. Mean annual temperature is 26.3°C, with a maximum temperature of 35.5°C and a minimum of 13°C in winter. Rains occur in summer and autumn (June-October); mean annual precipitation is 1,041 mm; cyclones and hurricanes are active from June to November (INEGI, 2017). For this study, we analyzed 87 adults (38 females and 49 males); these lizards came from scientific collections, including the Colección Nacional de Anfibios y Reptiles of the Instituto de Biología (CNAR-IBH) at the Universidad Nacional Autónoma de México (Appendix I). The first author verified the species identification in the scientific collection in 1999, which were collected from 1980 to 1992 (April, 1 female and 4 males; May, 14 females and 5 males; June, 14 females and 26 males; September, 9 females and 14 males). Because no differences were observed in the morphological and reproductive variables among years (ANCOVA, F=2.841, df=5, 84, P=0.211), they were pooled for analysis.

#### Sexual dimorphism

We took the following measurements of each lizard to the nearest 0.01 mm: SVL, head length (HL: distance from the anterior tip of the rostral scale to the posterior margin of the left ear), head width (HW: maximum width of the head measured as the distance between the posterior margin of the left and right ears), tibia length (TL: measured from the knee to the pad of the foot), and forearm length (FL: measured from the elbow to the pad of the foot) (Metzger and Herrel, 2005; Ramírez-Bautista et al., 2014). An analysis of covariance (ANCOVA) was conducted to analyze sexual dimorphism. The function of the ANCOVA was to eliminate the effect of SVL (covariate) on the dependent variables (HL, HW, TL, and FL) (Zar, 2010). The data are presented as mean  $\pm 1$ SE.

#### Reproduction

The smallest female containing enlarged vitellogenic follicles or oviductal eggs was used as an estimator of minimum SVL at maturity (Lozano et al., 2014; Ramírez-Bautista et al., 2015, 2017). Males were considered sexually mature if they contained enlarged testes and highly convoluted epididymides, which typically are associated with sperm production (Lozano et al., 2015). Testes, non-vitellogenic follicles (NVF) (previtellogenic follicle), vitellogenic follicles (VF), and eggs (E) were removed and measured. These classes of follicles (NVF, VF, and E) were also used to measure gonad volume (Ramírez-Bautista et al., 2015). In addition, liver and fat body mass were removed and weighed (to the nearest 0.0001 g) (Ramírez-Bautista et al., 2015). A one-way analysis of variance (ANOVA) was performed on organ masses with month as a factor to determine whether there was significant monthly variation (Ramírez-Bautista and Vitt, 1997; Ramírez-Bautista and Pavón, 2009). ANOVA was also used to determine variation of liver and fat body mass among months for each sex.

#### Clutch size

Clutch size was quantified by counting the number of eggs in the oviduct of adult females during the reproductive season. Females with eggs and VF simultaneously were considered to have at least two clutches. Due to data that were not normally distributed (by the Kolmogorov-Smirnov test), mean clutch size based on the counts of VF and eggs, as well as SVL of the females containing them, were compared using a Mann-Whitney U-test. Pearson's correlation coefficient was used to test for a possible relationship between clutch size and the SVL of females (Ramírez-Bautista et al., 2015, 2016). We assessed significance at P<0.05. All statistical analyses were performed using Statistica 7.0 (StatSoft, Inc., Tulsa, OK, USA).

#### Results

#### Sexual dimorphism

Males were larger ( $\bar{x}$ =48.1±0.67 mm; range=40.0–58.0) than females ( $\bar{x}$ =46.5± 0.42 mm; 40.0–52.0) in SVL (Mann-Whitney U-test, U=574, P=0.007). All characteristics that were measured exhibited sexual dimorphism, with males always being larger than females (Table 1).

#### Reproduction

Males reached sexual maturity at the same size as females at 40 mm. Reproductive activity for males and females was recorded from April to September. No differences in gonad volume in males ( $\bar{x}$ =58.0±32.3 mm<sup>3</sup>; range= 0.628–1571.2 mm<sup>3</sup>) were found among months (F=0.331, df=3, 44, P=0.994). The data showed that reproductive activity of males started in April (7.63±4.34 mm<sup>3</sup>, n=4) and increased in May (38.9±6.91 mm<sup>3</sup>, n=5), with a maximum in June (87.5±59.4 mm<sup>3</sup>,

TABLE 1. Mean $\pm$ 1SE, with range in parentheses, of morphological characteristics of adult females and males of *Sceloporus cozumelae* from Puerto Morelos, Quintana Roo, Mexico (SVL=snout-vent length, HL=head length, HW=head width, FL=forearm length, and TL=tibia length). Comparisons were made with an ANCOVA taking SVL as the covariate, except for SVL for which Mann-Whitney U-test was conducted. \*U value.

Characteristics	Females (n=38)	Malas (m. 40)	ANCOVA		
		Males (n=48)	F	df	Р
SVL	46.5±0.42 (40.0-52.0)	48.1±0.67 (40.0–58.0)	574*	na	0.007
HL	12.1±0.10 (10.8–13.6)	12.9±0.16 (10.7–15.9)	9.77	1,84	0.002
HW	8.3±0.11 (6.7–9.5)	9.1±0.13 (6.7–10.9)	11.53	1,84	0.001
FL	7.2±0.07 (6.6-8.2)	7.9±0.13 (5.7–9.8)	11.48	1,84	0.001
TL	10.8±0.13 (9.6–13.8)	11.9±0.29 (10.1–13.9)	4.53	1,84	0.036

n=26), followed by a decrease in September (21.6 mm<sup>3</sup>, n=13).

An ANOVA revealed no differences in gonad volume of females among months (F=1.684, df=3, 34, P=0.188). One female from April showed an egg volume of 15.97 mm<sup>3</sup>, female egg volume then increased in May  $(203.63 \pm 48.2 \text{ mm}^3, n=14)$ , decreased June  $(75.9 \pm 36.3 \text{ mm}^3, n=14)$ , in and increased again in September (168.81±59.7  $mm^3$ , n=9). One female from April showed VF: of 13 females from May, four had NVF and nine contained eggs; in June, of 14 females, four had NVF, and seven showed VF; and in September, of nine females, three had NVF, one showed VF, and five contained eggs. Females with NVF (SVL,  $\bar{x}=45.3\pm$ 0.91 mm, n=11), VF ( $\bar{x}=45.8\pm0.66$  mm, n=10), and E ( $\bar{x}=46.7\pm mm$ , n=17) did not differ in SVL (F=0.998, df=2, 33, P=0.379).

#### Clutch size

Clutch size in VF ( $\bar{x}=3.2\pm0.32$ , n=9) and eggs ( $\bar{x}=3.5\pm0.42$ ) were not different (Mann-Whitney U-test, U=37.5, P=0.567). Clutch size pooled from both VF and eggs was  $3.4\pm0.29$  (2–8 eggs), with egg volume of  $302.11\pm31.5$  mm<sup>3</sup> (145.2–506.1 mm<sup>3</sup>). SVL of the females that contained VF and eggs did not significantly differ from each other (Mann-Whitney U-test, U=75.5, P=0.913). Clutch size was correlated with females' SVL (r=0.51, F=8.36, df=1, 25, P=0.008). Fat body mass was not different among months during reproductive activity for males (F=0.580, df=3, 25, P=0.634) or females (F=0.81, df=3, 22, P=0.503). A similar pattern occurred for liver mass in both males (F=1.9, df=3, 25, P=0.173) and females (F=0.407, df=3, 22, P=0.749).

#### DISCUSSION

We know practically nothing about the natural history of S. cozumelae (Lee, 1996). and thus, our study on sexual dimorphism and reproduction represents the only information on those topics for the species. It is well known that in the genus Sceloporus sexual size dimorphism can follow any of three patterns; male-biased, female-biased, or no dimorphism (Fitch, 1978; Ramírez-Bautista et al., 2013; Jiménez-Arcos et al., 2017). Males of S. cozumelae were larger than females in all analyzed characteristics. This pattern in sexual size dimorphism is the most common in species of Sceloporus (Fitch, 1978; Ramírez-Bautista et al., 2013). For example, in S. variabilis (Cruz-Elizalde et al., 2017), S. siniferus (Ramírez-Bautista et al., 2015), and S. aeneus (Ramírez-Bautista et al., 2016), males were larger than females.

Males of many lizard species of the Phrynosomatidae family are known to be territorial (Fitch, 1978), and they are usually larger in many morphological traits and often brighter in color pattern (belly, chest, and throat) than are females (e.g., *S. formosus*, Ramírez-Bautista and Pavón, 2009; *Urosaurus bicarinatus*, Ramírez-Bautista et al., 1995). These patterns of morphology and coloration (bright colors) differences between males and females in phrynosomatid species have been favored mainly by male-biased sexual selection (Olsson et al., 2002; García-Rosales et al., 2017). Males of *S. cozumelae* might follow the same pattern, at least in morphology, because they are territorial, but the color patch has been reported to be lost in males (Ossip-Drahos et al., 2016).

Our data on reproduction show that males and females of *S. cozumelae* are synchronized with respect to gonadic activity. This species belongs to the *Sceloporus variabilis* group, in which males are reproductively active throughout the whole year (Ramírez-Bautista et al., 2006; Cruz-Elizalde and Ramírez-Bautista, 2016). Minimum SVL at sexual maturity for males and females were similar (40 mm), which is smaller when compared to populations of *S. variabilis* (42– 57 mm) (Cruz-Elizalde and Ramírez-Bautista, 2016).

Male reproductive activity determined by high testes volume was observed during May, June, and September, a pattern similar to those found in populations of S. variabilis (Cruz-Elizalde and Ramírez-Bautista, 2016) and other species that display continuous reproduction, such as S. siniferus (Ramírez-Bautista et al., 2015). This continuous reproduction, as in many oviparous species, is related to the availability of food resources in the environment (Ballinger, 1979; Ramírez-Bautista and Vitt, 1997). In S. cozumelae, a high energetic cost would be invested in reproduction because minimum fat body size was in May and September. However, males showed the highest fat body and liver mass in June, which was the month of the reproductive peak. This pattern could also be related to and explained by the abundance and quality of food (insects) during the rainy season (Ballinger, 1977), at the beginning of June, as it is important for spermatogenesis, as well as vitellogenesis and embryonic development in females (Guillette and Casas-Andreu, 1987). Reproductive activity of females was similar to that of the males; i.e., synchronized. Females with VF were found in April, May, June, and September, and all females showed VF (in ovary) and eggs in the oviduct. Females produced the highest number of VF and eggs in May (9/13), June (10/14) and September (6/9) when fat body and liver mass decreased. Overall, continuous rain throughout the year with particularly high precipitation from June to October may lead to the high availability of food resources throughout the year and would enable males and females to have a long reproductive period, as occurs in other species of lizards (Méndez-de La Cruz et al., 1992; Ramírez-Bautista et al., 2006; Hernández-Salinas et al., 2010; Cruz-Elizalde and Ramírez-Bautista, 2016).

Females of S. cozumelae from this population had a mean clutch size of 3.4 eggs, which is similar to females in populations of S. variabilis (Benabib, 1994; Cruz-Elizalde and Ramírez-Bautista, 2016). However, this similarity in clutch size (3.3 eggs, Ramírez-Bautista and González-Romero, 1991; 3.4, García-Collazo et al., 1993; 3.4 and 4.3, Cruz-Elizalde and Ramírez-Bautista, 2016) varied by female SVL, with S. cozumelae being the smallest (Table 2). These results could be related to clutch frequencies, because females of S. variabilis have at least three clutches during the reproductive season (Cruz-Elizalde and Ramírez-Bautista, 2016), and female S. cozumelae very likely have at least two clutches each year, based on two females from our sample that had both eggs and vitellogenic follicles at the same time. Variations in clutch size and frequency have been found to be associated to the availability of food in the environment (Ballinger, 1977; Hernández-Salinas and Ramírez-Bautista, 2015). Small clutches in species with continuous reproduction are advantageous for females because they allow them to spread the reproductive effort over time and space, and

TABLE 2. Reproductive characteristics of females of *Sceloporus variabilis* from different populations (upper five) compared to *S. cozumelae* (Puerto Morelos).

Population	Snout-vent length (mm)	Clutch size	Reproductive season	Source
Bastonal	53.1±0.49 (44–68)	4.6±0.14 (3-7)	November-September	Benabib (1994)
Los Tuxtlas	56.6±0.35 (43.8-71)	3.7±0.11 (2–6)	January-December	Ramírez-Bautista et al. (2006)
Atlapexco	53.6±0.52 (45-63)	3.4±0.21 (2-5)	January-December	Cruz-Elizalde and Ramírez- Bautista (2016)
San Pablo Tetlapayac	52.7±0.51 (45-57)	4.3±0.28 (3–6)	January-September	Cruz-Elizalde and Ramírez- Bautista (2016)
Santa Catarina	54.5±0.57 (47-62)	3.4±0.24 (2-5)	January-December	Cruz-Elizalde and Ramírez- Bautista (2016)
Puerto Morelos	46.5±0.42 (40–52)	3.4±0.29 (2-8)	April–September	This study

consequently they increase the survival probabilities of the eggs and offspring (Anguilletta et al., 2001; Du et al., 2005). In many lizard species with continuous reproduction (multiple clutches), clutch size is not correlated with female SVL; for example, in Urosaurus bicarinatus (Ramírez-Bautista et al., 1995; Ramírez-Bautista and Vitt, 1998) and S. sini-(Ramírez-Bautista et al., ferus 2016). However, clutch size of S. cozumelae was correlated with female SVL, similar to other small-bodied lizards with continuous reproduction, such as S. aeneus (Ramírez-Bautista et al., 2016).

In summary, sexual size dimorphism of S. cozumelae is male-biased. Females and males reach sexual maturity at similar body size. Males and females are synchronized in their reproductive activity, indicating that this species presumably has continuous reproduction, similar to that observed in populations of S. variabilis, where females have multiple small clutches. Mean clutch size was similar to that in other female populations of S. variabilis with larger SVL, and mean clutch size was correlated with female SVL, a pattern that is not commonly observed in small-bodied species with continuous reproduction. Indeed, more studies on S. cozumelae are needed to fully understand their reproductive cycle, as well as on the rest of the species of the Sceloporus variabilis group. These studies could help us understand the extent of the role that phylogeny and the environment play in patterns of sexual dimorphism (Cox et al., 2003) and life history characteristics (Zamora-Abrego et al., 2007; Zuñiga-Vega et al., 2016) of populations and closely related species.

#### **ACKNOWLEDGMENTS**

We thank Victor Hugo Reynoso for permission to examine specimens under his care in the Colección Nacional de Anfibios y Reptiles, Instituto de Biología (CNAR-IBH), Universidad Nacional Autónoma de México. We thank to Edmundo Pérez Ramos for his logistic help and to Larry David Wilson for reviewing an early version of the manuscript. We thank the anonymous reviewers for greatly improving the manuscript. Finally, we thank Programa para el Desarrollo Profesional Docente (PRODEP) at Universidad Autónoma del Estado de Hidalgo for their support.

## LITERATURE CITED

- ANGUILLETTA, M, J., SEARS, M. W., AND WINTERS, R. S. 2001. Seasonal variation in reproductive effort and its effect on offspring size in the lizard Sceloporus undulatus. Herpetologica 57: 365–375.
- BALLINGER, R. E. 1977. Reproductive strategies: Food availability as a source of proximal variation in a lizard. *Ecology* 58: 628–635.
- BALLINGER, R. E. 1979. Intraspecific variation in demography and life history of the lizard *Sceloporus jarrovi* along an altitudinal gradient in

southeastern Arizona. Ecology 60: 901-909.

- BENABIB, M. 1994. Reproduction and lipid utilization of tropical populations of *Sceloporus variabilis*. *Herpetological Monographs* 8: 160–180.
- COX, R. M., SKELLY, S. L., AND JOHN-ADLER, H. B. 2003. A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution* 57: 1653–1669.
- CRUZ-ELIZALDE, R. AND 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.
- CRUZ-ELIZALDE, R., RAMÍREZ-BAUTISTA, A., AND LOZANO, A. 2017. Sexual size dimorphism among populations of the rose-bellied lizard *Sceloporus variabilis* (Squamata: Phrynosomatidae) from high and low elevations in Mexico. *Herpetological Journal* 27: 252–257.
- DU, W. G., JI, X., ZHANG, Y. P., XU, X. F., AND 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: 443–453.
- FITCH, H. S. 1970. Reproductive cycles in lizards and snakes. University of Kansas Museum of Natural History, Miscellaneous Publications 52: 1–247.
- FITCH, H. S. 1978. Sexual size differences in the genus Sceloporus. University of Kansas Science Bulletin 51: 441–461.
- GARCÍA-COLLAZO, R., ALTAMIRANO ÁLVAREZ, T., AND GÓMEZ SOTO, M. 1993. Reproducción continua en Sceloporus variabilis variabilis (Sauria: Phrynosomatidae) en Alvarado, Veracruz, México. Boletín de la Sociedad Herpetológica Mexicana 5: 51–59.
- GARCÍA-ROSALES, A., RAMÍREZ-BAUTISTA, A., STEPHENSON, B. P., MEZA-LÁZARO, R. N., AND NIETO-MONTES DE OCA, A. 2017. Comparative morphology and genetics of two populations of spiny lizards (genus *Sceloporus*) from Central Mexico. *Zoologischer Anzeiger* 267: 21–30.
- GUILLETTE, L. J. JR. AND CASAS-ANDREU, G. 1987. Reproductive biology of the high elevation mexican lizard *Barisia imbricata*. *Herpetologica* 43: 29–38.

- HERNÁNDEZ-SALINAS, U. AND RAMÍREZ-BAUTISTA, A. 2015. Variation in morphological and reproductive characteristics of females of *Anolis nebulosus* (Squamata: Dactyloidae) from island and mainland populations near the Pacific Coast of Mexico. *Acta Zoologica Hungary* 96: 428–435.
- HERNÁNDEZ-SALINAS, U., RAMÍREZ-BAUTISTA, A., LEYTE-MANRIQUE, A., AND SMITH, G. R. 2010. Reproduction and sexual dimorphism in two populations of *Sceloporus grammicus* (Sauria: Phrynosomatidae) from Hidalgo, México. *Herpetologica* 66: 12–22.
- HIERLIHY, C. A., GARCÍA-COLLAZO, R., CHAVEZ-TAPIA, C. B., AND 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. 2017. Anuario Estadístico y Geográfico de Yucatán, México. Instituto Nacional de Estadística y Geografía, Aguascalientes.
- JIMÉNEZ-ARCOS, V. H, SANABRIA-URBÁN, S., AND CUEVA DEL CASTILLO, R. 2017. The interplay between natural and sexual selection in the evolution of sexual size dimorphism in *Sceloporus* lizards (Squamata: Phrynosomatidae). *Ecology* and Evolution 7: 905–917.
- LEACHÉ, A. D., BANBURY, B. L., LINKEM, C. W., AND 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.
- LEE, J. C. 1996. *The Amphibians and Reptiles of the Yucatán Peninsula*. Cornell University Press, Ithaca.
- LOZANO, E. A., RAMÍREZ-BAUTISTA, A., AND URIBE, M. C. 2014. Oogenesis and ovarian histology in two populations of the viviparous lizard *Sceloporus grammicus* (Squamata: Phrynosomatidae) from the central Mexican plateau. *Journal of Morphology* 275: 949–960.
- LOZANO, A., URIBE, M. C., AND RAMÍREZ-BAUTISTA, A. 2015. Seasonal and continuous spermatogenesis in the viviparous lizard Sceloporus grammicus, a study of two populations in contrasting environments from the central Mexican plateau. Zoologischer Anzeiger 254: 72–85.

- MANRÍQUEZ-MORÁN, N. L., VILLAGRÁN-SANTA CRUZ, M., AND MÉNDEZ-DE LA CRUZ, F. R. 2013. Reproductive activity in females of the oviparous lizard Sceloporus aeneus. Southwestern Naturalist 58: 325–329.
- MÉNDEZ-DE LA CRUZ, F. R., CASAS-ANDREU, G., AND VILLAGRÁN-SANTA CRUZ, M. 1992. Variación anual en la alimentación y condición física de Sceloporus mucronatus (Sauria: Iguanidae) en la Sierra del Ajusco, Distrito Federal, México. Southwestern Naturalist 37: 349–355.
- METZGER, K. AND HERREL, A. 2005. Correlations between lizard cranial shape and diet: A quantitative, phylogenetically informed analysis. *Biological Journal of the Linnean Society* 86: 433– 466.
- OLSSON, M., SHINE, R., WAPSTRA, E., UJVARI, B., AND MADSEN, T. 2002. Sexual dimorphism in lizard body shape: The role of sexual selection and fecundity selection. *Evolution* 56: 1538– 1542.
- OSSIP-DRAHOS, A. G., OYOLA MORALES, J. R., VITAL-GARCÍA, C., ZÚÑIGA-VEGA, J. J., HEWS, D. K., AND MARTINS, E. P. 2016. Shaping communicative colour signals over evolutionary time. *Royal Society Open Science* 3: 160728.
- PÉREZ-MENDOZA, H. A. AND ZÚÑIGA-VEGA, J. J. 2014. A test of the fast-slow continuum model of life-history variation in the lizard Sceloporus grammicus. Evolutionary Ecology 16: 235–248.
- PÉREZ-MENDOZA, H. A., ZÚÑIGA-VEGA, J. J., ZURITA-GUTIÉRREZ, Y. H., FORNONI, J., SOLANO-ZAVALETA, I., HERNÁNDEZ-ROSAS, A. L., AND MOLINA-MOCTEZUMA, A. 2013. Demographic importance of the life-cycles components in *Sceloporus grammicus*. *Herpetologica* 69: 411–35.
- PINCHEIRA-DONOSO, D. AND HUNT, J. 2017. Fecundity selection theory: Concepts and evidence. *Biological Reviews* 92: 341–356.
- RAMÍREZ-BAUTISTA, A., CRUZ-ELIZALDE, R., HERNÁNDEZ-SALINAS, U., LOZANO, A., AND GRUMMER, J. A. 2017. Reproductive trait variation in the Sceloporus scalaris species group (Squamata: Phrynosomatidae) from the Transvolcanic Belt, Mexico. Biological Journal of the Linnean Society 122: 838–849.
- RAMÍREZ-BAUTISTA, A., GARCÍA-COLLAZO, R., AND GUILLETTE, L. J. JR. 2006. Reproductive, fat and

liver cycles of male and female rose-bellied lizards, *Sceloporus variabilis*, from coastal areas of southern Veracruz, México. *Southwestern Naturalist* 51: 163–171.

- RAMÍREZ-BAUTISTA, A. AND GONZÁLEZ-ROMERO, A. 1991. Notes on the reproduction of the rose belly lizard, *Sceloporus variabilis* (Sauria: Iguanidae) from Dos Bocas, Tabasco, México. *Bulletin of Chicago Herpetological Society* 26: 270–272.
- RAMÍREZ-BAUTISTA, A., LEYTE-MANRIQUE, A., MARSHALL, J. C., AND 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., LOZANO, A., HERNÁNDEZ-SALINAS, U., AND CRUZ-ELIZALDE, R. 2016. Female reproductive characteristics among populations of the oviparous lizard Sceloporus aeneus (Squamata: Phrynosomatidae) from central Mexico. Herpetologica 72: 196–201.
- RAMÍREZ-BAUTISTA, A., LURÍA-MANZANO, R., CRUZ-ELIZALDE, R., PAVÓN, N. P., AND WILSON, L. D. 2015. Variation in reproduction and sexual dimorphism in the long-tailed spiny lizard *Sceloporus siniferus* (Squamata: Phrynosomatidae) from the Southern Pacific Coast of Mexico. *Salamandra* 51: 73–82.
- RAMÍREZ-BAUTISTA, A. AND 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., SMITH, G. R., LEYTE-MANRIQUE, A., AND HERNÁNDEZ-SALINAS, U. 2013. No sexual dimorphism in the eastern spiny lizard, *Sceloporus spinosus*, from Guadalcázar, San Luis Potosí. *Southwestern Naturalist* 58: 505–508.
- RAMÍREZ-BAUTISTA, A., STEPHENSON, B. P., SERRANO MUÑOZ, C., CRUZ-ELIZALDE, R., AND HERNÁNDEZ-SALINAS, U. 2014. Reproduction and sexual dimorphism in two populations of the polymorphic spiny lizard *Sceloporus minor* from Hidalgo, México. *Acta Zoologica (Stockholm)* 95: 397–408.

- RAMÍREZ-BAUTISTA, A., URIBE-PEÑA, Z., AND GUILLETTE, L. J. JR. 1995. Reproductive biology of the lizard Urosaurus bicarinatus bicarinatus (Reptilia: Phrynosomatidae) from Río Balsas Basin, México. Herpetologica 51: 24–33.
- RAMÍREZ-BAUTISTA, A. AND VITT, L. J. 1997. Reproduction in the lizard *Anolis nebulosus* (Polychrotidae) from the Pacific coast of México. *Herpetologica* 53: 423–431.
- RAMÍREZ-BAUTISTA, A. AND VITT, L. J. 1998. Reproductive biology of Urosaurus bicarinatus (Sauria: Phrynosomatidae) from a tropical dry forest of México. Southwestern Naturalist 43: 381–390.
- ROITBERG, E. S., EPLANOVA, G. V., KOTENKO, T. I., AMAT, F., CARRETERO, M. A., KURANOVA, V. N., BULAKHOVA, N. A., ZINENKO, O. I., AND YAKOVLEV, V. A. 2015. Geographic variation of life-history traits in the sand lizard, *Lacerta agilis*: Testing Darwin's fecundity-advantage hypothesis. *Journal of Evolutionary Biology* 28: 613–629.
- SCHWARZ, R. AND MEIRI, S. 2017. The fast-slow life-history continuum in insular lizards: A comparison between species with invariant and variable clutch sizes. *Journal of Biogeography* 44: 2808–2815.
- TINKLE, D. W., WILBUR, H. M., AND TILLEY, S. G. 1970. Evolutionary strategies in lizard reproduction. *Evolution* 24: 55–74.
- VALDÉZ-GONZÁLEZ, M. A. AND 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.
- VALENCIA-LIMÓN, E. R., CASTRO-FRANCO, R., AND BUSTOS ZAGAL, M. G. 2014. Dimorfismo sexual y ciclo reproductor de *Sceloporus horridus horridus* (Wiegmann 1939) (Sauria: Phrynosomatidae). Acta Zoológica Mexicana 30: 91–105.
- WANG, Y., JI, W., ZHAO, W., YU, N., AND LIU, N. 2011. Geographic variation in clutch and egg size for the lizard *Phrynocephalus przewalskii* (Squamata: Agamidae). *Asian Herpetological Research* 2: 97–112.
- ZAMORA-ABREGO, J. G., ZÚÑIGA-VEGA, J. J., AND NIETO-MONTES DE OCA, A. 2007. Variation in reproductive traits within the lizard genus *Xeno*-

saurus. Journal of Herpetology 41: 630-637.

- ZAR, J. H. 2010. *Biostatistical Analysis. 5th Edition*, Prentice Hall, Upper Saddle River.
- ZÚÑIGA-VEGA, J. J., FUENTES-G, J. A., OSSIP-DRAHOS, A. G., AND MARTINS, E. P. 2016. Repeated evolution of viviparity in phrynosomatid lizards constrained interspecific diversification in some life history traits. *Biology Letters* 12: 20160653.
- ZÚÑIGA-VEGA, J. J., FUENTES-G, J. A., ZAMORA-ABREGO, J. G., GARCÍA-VÁZQUEZ, U. O., NIETO-MONTES DE OCA, A., AND MARTINS, E. P. 2017. Evolutionary patterns in life-history traits of lizards of the genus *Xenosaurus*. *Herpetological Journal* 27: 346–360.

Accepted: 24 October 2019

#### Appendix 1

Voucher numbers of the individuals of *Sceloporus cozumelae* used in this study. Specimens were obtained from Colección Nacional de Anfibios y Reptiles, Instituto de Biología, Universidad Nacional Autónoma de México.

Males: CNAR-IBH (4131, 4132, 5485, 5506, 5507, 5544, 5545, 6172, 6355, 7404, 7698, 7702, 7705, 7707, 05485-2, 05485-95, 05506-10, 05506-4, 05507-11, 05507-12, 05507-2, 05507-3, 05544-2, 05544-4, 05545-2, 05545-5. 05545-8, 05794-12, 05794-16. 05794-18, 4131-10, 4131-13. 4131-14, 4131-15, 4131-17, 4131-20, 4131-24, 4131-4, 4131-6, 4131-70, 4131-8, 6172-3, 6172-7, 6172-9, 6173-10, 6173-11).

Females: CNAR-IBH (5749, 5794, 6353, 6354, 7697, 7701, 05485-3, 05506-2, 05506-8, 05506-9, 05507-6, 05543-3, 05794-11, 05794-13, 05794-14, 05794-15, 05794-4, 05794-5, 05794-7, 06355-2, 06356-2, 06356-3, 4131-11, 4131-12, 4131-16, 4131-18, 4131-2, 4131-21, 4131-3, 4131-5, 4131-9, 5507-7, 6172-2, 6172-4, 6172-5, 6172-6, 6172-8, 7696-2).