Sexual Dimorphism and Feeding Ecology of the Black-bellied Bunchgrass Lizard Sceloporus aeneus (Squamata: Phrynosomatidae) in Central Mexico

Authors: Cruz-Elizalde, Raciel, Ramírez-Bautista, Aurelio, and Núñez de Cáceres-González, Francisco F.

Source: South American Journal of Herpetology, 18(1) : 46-55

Published By: Brazilian Society of Herpetology

URL: https://doi.org/10.2994/SAJH-D-18-00056.1

South American Journal of Herpetology, 18, 2020, 46–55

Sexual Dimorphism and Feeding Ecology of the Black-bellied Bunchgrass Lizard *Sceloporus aeneus* (Squamata: Phrynosomatidae) in Central Mexico

Raciel Cruz-Elizalde[1],*, Aurelio Ramírez-Bautista[2], Francisco F. Núñez de Cáceres-González[3]

[1] *Museo de Zoología "Alfonso L. Herrera", Facultad de Ciencias, Universidad Nacional Autónoma de México, A.P. 70–399, Ciudad de México CP 04510, México.*
[2] *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.
[3] *Laboratorio de Genética, 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.
* *Corresponding author. Email: cruzelizalde@gmail.com*

Abstract. Morphology and resource use have a significant influence on lizard population dynamics. In this study, sexual dimorphism and feeding ecology were assessed in a population of *Sceloporus aeneus* from central Mexico. Sexual dimorphism was recorded, with males being larger than females in several morphological characteristics, such as jaw width, femur length, tibia length, and forearm length, but not snout–vent length (SVL) or jaw length, which were similar in both sexes. The stomach contents analysis indicated an insectivorous diet composed of 11 prey categories, of which females consumed 11 and males consumed 9. Low values of feeding niche breadth were found, as well as high overlap between sexes and seasons. For the whole population, adult preys of the family Formicidae and orders Coleoptera and Hemiptera showed the highest values of food importance and abundance. A higher volume of stomach contents was recorded during the dry season than the wet season in both females and males. Results showed a pattern of sexual dimorphism similar to that of other species of the genus *Sceloporus,* but different from those of other populations of the same species. Morphological variation in jaw length and width seems to be related to food resources use because, in spite of the high similarity in the diet between sexes, the volume of stomach contents was not correlated with SVL in females. These findings suggest a constant consumption of food that is subsequently invested in reproduction. Further studies analyzing morphology and diet and their effect on reproductive characteristics such as clutch size, eggs mass, and volume are needed among populations of this species. The results obtained in this research could help explain the differences and similarities previously reported on the morphology and reproductive characteristics for *S. aeneus* and other species of the *S. scalaris* group.

Keywords. Body size; Diet; Niche overlap; Squamata; *Scalaris* group; Seasonal variation.

Resumen. La morfología y el uso de los recursos son dos factores que tienen influencia en la dinámica de las poblaciones de lagartijas. En este estudio, se determinó el dimorfismo sexual, así como la ecología alimentaria en una población de *Sceloporus aeneus* del centro de México. El dimorfismo sexual se sesgó hacia los machos, siendo estos más grandes que las hembras en varias características morfológicas, tales como el ancho de la mandíbula, longitud del fémur, longitud de la tibia y longitud del antebrazo, pero no en la longitud hocico-cloaca (LHC), y la longitud de la mandíbula, las que fueron similares en ambos sexos. Los análisis del contenido estomacal indicaron una dieta insectívora, compuesta por 11 categorías de presa, de las que las hembras consumieron 11 categorías y los machos nueve. Se reportaron bajos valores de amplitud de nicho alimentario, así como un alto solapamiento entre sexos y estaciones. Para la población, las presas adultas de la familia Formicidae, y de los órdenes Coleoptera y Hemiptera mostraron los mayores valores de importancia alimentaria, así como las mayores abundancias. Un alto volumen del contenido estomacal se registró durante la estación de secas, comparado con la de lluvias, tanto en hembras como machos. Los resultados mostraron un patrón de dimorfismo sexual similar a otras especies del género *Sceloporus,* pero distinta a otras poblaciones de la especie. La variación morfológica en el largo y ancho de la mandíbula, parece estar relacionada con el uso de recurso alimento, debido a que, a pesar de la alta similitud en la dieta entre sexos, el volumen del contenido estomacal no estuvo correlacionado con la LHC de las hembras. Estos hallazgos indican un consumo constante de alimento para luego invertir la energía en la reproducción. Se necesitan estudios adicionales que analicen la morfología y la dieta, así como sus efectos sobre las características reproductivas, como el tamaño de la puesta, y masa y volumen del huevo entre las poblaciones de esta especie. Los resultados obtenidos en este estudio proporcionan información para explicar las variaciones y similitudes previamente reportadas sobre morfología y características reproductivas de *S. aeneus,* así como para otras especies relacionadas del grupo *scalaris.*

INTRODUCTION

The genus *Sceloporus* Wiegmann, 1828 is composed of 97 species (Leaché et al., 2016). These species have shown high variation in ecological, morphological, and reproductive attributes (Benabib, 1994; Leyte-Manrique and Ramírez-Bautista, 2010; Zúñiga-Vega et al., 2016; García-Rosales et al., 2017) both at the intraspecific (Stephenson, 2010; García-Rosales et al., 2017) and the intrapopulation level (Ramírez-Bautista et al., 2008, 2014, 2016a, b).

With respect to lizard species (Cox et al., 2003, 2007), in the genus *Sceloporus* (Fitch, 1978; Jiménez-Ar-

How to cite this article: Cruz-Elizalde R., Ramírez-Bautista A., Cáceres-González F.F.N. Sexual dimorphism and feeding ecology of the black-bellied bunchgrass lizard *Sceloporus aeneus* (Squamata: Phrynosomatidae) in central Mexico. *South American Journal of Herpetology* 18: 46–55. http://doi.org/10.2994/SAJH-D-18-00056.1

Submitted: 09 August 2018
Accepted: 04 April 2019
Available Online: 31 December 2020

Handling Editor: Gabriel Costa
http://doi.org/10.2994/SAJH-D-18-00056.1

cos et al., 2017) morphological variation between sexes, also called sexual dimorphism, has been explained by two main hypotheses: (*i*) male-biased dimorphism by sexual selection, which gives advantages in male-male competition for territory and access to females (Endler and Houde, 1995) and (*ii*) female-biased dimorphism explained by fecundity advantage, where larger females are favored by natural selection (Du et al., 2005; Pincheira-Donoso and Hunt, 2017). A third hypothesis proposed by Rand (1967) and Schoener (1967) suggests that sexual dimorphism in lizards has evolved by intraspecific niche divergence, in which each sex is able to use the same or different resources with different degrees, such as food, microhabitat, and territory (Schoener, 1967; Hierlihy et al., 2013); however, this hypothesis has only been tested in a few studies (Herrel et al., 2001; Edwards et al., 2013).

According to Fitch (1978), the genus *Sceloporus* shows three patterns of sexual dimorphism that have been confirmed in recent years by several studies: (*i*) larger snout–vent length (SVL) in males than in females found in *S. torquatus* Wiegmann, 1828, *S. grammicus* Wiegmann, 1828, and *S. minor* Cope, 1885 (Feria-Ortíz et al., 2001; Hernández-Salinas et al., 2010; Ramírez-Bautista et al., 2014); (*ii*) larger female SVL than male SVL found in *S. undulatus* (Bosc and Daudin in Sonnini and Latrelle, 1801), *S. graciosus* Baird and Girard, 1852, and *S. virgatus* Smith, 1938 (Fitch, 1978; Cox and John-Alder, 2007); and (*iii*) lack of sexual dimorphism found in *S. taeniocnemis* Cope, 1885, *S. formosus* Wiegman, 1834, and *S. spinosus* Wiegmann, 1828 (Fitch, 1978; Ramírez-Bautista and Pavón, 2009; Ramírez-Bautista et al., 2013). Likewise, at the population level several studies have reported temporal (Ramírez-Bautista et al., 2016a) and geographic variation in sexual dimorphism (Valdéz-González and Ramírez-Bautista, 2002; Ramírez-Bautista et al., 2013). These patterns have been explained by the effect of sexual competition (Fitch, 1978; Ramírez-Bautista et al., 2008; Ramírez-Bautista and Pavón, 2009), different degrees of growth rate between sexes (Ruby and Dunham, 1984; Smith and Ballinger, 1994), fecundity (Olsson et al., 2002; Pincheira-Donoso and Hunt, 2017), and niche divergence (Camilleri and Shine, 1990; Hierlihy et al., 2013).

Morphological variation and sexual dimorphism can affect the ecology and behavior of individuals, mainly in the use of food resources (Edwards et al., 2013; Scali et al., 2016). This parameter is indispensable for maintenance and development, such as growth, reproduction, and tissue repair in lizard species (Vitt and Caldwell, 2009); therefore, the quantity and quality of consumed food are important parameters influencing these activities (Ballinger and Congdon, 1980). Use of food resources by both sexes and among populations are determined by food availability in the environment. Such availability might be influenced by the dry and wet seasons as well as intra-interspecific competition (Huey and Pianka, 1981; Ngo et al., 2015). For example, variation has been recorded in the diet composition between insular and mainland populations (Dutra et al., 2011; Hernández-Salinas et al., 2016) or among populations from different mainland environments (Parker and Pianka, 1975; Ngo et al., 2015). Likewise, diet type can vary in relation to type, size, and abundance of prey consumed between sexes and populations (Vitt and Colli, 1994; Herrel et al., 2001).

Sceloporus aeneus Wiegmann, 1828 is an endemic species of Mexico, oviparous, and of small size in SVL (47–50 mm). Its distribution occurs in the central and northern regions of the country, in the states of Puebla, Michoacán, Guanajuato, Morelos, Estado de México, Distrito Federal, and Hidalgo (Smith et al., 1993). It inhabits temperate environments from high elevation with vegetation types of pine, oak, and pine-oak forests (Sites et al., 1992). Studies carried out among populations of this species have shown similarities in reproductive characteristics, such as clutch size, egg mass, and volume (Rodríguez-Romero et al., 2002; Manríquez-Morán et al., 2013; Ramírez-Bautista et al., 2016b) as well as differences in minimum SVL at sexual maturity (Manríquez-Morán et al., 2013; Ramírez-Bautista et al., 2016a, b). Regarding sexual dimorphism, it has been reported that males show larger SVL than females (Ramírez-Bautista et al., 2016a). Despite showing similarities in reproductive characteristics and morphological variation among populations, there is no information to date on the use of food resources between sexes and/or seasons within a population. Such ecological studies are needed to determine possible interactions that could help interpret the variations/similarities of the reproductive and morphological attributes, which will also generate information on the feeding behavior of the species, and between sexes and seasons within the same population.

Therefore, the goal of this study was to analyze sexual dimorphism as well as feeding ecology between sexes and seasons of *Sceloporus aeneus* from central Mexico. The objectives comprised: (*i*) to analyze sexual dimorphism, (*ii*) to determine the diet in both females and males within seasons, (*iii*) to determine the degree of overlap of the food niche between sexes and seasons, and (*iv*) to determine the relationship between sizes (SVL) of the individuals and the volume and weight of stomach contents, as well as abundance of consumed prey. According to the hypothesis on variation of morphological characteristics previously found between sexes (Ramírez-Bautista et al., 2016a), we expected to find differences in the diet between sexes and seasons, as well as a low overlap in the use of food resources.

MATERIALS AND METHODS

Study area

The present study was carried out in the community of El Encinal (20°03′54.17″N, 98°12′21.99″W) located in the municipality of Cuautepec de Hinojosa, Hidalgo, Mexico. El Encinal is situated at an elevation of 2,474 m, presenting a vegetation type of pine-oak forest (Rzedowski, 1978). Mean annual temperature is 13.6°C, and the mean annual precipitation is 714.5 mm (Pavón and Meza Sánchez, 2009).

Field work

Samples were collected on 13 different dates in November 2008, February, April, June, and August 2009, and in April–November 2010 (seven samples were from the dry season, from January–May and October–December, and six from the wet season, from June–September). Capture of organisms was at 10:00–17:00 h in order to increase the possibility of finding individuals with food in their stomach. Specimens were captured under the collection permit SGPA/DGVS/02726/10 issued by Secretaría del Medio Ambiente y Recursos Naturales (SEMARNAT). Lizards were humanely euthanized in the laboratory by an intracelomic injection of sodium pentobarbital. This study was conducted according to the ethics and regulations for animal research of the Universidad Autónoma del Estado de Hidalgo and AVMA Guidelines on Euthanasia (AVMA, 2013), and Norma Oficial Mexicana NOM-033-SAG/ZOO-2014 (DOF, 2015), for handling specimens. Specimens were fixed in 10% formalin and then preserved in 70% ethanol (Ramírez-Bautista et al., 2014). All specimens were deposited at the collection of Amphibians and Reptiles of the Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo.

Morphological analyses

Morphological description and comparison were restricted to adult males and females. Males were regarded as adults if they had enlarged testes and convoluted epididymides consistent with sperm production (Lozano et al., 2015). Adult females were those with vitellogenic follicles in ovaries, or eggs in oviducts (unpublished data; Goldberg and Lowe, 1966; Ramírez-Bautista et al., 2016a, b). Morphological measures were: SVL (± 0.1 mm), jaw length (JL; ± 0.1 mm), jaw width (JW; ± 0.1 mm), femur length (FEL; ± 0.1 mm), tibia length (TL; ± 0.1 mm), and forearm length (FL; ± 0.1 mm).

Analysis of stomach contents

The stomachs of collected individuals were removed and weighed using an analytic balance (precision: 0.0001 g). The stomach contents were then placed in a Petri dish where length, width, and height were measured with a digital caliper. The same measurements were also taken for each prey category (Leyte-Manrique and Ramírez-Bautista, 2010). Different types of prey were identified at the taxonomic level of order using the dichotomous keys by Triplehorn and Johnson (2005). In the case of holometabolous individuals, they were classified as larvae and adult (Leyte-Manrique and Ramírez-Bautista, 2010; Gadsden et al., 2011). Likewise, within the order Hymenoptera, the family Formicidae was considered a different prey category because of its importance in the diet composition of other lizard species of the genus *Sceloporus* (Leyte-Manrique and Ramírez-Bautista, 2010; Gadsden et al., 2011). Plant material was also considered a prey category for the diet analysis (Feria-Ortíz et al., 2001).

Data analysis

An analysis of covariance (ANCOVA) was conducted to analyze sexual dimorphism. The function of the ANCOVA was to eliminate, through linear regressions, the effect of SVL (covariate) on the dependent variables (JL, JW, FEL, TL, and FL) and to check whether the regression slopes were different between sexes (factor; Zar, 2009). The data were presented as mean ± 1 SE.

To assess food importance, the relative index importance (I) of each category of the consumed prey was used. This index includes three parameters of the consumed prey (frequency, number, and volume; Biavati et al., 2004; Ngo et al., 2014). The formula is represented as I: $(\%F + \%N + \%V)/3$, where $\%F$ is the percentage of occurrence, $\%N$ the numerical percentage, and $\%V$ the volumetric percentage. The importance index (I) was calculated for each population, sex, and season (dry and wet). Likewise, the breadth and overlap of the food niche of the sexes and seasons were analyzed. The food niche breadth was measured with the standardized Levin's index by using the formula $B_A = ((1/\sum pi2)-1)/n\text{-}1$, where B_A is the measurement of niche breadth, pi is the proportion of each prey category with respect to the total number of prey found in each group (sex or season), and n is the number of prey category in the diet of individuals (Hurlbert, 1978). The overlap of eating habits between the sexes was analyzed with Pianka's index (1986): $O_{jk} = \sum pijPik/\sum pi^2j \sum pi^2k$, where O_{jk} represents the value of food niche overlap, and pij and Pik are the proportions of prey belonging to the first category (food groups) that were used by the organisms j and k (sexes or seasons, Gadsden and Palacios-Orona, 1997). Numbers of prey by sex and season were compared using a Mann-Whitney test (Zar, 2009). The breadth of the diet and diet overlap was determined for males, females, and for dry (January–May and October–December) and wet (June–September) seasons using the Ecological Methodology software v.7 (Krebs, 1999).

RESULTS

Sexual dimorphism

According to the results, females and males of *Sceloporus aeneus* showed sexual dimorphism, and males were larger in the morphological characteristics JW, FEL, TL, and FL, except in SVL and JL (Table 1). In size (SVL), females (48.55 ± 0.45; range 40.57–55.27, *n* = 47) were similar to males (49.48 ± 0.73; range 44.21–54.68, *n* = 20; *U* = 347, *P* = 0.091).

Diet

A total of 62 (42 females and 20 males) lizards were collected for the analyses of stomach contents. These lizards fed on a total of 783 prey items belonging to 11 categories (Table 2). The diet of *Sceloporus aeneus* (Table 2) was composed primarily of insects (70%), followed by arachnids (20%), and plant material (10%).

For the population estimate, the prey categories Formicidae, Coleoptera (adult; A), and Hemiptera showed the highest values of food importance (I), as well as being the most consumed prey in the population (Table 2). When diet was analyzed by sex, females consumed 11 prey categories, and males 9; however, no significant difference was found (*U* = 42.5, *P* = 0.250). According to the abundance of prey consumed, no significant difference was found (*U* = 42.5, *P* = 0.621) between males (38.22 ± 28.05) and females (39.90 ± 21.28; Table 2). The categories Formicidae, Coleoptera (A), and Hemiptera in females, and Orthoptera in males showed the highest values of I. For females, these values were 28.63, 23.62, and 22.62 for Formicidae, Coleoptera (A), and Hemiptera, respectively. In males, the values for Formicidae, Coleoptera (A), and Orthoptera were 44.64, 26.61, and 8.65, respectively (Table 2).

Diet composition by season

Diet composition showed similarity between seasons (*U* = 42, *P* = 0.838). In the dry season, a lower number of prey categories (eight) but more prey items (439) were found compared to the wet season (10 prey categories and 340 prey items; Table 3). The number of prey items consumed in the dry (54.87 ± 34.99) and the wet (34 ± 20.04) season did not differ significantly (*U* = 32, *P* = 0.505). For the dry season, the categories Formicidae, Hemiptera, Coleoptera (A), and Orthoptera showed the highest values of I (Table 3). For the wet season, the results revealed a

Table 1. Mean values ± 1 SE and range of morphological characteristics (SVL = snout–vent length, JW = jaw width, JL = jaw length, FEL = femur length, TL = tibia length, FL = forearm length) of adult female and male *Sceloporus aeneus* from El Encinal, Cuautepec de Hinojosa, Hidalgo, Mexico. Comparisons were made with ANCOVA with SVL as the covariate.

Morphological characteristics	**Female (*n* = 47)**	**Male (*n* = 20)**	**ANCOVA**		
			F	**df**	***P***
SVL	48.55 ± 0.45 (40.57–55.27)	49.48 ± 0.73 (44.21–54.68)			
JW	8.49 ± 0.21 (7.14–9.82)	9.41 ± 0.22 (6.89–10.78)	8.37	1, 64	0.005
JL	9.43 ± 0.22 (7.53–11.13)	10.03 ± 0.17 (8.51–11.11)	2.342	1, 64	0.132
FEL	8.39 ± 0.11 (6.86–9.99)	9.40 ± 0.19 (7.81–10.89)	21.01	1, 64	< 0.001
TL	9.83 ± 0.08 (8.25–10.77)	10.59 ± 0.17 (8.62–11.85)	18.15	1, 64	< 0.001
FL	7.66 ± 0.07 (6.48–8.61)	8.02 ± 0.12 (7.27–9.10)	4.67	1, 64	0.034

Table 2. Diet composition of the species, females, and males of *Sceloporus aeneus* from El Encinal, Cuautepec de Hinojosa, Hidalgo, Mexico. N = number of items, F = frequency of occurrence, and I = value of feeding importance. A = adult, L = larvae.

Prey Category	**Species (*n* = 62)**			**Female (*n* = 42)**			**Male (*n* = 20)**		
	N	**F**	**I**	**N**	**F**	**I**	**N**	**F**	**I**
Acari	1	1	0.25	1	1	0.38			
Aranae	17	16	4.94	12	12	5.96	5	4	3.13
Coleoptera (A)	137	48	24.52	87	31	23.62	50	17	26.61
Coleoptera (L)	14	6	4.68	7	4	4.44	7	2	5.08
Diptera	3	2	0.58	2	1	0.54	1	1	0.70
Hemiptera	54	24	16.39	44	17	22.62	10	7	5.85
Hymenoptera	31	10	4.19	29	8	5.94	2	2	1.44
Formicidae	497	31	34.91	238	19	28.63	259	12	44.64
Lepidoptera (L)	2	1	0.31	2	1	0.45			
Orthoptera	11	11	4.57	5	5	2.35	6	6	8.65
Plant material	16	16	4.64	12	12	5.06	4	4	3.90
Total	**783**	**166**		**233**	**43**		**344**	**55**	

Table 3. Diet composition of *Sceloporus aeneus* from El Encinal per season (Dry [January–June and October–December] and Wet [July–September]). *n* = number of items, I = Value of feeding importance. A = adult, L = larvae.

Sex	**Female**				**Male**			
Season	**Dry**		**Wet**		**Dry**		**Wet**	
Prey Category/Values	***n***	**I**	***n***	**I**	***n***	**I**	***n***	**I**
Acari			1	0.69				
Aranae	2	2.14	10	10.39	3	2.91	2	3.45
Coleoptera (A)	29	14.17	58	37.23	29	29.03	21	25.38
Coleoptera (L)			7	10.87			7	10.37
Diptera	2	1.20			1	1.24		
Hemiptera	33	33.33	11	6.97	6	6.48	4	4.81
Hymenoptera	24	9.22	5	3.59	1	1.31	1	1.64
Formicidae	135	31.44	103	25.73	160	42.46	99	45.41
Lepidoptera (L)			2	0.85				
Orthoptera	1	1.35			4	13.91	2	3.83
Plant material	7	7.15	5	3.68	2	2.67	2	5.12
Total	**233**		**202**		**206**		**138**	

very similar composition of prey categories to those of the dry season (Formicidae, Coleoptera [A], and Orthoptera); however, the category Coleoptera (larva; L) also recorded high values of I (Table 3).

Breadth and overlap of dietary niche

The food niche breadth was higher in females ($B = 0.186$) than males ($B = 0.087$). Seasonally, females showed similar values in both dry and wet seasons (dry, $B = 0.230$; wet, $B = 0.235$), whereas males had lower breadth values than females, but these values were higher in the wet season ($B = 0.121$) than the dry season ($B = 0.086$). According to the food niche overlap, a high value of $O_{jk} = 0.972$ was shown between sexes. These high values of overlap were also recorded between seasons for females ($O_{jk} = 0.935$) and males ($O_{jk} = 0.997$).

Variation in stomach content, number of prey items, and correlation analyses

There were no differences with respect to stomach content volume (females: 1,332.6 ± 362.44 mm^3; males: 1,202.55 ± 351.18 mm^3; $U = 407$, $P = 0.850$), or in the consumed prey (females: 4.59 ± 1.44; males: 9.21 ± 3.98, $U = 382.5$, $P = 0.803$) between sexes.

Considering the dry and wet seasons, differences were found in stomach content volume ($U = 193.5$, $P = 0.001$) and number of prey consumed by season ($U = 252.5$, $P = 0.034$), with a higher volume and abundance in the dry season (2,649.8 ± 742.52 mm^3; 9.33 ± 3.56) than in the wet season (690.09 ± 137.48 mm^3; 4.65 ± 1.68). By sex and seasons, females showed a larger volume of stomach contents in the dry season (3,302.15 ± 1150.58 mm^3) than in the wet season (633.72 ± 156.49 mm^3; $U = 55$, $P = 0.001$), as well as a higher number of prey items (dry, 6.81 ± 3.23; wet, 3.80 ± 1.58; $U = 102$, $P = 0.05$). In males, there were no significant differences in the volume of stomach contents (dry: 1,976.29 ± 831.29 mm^3; wet: 835.71 ± 288.76 mm^3; $U = 28$, $P = 0.253$) nor in the number of consumed prey between seasons (dry: 13.28 ± 7.78; wet: 6.83 ± 4.51; $U = 32$, $P = 0.422$).

The correlation between SVL of the individuals and volume of stomach contents did not show statistical significance in females ($r = 0.252$, $P = 0.151$; Fig. 1A); however, a significant negative correlation occurred in males ($r = -0.588$, $P = 0.006$; Fig. 1B). A similar pattern was observed in mass (weight) of stomach contents for females ($r = 0.213$, $P = 0.174$; Fig. 1C) and males ($r = -0.673$, $P = 0.001$; Fig. 1D).

DISCUSSION

Sceloporus aeneus, like other species of the genus, shows male-biased sexual dimorphism (Fitch, 1978; Ramírez-Bautista et al., 2016a; Jiménez-Arcos et al., 2017). This pattern is similar to that of other small-sized species, such as *S. gadoviae* Boulenger, 1905 (Lemos-Espinal et al., 1999), *S. siniferus* Cope, 1870 (Hierlihy et al., 2013; Ramírez-Bautista et al., 2015), and *S. variabilis* Wiegmann, 1834 (Ramírez-Bautista et al., 2006; Cruz-Elizalde et al., 2017).

Males of *Sceloporus aeneus* showed sexual dimorphism in dimensions of the jaws and limbs, but not in SVL or JL (see Table 1). This pattern of sexual dimorphism is similar to that found in other populations of the same species from central Mexico (Ramírez-Bautista et al., 2016a). As in other species of the genus, in addition to the morphological characteristics, sexual dimorphism can be expressed in other attributes such as color pattern (Stephenson and Ramírez-Bautista, 2012; Jiménez-Arcos

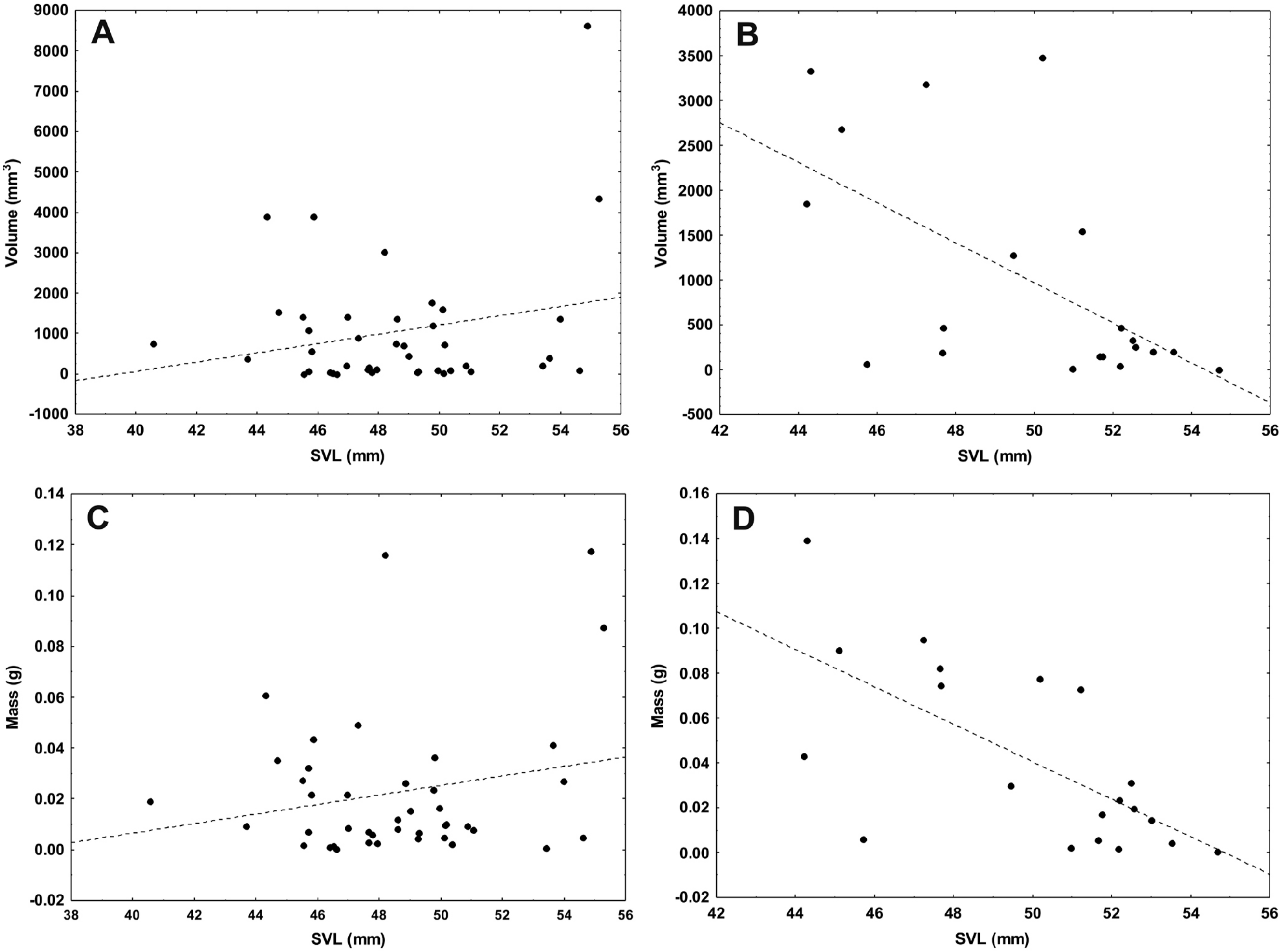

Figure 1. Relationships between snout–vent length (SVL) and volume of stomach contents of females **(A)** and males **(B)**, and SVL vs. mass of stomach content in females **(C)** and males **(D)**.

et al., 2017). Males of *S. aeneus* show more conspicuous ventral and gular patches than females (Smith et al., 1993). This color pattern has been evaluated for species that lack sexual dimorphism in body size like *S. torquatus* (Feria-Ortíz et al., 2001), *S. formosus* (Ramírez-Bautista and Pavón, 2009), and *S. spinosus* (Ramírez-Bautista et al., 2013). These color patterns are used by males for intra-interspecific recognition, care, and defense of territory and courtship (Martins, 1994; Cox et al., 2003; García-Rosales et al., 2017).

Despite not showing significant differences in SVL and JL between sexes, the rest of the analyzed characteristics varied, with the males having the greatest morphological dimensions. These results can be explained by the sexual selection hypothesis (Cox et al., 2003, 2007), because the greatest dimensions in the jaw (or the head) give an advantage in the male-male combat to gain access to the females and in the defense of the territory (Fitch, 1978; Cox et al., 2003). This pattern occurs in other species of the genus such as *Sceloporus minor* (Ramírez-Bautista et al., 2014) and *S. grammicus* (Hernández-Salinas et al., 2010; Bastiaans et al., 2014), as well as in other lizard species like *Zootaca vivipara* (Lichtenstein, 1823) (Gvozdik and Van Damme, 2003) and *Lacerta agilis* Linnaeus, 1758 (Borczyk et al., 2014). In this sense, intersexual competition (Fitch, 1978; Ramírez-Bautista et al., 2008; Ramírez-Bautista and Pavón, 2009), unlike fecundity (Olsson et al., 2002) and different growth rates in each sex (Ruby and Dunham, 1984; Cox and John-Adler, 2007), may be determining the morphological differences between the sexes of this species (Ramírez-Bautista et al., 2016a).

Morphological variation can be influenced by diverse factors, such as sexual selection (Fitch, 1978; Cox et al., 2003), competition (Parker and Pianka, 1975; Olsson et al., 2002), or use of resources (Scali et al., 2016). Therefore, this morphological variation is highly related to the ecology and reproductive characteristics of the individuals, which is also reflected in the use of food resources (Miles et al., 2007). The analyzed population of *Sceloporus aeneus* showed an insectivore diet, similar to other species of the genus, like *S. grammicus* (Leyte-Manrique and Ramírez-Bautista, 2010) and *S. jarrovii* Cope in Yarrow, 1875 (Gadsden et al., 2011), as well as other lizard species such as *Eutropis multifasciata* (Kuhl, 1820) (Ngo et al., 2014), *Anolis nebulosus* (Wiegmann, 1834) (Hernández-Salinas et al., 2016), *Xenosaurus mendozai* Nieto-Montes de Oca et al., 2013 (Zamora-Abrego and Ortega-León, 2016), and *Tropidurus torquatus* (Wied, 1821) (Siqueira et al., 2013).

The main prey categories consumed by *Sceloporus aeneus* were from the Formicidae family and the orders Hemiptera and Coleoptera (A), which coincides with the diet patterns of other species of the genus like *S. grammicus* (Leyte-Manrique and Ramírez-Bautista, 2010) and *S. jarrovii* (Gadsden et al., 2011). These results are also similar to those reported for other species from temperate environments of central Mexico, such as *S. mucronatus* Cope, 1885 (Méndez-de La Cruz et al., 1992) and *S. torquatus* (Feria-Ortíz et al., 2010). Diet composition may be influenced by the foraging mode of the species, which are classified as "sit and wait" (Huey and Pianka, 1981; Reilly et al., 2007), a characteristic of the genus *Sceloporus*. In addition, diet might also be determined by the availability of the resources in the environment (Ballinger and Ballinger, 1979) because variation in precipitation or temperature modifies the biomass of the food that lizards can consume (Ballinger, 1977; Benabib, 1994).

Diet composition similar to that indicated above has been observed in other lizard species of the same genus, such as *Sceloporus gadoviae, S. horridus* Wiegmann, 1834, *S. jalapae* Günther, 1890 (Serrano-Cardozo et al., 2008), *S. grammicus* (Leyte-Manrique and Ramírez-Bautista, 2010), and *S. jarrovii* (Gadsden et al., 2011), and in species of a different genus, such as *Xenosaurus mendozai* (Zamora-Abrego and Ortega-León, 2016). In these species, seasonal changes in diet have been reported in relation to prey availability of Hymenoptera, Formicidae, Coleoptera, or Hemiptera, whose abundances are influenced by rains or droughts throughout the year. The latter results in a diet composition that is significantly shaped by the occurrence and abundance of the available categories in the environment (Ballinger and Ballinger, 1979). This pattern of seasonal change might also occur in this population of *S. aeneus,* because even though they consumed a smaller number of prey categories (8) in the dry season than in the wet season (10), total abundance of prey was greater in the dry period than during the rains, and no significant difference was found. Ballinger and Ballinger (1979) pointed out that the differences in the number of consumed prey by season might be affected by the low availability of prey in the environment, especially of prey that are gregarious such as ants, hemipterans, and coleopterans. Therefore, individuals in the population would consume a high number of prey of small size, such as ants, to compensate for the nutritional value that larger prey can provide, such as members of Coleoptera or Lepidoptera (Maury, 1995; Gadsden et al., 2011).

Similarly, an increase in the volume of stomach contents, as well as the consumption of a higher number of prey categories, might be related to the different phases of the reproductive period, and, thus, to the different types of diet between sexes. For example, in viviparous species such as *Sceloporus mucronatus* (Méndez-de La Cruz et al., 1992), *S. torquatus* (Feria-Ortíz et al., 2001), and *S. jarrovii* (Gadsden and Estrada-Rodríguez, 2008) the lowest volume of stomach content in females coincides with the gestation period; therefore, the embryos would displace the stomach of the lizards and occupy more space inside the females. When neonates are born, the production of progesterone in the females decreases (Crews and Garrick, 1980) and feeding increases, as does the volume of stomach contents (Méndez-de La Cruz et al., 1992). With regard to *S. aeneus,* it has been reported that different populations in central Mexico produce at least two clutches (frequencies) during the reproductive season (Rodríguez-Romero et al., 2002; Manríquez-Morán et al., 2013; Ramírez-Bautista et al., 2016b). This reproductive pattern allows females to consume a constant volume of food, and this consumption rate can be increased and converted to energy invested in reproduction, as has been observed in oviparous species like *S. variabilis* (Benabib, 1994). These results might explain the higher value reported for breadth of food niche in females than in males at the population and season level, and the higher volume of stomach contents in the dry season and previous to the months of the reproductive activity of the females (April–September; Ramírez-Bautista et al., 2016b); also, no correlation was observed between female SVL and volume of stomach contents. The above indicates that the females might feeding continuously throughout the year (Benabib, 1994) and investing energy on egg production (clutch size, egg mass and volume) without significant changes among reproductive periods or populations (Manríquez-Morán et al., 2013; Ramírez-Bautista et al., 2016a, b).

In males, the diet was composed of a smaller number of categories, but with greater abundance of prey consumed than in females, until no significant difference was found. Similar pattern has been reported for other species, such as *Anolis nebulosus* (Lister and Aguayo, 1992), *A. humilis* Peters, 1863 (Parmerlee and Guyer, 1995), and *A. polylepis* Peters, 1874 (Perry, 1996). This result may be due to the fact that reproduction in males of *Sceloporus aeneus* represents a higher energy cost, mainly for defense of territory and access to females (Martori and Aun, 1997). This energy cost is compensated by feeding on a smaller number of prey but containing a higher nutritional value, such as members of Orthoptera or Coleoptera (Maury, 1995). In addition, the foraging time invested by males can be different from that of females, which modifies the number of prey consumed, as well as the values of breadth of food niche between seasons (Perry, 1996; Hierlihy et al., 2013).

Sceloporus aeneus, like other species of the *S. scalaris* group (Benabib et al., 1997; Rodríguez-Romero et al., 2002; Leaché et al., 2016), maintains similar characteristics among its populations, such as body size (SVL; Rodríguez-Romero et al., 2002; Ramírez-Bautista et al., 2016a), reproductive characteristics (Manríquez-Morán et al., 2013; Ramírez-Bautista et al., 2016a, b), and ecological characteristics (Smith et al., 1993; Benabib et al., 1997; Rodríguez-Romero, 1999). The absence of sexual dimorphism with respect to body size (SVL) recorded in this study was different to the general pattern reported in the genus *Sceloporus,* where males are larger than females in SVL (Fitch, 1978; Jiménez-Arcos et al., 2017). However, in this study the rest of the morphological structures (mandibular and body extremities) coincide with male-biased dimorphism in the genus (Fitch, 1978; Wiens, 1999). Morphological differences can influence other activities, such as the use of available resources both at the intrapopulation and interpopulation level; therefore, alongside analyzing the use of food resources between sexes and seasons, further studies are needed aiming to evaluate different populations of single species, as well as the effect of food on reproductive characteristics (e.g., clutch size, egg mass and volume; Hernández-Salinas et al., 2016), growth rate (Ballinger and Congdon, 1980; Duncan et al., 2015), and cranial morphology (Herrel et al., 2008; Edwards et al., 2013).

ACKNOWLEDGMENTS

The authors thank Itzel Magno Benitez, Uriel Hernández Salinas, Osiel Barrera Hernández, and Gustavo Rivas for their help in the field and laboratory work. We also thank two anonymous reviewers for their helpful comments. This research was supported by project Fomix-CONACyT-191908 Biodiversidad del Estado de Hidalgo-3a.

REFERENCES

AVMA (American Veterinary Medical Association). 2013. Guidelines for the Euthanasia of Animals. Accessible at www.avma.org/KB/Policies/Documents/euthanasia.pdf. Accessed: 15 June 2018.

Baird S.F., Girard C. 1852. Characteristics of some new reptiles in the Museum of the Smithsonian Institution. *Proceedings of the American Philosophical Society* 6:68–70.

Ballinger R.E. 1977. Reproductive strategies: food availability as a source of proximal variation in a lizard. *Ecology* 58:628–635. DOI

Ballinger R.E., Ballinger R.A. 1979. Food resource utilization during periods of low and high food availability in *Sceloporus jarrovi* (Sauria: Iguanidae). *The Southwestern Naturalist* 24:347–363.

Ballinger R.E., Congdon J.D. 1980. Food resource limitation of body growth rates in *Sceloporus scalaris* (Sauria: Iguanidae). *Copeia* 1980:921–923. DOI

Bastiaans E., Bastiaans M.J., Morinaga G., Gaytán J.G.C., Marshall J.C., Bane B., … Sinervo B. 2014. Female preference for sympatric vs. allopatric male throat color morphs in the mesquite lizard (*Sceloporus grammicus*) species complex. *PLoS One* 9:e93197. DOI

Benabib M. 1994. Reproduction and lipid utilization of tropical population of *Sceloporus variabilis. Herpetological Monographs* 8:160–180. DOI

Benabib M., Kjer K.M., Sites J.W. Jr. 1997. Mitochondrial DNA sequence-based phylogeny and the evolution of viviparity in the *Sceloporus scalaris* group (Reptilia, Squamata). *Evolution* 51:1262–1275. DOI

Biavati G.M., Wiederhecker H.C., Colli G.R. 2004. Diet of *Epipedobates flavopictus* (Anura: Dendrobatidae) in Neotropical Savanna. *Journal of Herpetology* 38:510–518. DOI

Borczyk B., Kusznierz J., Paśko Ł., Turniak E. 2014. Scaling of the sexual size and shape skull dimorphism in the sand lizard (*Lacerta agilis* L.). *Vertebrate Zoology* 64:221–227.

Boulenger G.A. 1905. Descriptions of new reptiles discovered in Mexico by Dr. H. Gadow, F.R.S. *Proceedings of the Zoological Society London* 1905:245–247. DOI

Camilleri C., Shine R. 1990. Sexual dimorphism and dietary divergence: differences in trophic morphology between male and female snakes. *Copeia* 1990:649–658. DOI

Cope E.D. 1870. Seventh contribution to the herpetology of tropical America. *Proceedings of the American Philosophical Society* 11:147–169.

Cope E.D. 1885. A contribution to the herpetology of Mexico. *Proceedings of the American Philosophical Society* 22: 379–404.

Cox R.M., John-Alder H.B. 2007. Growing apart together: the development of contrasting sexual size dimorphisms in sympatric *Sceloporus* lizards. *Herpetologica* 63:245–257. DOI

Cox R., Skelly S.L., John-Alder H.B. 2003. A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution* 57:1653–1669. DOI

Cox R.M., Butler M.A., John-Alder H.B. 2007. The evolution of sexual size dimorphism in reptiles. Pp. 38–49, in Fairbairn D.J., Blanckenhorn W.U., Székely T. (Eds.), Sex, Size & Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford University Press, Oxford. DOI

Crews D., Garrick L.D. 1980. Methods of inducing reproduction in captive reptiles. Pp. 49–70, in Murphy J.B., Collins J.T. (Eds.), Reproductive Biology and Diseases of Captive Reptiles. Society for the Study of Amphibians and Reptiles, Lawrence.

Cruz-Elizalde R., Ramírez-Bautista A., 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.

DOF (Diario Oficial de la Federación). 2015. NORMA Oficial Mexicana NOM-033-SAG/ZOO-2014. Métodos para dar muerte a los animales domésticos y silvestres. Accessible at: https://www.gob.mx/profepa/documentos/norma-oficial-mexicana-nom-033-sag-zoo-2014-metodos-para-dar-muerte-a-los-animales-domesticos-y-silvestres. Accessed: 21 June 2014.

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* 85:443–453. DOI

Duncan C.A., Jetzt A.E., Cohick W.S., John-Alder H.B. 2015. Nutritional modulation of IGF-1 in relation to growth and body condition in *Sceloporus* lizards. *General and Comparative Endocrinology* 216:116–124. DOI

Dutra F., Siqueira C.C., Vrcibradic D., Kiefer M.C., Rocha C.F.D. 2011. Plant consumption of insular and mainland populations of a tropical lizard. *Herpetologica* 67:32–45. DOI

Edwards S., Tolley K.A., Vanhooydonck B., Measey G.J., Herrel A. 2013. Is dietary niche breadth linked to morphology and performance in Sandveld lizards *Nucras* (Sauria: Lacertidae)? *Biological Journal of the Linnean Society* 110:674–688. DOI

Endler J.A., Houde A.E. 1995. Geographic variation in female preferences for male traits in *Poecilia reticulata*. *Evolution* 49:456–468. DOI

Feria-Ortiz M., Nieto-Montes de Oca A., Salgado-Ugarte I.H. 2001. Diet and reproductive biology of the viviparous lizard *Sceloporus torquatus torquatus* (Squamata: Phrynosomatidae). *Journal of Herpetology* 35:104–112. DOI

Fitch H.S. 1978. Sexual size differences in the genus *Sceloporus*. *University of Kansas Science Bulletin* 561:441–461. DOI

Gadsden H., Estrada-Rodríguez J.L. 2008. Demography of the yarrow's spiny lizard *Sceloporus jarrovii* from the central Chihuahuan desert. *Western North American Naturalist* 68:46–57. DOI

Gadsden H.E., Palacios-Orona L.E. 1997. Seasonal dietary patterns of the Mexican fringe-toed (*Uma paraphygas*). *Journal of Herpetology* 31:1–9. DOI

Gadsden H., Estrada-Rodríguez J.L., Quezada-Rivera D.A., Leyva-Pacheco S.V. 2011. Diet of the yarrow's spiny lizard *Sceloporus jarrovii* in the Central Chihuahuan Desert. *The Southwestern Naturalist* 56:89–94. DOI

García-Rosales A., Ramírez-Bautista A., Stephenson B.P., Meza-Lázaro R.N., 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. DOI

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. DOI

Günther A.C.L.G. 1885. Reptilia and Batrachia. Biologia Centrali-Américana. Taylor & Francis, London. DOI

Gvozdík L., Van Damme R. 2003. Evolutionary maintenance of sexual dimorphism in head size in the lizard *Zootaca vivipara:* a test of two hypotheses. *Journal of Zoology* 259:7–13. DOI

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. DOI

Hernández-Salinas U., Ramírez-Bautista A., Cruz-Elizalde R. 2016. Variation in feeding habits of the arboreal lizard *Anolis nebulosus* (Squamata: Dactyloidae) from island and mainland populations in Mexican Pacific. *Copeia* 104:831–837. DOI

Herrel A., De Grauw E., Lemos-Espinal J.A. 2001. Head shape and bite performance in xenosaurid lizards. *Journal of Experimental Zoology* 290:101–107. DOI

Herrel A., Huyghe K., Vanhooydonck B., Backeljau T., Breugelmans K., Grbac I., … Irschick D.J. 2008. Rapid large-scale evolutionary divergence in morphology and performance associated with exploitation of a different dietary resource. *Proceedings of the National Academy of Sciences of the United States of America* 105:4792–4795. DOI

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.

Huey R.B., Pianka E.R. 1981. Ecological consequences of foraging mode. *Ecology* 62:991–999. DOI

Hurlbert S.H. 1978. The measurement of niche overlap and some relatives. *Ecology* 59:67–77. DOI

Jiménez-Arcos V.H., Sanabria-Urbán S., 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. DOI

Krebs C.J. 1999. Ecological Methodology, Version 7. Available from: http://www.exetersoftware.com/cat/ecometh/ecomethodology.html.

Kuhl H. 1820. Beiträge zur Zoologie und vergleichenden Anatomie. Hermannsche Buchhandlung, Frankfurt. DOI

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. DOI

Lemos-Espinal J.A., Smith G.R., Ballinger R.E. 1999. Reproduction in Gadow's spiny lizard, *Sceloporus gadoviae* (Phrynosomatidae), from arid tropical México. *The Southwestern Naturalist* 44:57–63.

Leyte-Manrique A., Ramírez-Bautista A. 2010. Diet of two populations of *Sceloporus grammicus* (Squamata: Phrynosomatidae) from Hidalgo, Mexico. *The Southwestern Naturalist* 55:98–103. DOI

Lichtenstein H. 1823. Verzeichniss der Doubletten des zoologischen Museums der Königl. Universität zu Berlin nebst Beschreibung vieler bisher unbekannter Arten von Säugethieren, Vögeln, Amphibien und Fischen. Königl. T. Trautwein, Berlin. DOI

Linnaeus C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differential, synonymis, locis, Tomus I. Editio decima, reformata. Laurentiis Salvii, Holmiae. DOI

Lister B.C., Aguayo A.G. 1992. Seasonality, predation, and the behaviour of a tropical mainland anole. *Journal of Animal Ecology* 61:717–733. DOI

Lozano A., Uribe M.C., 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. DOI

Manríquez-Morán N.L., Villagrán-Santa Cruz M., Méndez-de la Cruz F.R. 2013. Reproductive activity in females of the oviparous lizard *Sceloporus aeneus*. *The Southwestern Naturalist* 58:325–329. DOI

Martins E.P. 1994. Phylogenetic perspectives on the evolution of lizard territoriality. Pp. 117–144, in Vitt L.J., Pianka E.R. (Eds.), Lizard Ecology: Historical and Experimental perspectives. Princeton University Press, Princeton. DOI

Martori R.A., Aún L. 1997. Reproduction and fat body cycle of *Liolaemus wiegmannii* in central Argentina. *Journal of Herpetology* 31:578–581. DOI

Maury M.E. 1995. Diet composition of the greater earless lizard (*Cophosaurus texanus*) in the central Chiuhahuan Desert. *Journal of Herpetology* 29:266–272. DOI

Méndez-de La Cruz F.R., Casas-Andreu G., 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. *The Southwestern Naturalist* 37:349–355. DOI

Miles D.B., Losos J.B., Irschick D.J. 2007. Morphology, performance, and foraging mode. Pp. 49–93, in Reilly S.M., McBrayer L.D., Miles D.B. (Eds.), Lizard Ecology: The Evolutionary Consequences of Foraging Mode. Cambridge University Press, Cambridge.

Ngo C.D., Ngo B.V., Truong P.B., Duong L.D. 2014. Sexual size dimorphism and feeding ecology of *Eutropis multifasciata* (Reptilia: Squamata: Scincidae) in the Central Highlands of Vietnam. *Herpetological Conservation and Biology* 9:322–333.

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. DOI

Nieto-Montes de Oca A., García-Vázquez UO, Zúñiga-Vega J., Schmidt-Ballardo W. 2013. A new species of *Xenosaurus* (Squamata: Xenosauridae) from the Sierra Gorda Biosphere Reserve of Querétaro, Mexico. *Revista Mexicana de Biodiversidad* 84:485–498.

Olsson M., Shine R., Wapstra E., Ujvari B., Madsen T. 2002. Sexual dimorphism in lizard body shape: The role of sexual selection and fecundity selection. *Evolution* 56:1538–1542. DOI

Parker W.S., Pianka E.R. 1975. Comparative ecology of populations of the lizard *Uta stansburiana*. *Copeia* 1975:615–632. DOI

Parmerlee J.R., Guyer C. 1995. Sexual differences in foraging behavior of an anoline lizard, *Norops humilis*. *Journal of Herpetology* 29:619–621. DOI

Pavón N.P., Meza Sánchez M. 2009. Cambio Climático en el Estado de Hidalgo: Clasificación y Tendencias Climáticas. Universidad Autónoma del Estado de Hidalgo, Pachuca.

Perry G. 1996. The evolution of sexual dimorphism in the lizard *Anolis polylepis* (Iguania): evidence from intraspecific variation in foraging behavior and diet. *Canadian Journal of Zoology* 74:1238–1245. DOI

Peters W.C.H. 1863. Über einige neue Arten der Saurier-Gattung Anolis. Monatsberichte der Königlichen Preussische Akademie des Wissenschaften zu Berlin 1864:135–149.

Peters W.C.H. 1874. Über neue Saurier (Spæriodactylus, Anolis, Phrynosoma, Tropidolepisma, Lygosoma, Ophioscincus) aus Centralamerica, Mexico und Australien. Monatsberichte der Königlichen Preussische Akademie des Wissenschaften zu Berlin 1873:738–747.

Pianka E.R. 1986. Ecology and Natural History of Desert Lizards. Princeton University Press, Princeton. DOI

Pincheira-Donoso D., Hunt J. 2017. Fecundity selection theory: concepts and evidence. *Biological Reviews* 92:341–356. DOI

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. DOI

Ramírez-Bautista A., García-Collazo R., 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. *The Southwestern Naturalist* 51:163–171.

Ramírez-Bautista A., Ramos-Flores O., Stephenson B.P., Smith G.R. 2008. Reproduction and sexual dimorphism in two populations of *Sceloporus minor* of the Guadalcázar Region, San Luis Potosí, México. *The Herpetological Journal* 18:121–127.

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 Potosi, Mexico. *The Southwestern Naturalist* 58:505–508. DOI

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 Zoológica* 95:397–408. DOI

Ramírez-Bautista A., Luría-Manzano R., Cruz-Elizalde R., Pavón N.P., 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., Hernández-Salinas U., Cruz-Elizalde R., Lozano A., Rodríguez-Romero F.J. 2016a. Sexual dimorphism and reproductive traits over time in *Sceloporus aeneus* (Squamata: Phrynosomatidae), based on a population in the Transmexican Volcanic Belt, Mexico. *Salamandra* 52:197–203.

Ramírez-Bautista A., Lozano A., Hernández-Salinas U., Cruz-Elizalde R. 2016b. Female reproductive characteristics among populations of the oviparous lizard *Sceloporus aeneus* (Squamata: Phrynosomatidae) from Central Mexico. *Herpetologica* 72:196–201. DOI

Rand A.S. 1967. Ecology and social organization in *Anolis lineatopus. Proceedings of the United States National Museum* 122:1–79. DOI

Reilly S.M., McBrayer L.B., Miles D.B. 2007. Lizard Ecology: The Evolutionary Consequences of Foraging Mode. Cambridge University Press, Cambridge. DOI

Rodríguez-Romero F. 1999. Estudio comparativo de algunos aspectos de la inversión parental en lacertilios de ambientes tropical y templado. M.Sc. Dissertation, Universidad Nacional Autónoma de México, México.

Rodríguez-Romero F., Méndez F.R., García-Collazo R., Villagrán-Santa Cruz M. 2002. Comparación del esfuerzo reproductor en dos especies hermanas del género *Sceloporus* (Sauria: Phrynosomatidae) con diferente modo reproductor. *Acta Zoológica Mexicana* 85:181–188.

Ruby D.E., Dunham A.E. 1984. A population analysis of the ovoviviparous lizard *Sceloporus jarrovi* in the Pinaleño mountains of southeastern Arizona. *Herpetologica* 40:425–436.

Rzedowski J. 1978. Vegetación de México. Limusa Wiley, México City.

Scali S., Sacchi R., Mangiacotti M., Pupin F., Gentilli A., Zucchi C., … Zuffi M.A.L. 2016. Does a polymorphic species have a ‘polymorphic’ diet? A case study from a lacertid lizard. *Biological Journal of the Linnean Society* 117:492–502. DOI

Schoener T.W. 1967. The ecological significance of sexual size dimorphism in the lizard *Anolis conspersus. Science* 155:474–477. DOI

Serrano-Cardozo V.H., Lemos-Espinal J.A., Smith G.R. 2008. Comparative diet of three sympatric *Sceloporus* in the semiarid Zapotitlán Valley, Mexico. *Revista Mexicana de Biodiversidad* 79:427–434.

Siqueira C.C., Kiefer M.C., Van Sluys M., Duarte Rocha C.F. 2013. Variation in the diet of the lizard *Tropidurus torquatus* along its coastal range in Brazil. *Biota Neotropical* 13:93–101. DOI

Sites J.W., Archie J.W., Cole C.L., Flores-Villela O. 1992. A review of phylogenetic hypotheses for lizards of genus *Sceloporus* (Phrynosomatidae): implications for ecological and evolutionary studies. *Bulletin of the American Museum of Natural History* 213:1–110.

Smith H.M. 1938. Remarks on the status of the subspecies of *Sceloporus undulatus,* with descriptions of new species and subspecies of the Undulatus group. *Occasional Papers of the Museum of Zoology, University of Michigan* 387:1–17.

Smith G.R., Ballinger R.E. 1994. Temporal and spatial variation in individual growth in the spiny lizard, *Sceloporus jarrovi. Copeia* 1994:1007–1013. DOI

Smith H.M., Camarillo J.L.R., Chiszar D. 1993. The status of the members of the *Sceloporus aeneus* complex (Reptilia: Sauria) of Mexico. *Bulletin of Maryland Herpetological Society* 29:130–139.

Sonnini C.S., Latreille P.A. 1801. Histoire Naturelle des Reptiles, avec Figures Dissinées d’après Nature, Tome II. Deterville, Paris. DOI

Stephenson B. 2010. A study of the biological significance of a male color polymorphism in the lizard *Sceloporus minor.* Ph.D. Dissertation, University of Miami, USA.

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. DOI

Triplehorn C., Johnson N.F. 2005. Borror and Delong’s Introduction to the Study of Insects. Cengage Learning, Boston.

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. DOI

Vitt L.J., Caldwell J.P. 2009. Herpetology: An Introductory Biology of Amphibians and Reptiles. Elsevier Academic Press, Burlington. DOI

Vitt L.J., Colli G.R. 1994. Geographical ecology of a neotropical lizard: *Ameiva ameiva* (Teiidae) in Brazil. *Canadian Journal of Zoology* 72:1986–2008. DOI

Wied M. 1821. Reise nach Brasilien in den Jahren 1815 bis 1817. Volume 1. Heinrich Ludwig Bronner, Frankfurt. DOI

Wiegmann A.F.A. 1828. Beyträge zur Amphibienkunde. *Isis von Oken* 21:364–383.

Wiegmann A.F.A. 1834. Herpetologia Mexicana, seu Descriptio amphibiorum Novae Hispaniae: quae itineribus comitis de Sack, Ferdinandi Deppe et Chr. Guil. Schiede in Museum Zoologicum Berolinense pervenerunt. Pars prima, Saurorum species amplectens, adiecto systematis saurorum prodromo, additisque multis in hunc amphibiorum ordinem observationibus. Sumptibus C.G. Lüderitz, Berolini.

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. DOI

Yarrow H.C. 1875. Report upon the collections of batrachians and reptiles made in portions of Nevada, Utah, California, Colorado, New Mexico, and Arizona, during the years 871, 1872, 1873, and 1874. Government Printing Office, Washington D.C.

Zamora-Abrego J.G., Ortega-León A.M. 2016. Ecología trófica de la lagartija *Xenosaurus mendozai* (Squamata: Xenosauridae) en el estado de Querétaro, México. *Revista Mexicana de Biodiversidad* 87:140–149. DOI

Zar J.H. 2009. Biostatistical Analysis. Prentice-Hall, Upper Saddle River.

Zúñiga-Vega J.J., Fuentes-G J.A., Ossip-Drahos A.G., Martins E.P. 2016. Repeated evolution of viviparity in phrynosomatid lizards constrained interspecific diversification in some life-history traits. *Biology Letters* 12:20160653. DOI