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Sexual dimorphism and reproductive traits over time in *Sceloporus aeneus* (Squamata: Phrynosomatidae), based on a population in the Transmexican Volcanic Belt, Mexico

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Abstract. Very little information is documented about variation in sexual size dimorphism between years within populations of a single species, and studies covering related topics are very scarce. We present information on sexual size dimorphism and reproductive traits obtained during the years 1980–1983, in a population of the lizard *Sceloporus aeneus* from the Transmexican Volcanic Belt. Adult males of this species showed a snout–vent length (SVL) range from 37–55 mm, whereas adult females ranged from 40–55 mm. Males were larger than females in all morphometric features. Differences in SVL occurred between years for either sex, whereas no differences were found between years within either sex in all other morphological characteristics. Mean of vitellogenic follicles (VF) and oviductal eggs were similar over the years. Considering VF and eggs together, the mean clutch size was 6.4 ± 0.15 eggs. Clutch size was significantly related to female SVL. Females produce at least two clutches during the reproductive period every year. Clutch size varied between years with the mean clutch size from 1982 being greater than those of 1981 and 1983. Egg masses and volumes were similar over the years investigated. The results of this study suggest that environmental factors (precipitation and temperature) can influence morphological and reproductive traits of *Sceloporus aeneus* from one year to the next.

Key words. Body size, sexual dimorphism, clutch size, variation between years.

Introduction

Sexual dimorphism in body size has been well explained in studies of single populations of many species of the genus *Sceloporus* (Fitch 1978, Ramírez-Bautista & Pavón 2009). Fitch (1978) tried to evaluate potential causes of sexual size dimorphism in *Sceloporus* species and identified three patterns of sexual size dimorphism: male-biased, female-biased, or no size dimorphism. Fitch (1978) demonstrated that males are larger than females in many *Sceloporus* species. This concept has been confirmed for single populations of many species and over years (De Marco 1989). Moreover, there have been a few studies examining sexual size dimorphism in more than one population of one particular species of *Sceloporus* (Smith et al. 2003, Ramírez-Bautista et al. 2008, 2013). Patterns of "sexual size dimorphism" have been explained in different ways, such as being the effect of sexual selection (Anderson & Vitt 1990, Verrastro 2004, Ramírez-Bautista et al. 2008, Ramírez-Bautista & Pavón 2009), different growth rates between males and females (Ruby & Dunham 1984, Smith & Ballinger 1994), fecundity (heavier females facilitating the development of more eggs) (Olsson et al. 2002, Ramírez-Bautista & Pavón 2009), and niche divergence (Camilleri & Shine 1990, Hierlihy et al. 2013).

These sexual distinctions generally are attributed to morphology affecting individual fitness (Darwin 1871, Andersson 1994, Olsson et al. 2002). The relatively larger heads of males are believed to improve chances of success in male–male rivalry, which is explained to have arisen through sexual selection (Olsson et al. 2002). The longer and wider body proportions of females, on the other hand, have been attributed to selective forces impacting on fecundity whereby increased space will facilitate developing more or larger eggs/embryos, larger clutch/litter sizes, and/

or larger hatchlings/neonates (Andersson 1994, Olsson et al. 2002, Ramírez-Bautista et al. 2008). However, at this point of time there have been no direct tests of these hypotheses. To analyse them, we need to measure the effects of which morphological variations of females impact on their fitness (Olsson et al. 2002). Very little is known about variations in body size between populations of a single species (Dunham 1982, Michaud & Echternacht 1995) or long-term variation in SVL over years, and how these variations influence life history traits (egg size and clutch size).

This study reports on data of sexual size dimorphism and reproductive traits of *Sceloporus aeneus*, a small terrestrial lizard (adult SVL range 37–55 mm) with an oviparous mode of reproduction. This species inhabits high altitudes (2500–2950 m) of mountains in the Transmexican Volcanic Belt. Its range covers Puebla, central Michoacán, Guanajuato, Distrito Federal, State of Mexico, Morelos, and Hidalgo (Smith & Taylor 1966). This species typically inhabits vegetation types such as pine and pine-oak forest (Ramírez-Bautista et al. 2009). Considering the theory and lack of information described above, the goals of this study are: 1) to describe the general pattern of sexual size dimorphism, and reproductive traits of females in a population of *S. aeneus* from the Transmexican Volcanic Belt, Mexico; 2) to describe the variation over years (1980–1983) in female reproductive traits (clutch size, clutch frequency, egg mass, and egg volume), as well as body size and other morphological characteristics for both sexes; and 3) to relate reproductive (clutch size) and morphological (body size) characteristics to environmental variables (temperature and precipitation).

Material and methods

Study area

Herpetological surveys were carried out from May through August during the years 1980 to 1983, and adult lizards (n = 140) were collected near the locality of Cahuacán, Municipality Nicolás Romero (19°37'48" N, 99°25'54" W; datum WGS84), State of Mexico, Mexico. The altitude here is about 2,950 m and vegetation type is pine and pine-oak forest (Rzedowski 1978). The rainy season in this area extends from June through September. Mean annual precipitation and temperature varied between the years: 1980 (852.5 mm, 15.4°C), 1981 (1,035.2 mm, 15.0°C), 1982 (716.1 mm, 15.6°C), and 1983 (958.7 mm, 14.5°C; see Fig. 1; Conagua 2014).

Morphological analysis

Specimens of *S. aeneus* were examined that had originally been fixed (formalin 10%), conserved in alcohol (70%), and deposited in the Colección Nacional de Anfibios y Reptiles, Instituto de Biología (CNAR, IBH-1432-26; IBH-2681: 1 [3 individuals, same acronym], 2, 3, 5 to 10; IBH-3621: 1 to 7; IBH-3641: 1 [3 individuals, same acronym], 2, 3, 5 to 10; IBH-3646: 1 [2 individuals, same acronym], 3, 7 [3 individuals, same acronym]; IBH-3815: 1 to 4, 5 [3 individuals, same acronym], 6 to 10, 12, 13 [2 individuals, same acronym], 14 to 22, 24 to 26, 28 [2 individuals, same acronym], 29 [2 individuals, same acronym], 30 to 32, 33 [2 individuals, same acronym], 34, 35 [2 individuals, same acronym], 38, 40 to 42, 44, 46; IBH-3816: 1, 2, 4, 8, 13 [2 individuals, same acro-

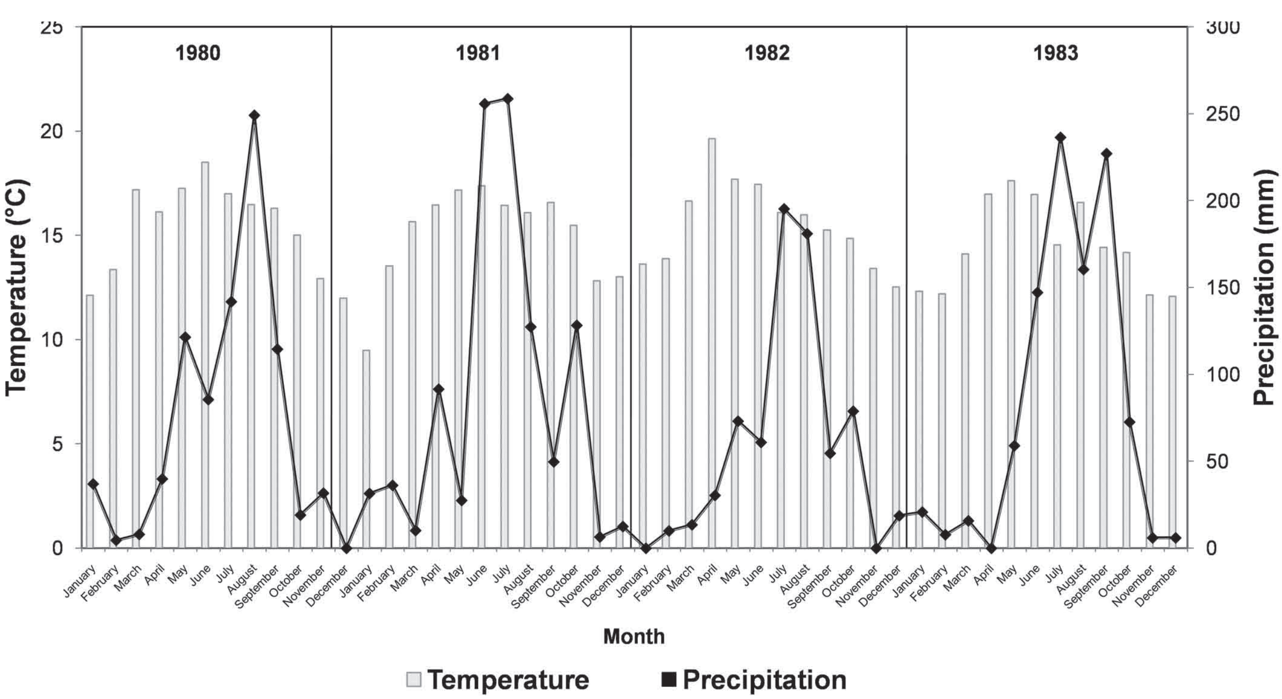

Figure 1. Annual variation in mean monthly temperature and precipitation for Cahuacán, State of Mexico, Mexico, in 1980–1983 (Conagua 2014).

Table 1. Morphological characteristics of adult females and males of *Sceloporus aeneus* from Cahuacán, Municipality of Nicolás Romero, State of Mexico, Mexico. Measurements for all characteristics are given in millimetres. Means are presented with ± 1 SE; intervals are in parenthesis; n – sample size; * – ANCOVA; ** – t-Student test.

Characteristics	Females (n=105)	Males (n=35)	F/t-value	p-value
Snout–vent length (SVL)	46.6±0.31 (40.0–55.0)	47.9±0.62 (37–55.0)	t=-2.03**	0.044**
Head length (HL)	11.5±0.06 (10.0–13.0)	12.4±0.16 (9.0–13.8)	$F_{1,137}$=75.86	<0.001*
Head width (HW)	8.6±0.06 (7.6–11.5)	9.5±0.11 (7.5–10.7)	$F_{1,137}$=71.32	<0.001*
Forearm length (FL)	6.4±0.05 (5.0–7.8)	7.0±0.15 (5.5–10.0)	$F_{1,137}$=16.3	<0.001*
Tibia length (TL)	8.6±0.06 (7.2–10.7)	9.5±0.14 (6.7–10.9)	$F_{1,137}$=40.24	<0.001*

nym], 14, 36; IBH-4432: 2, 3 [2 individuals, same acronym], 4 [2 individuals, same acronym], 5 to 10, 12 to 18, 19 to 21, 23, 24, 25 [2 individuals, same acronym], 27 [2 individuals, same acronym], 28, 29, 31, 32, 34 to 37, 38 [2 individuals, same acronym], 39, 40, 42 to 47; IBH-4447; and IBH-4513: 3, 4), and from the Museum of Zoología, Facultad de Ciencias (MZFC, MZFC-00770 [2 individuals, same acronym]; and MZFC-05784, both from the collection of the Universidad Nacional Autónoma de México. We collected a total of 105 adult females (1980 = 6, 1981 = 17, 1982 = 39, and 1983 = 43) and 35 adult males (1980 = 5, 1981 = 6, 1982 = 17, and 1983 = 7) of the species in the study area. We took the following measurements of each lizard to the nearest 0.1 mm: snout–vent length (SVL), head length (HL; distance from the anterior tip of the rostral scale to the posterior margin of the left ear opening), head width (HW; maximum width of the head, measured as the distance between the posterior margin of the left and right ear openings), and forearm length (FL) and tibia length (TL), were each measured from the elbow (FL) or knee (TL) to the sole of the foot (Ramírez-Bautista et al. 2014). To test for sexual size dimorphism, we compared the SVL of all adult males and females and by year using a t-Student test and Mann-Whitney U-test. An analysis of variance (ANOVA) was performed to compare the SVL between the years for each sex. Also, we used an analysis of covariance (ANCOVA) with SVL as the covariate to compare HW, HL, FL, and TL and possibly identify differences between males and females (Zar 1999), and each one of these morphological characteristics between years for each sex. Post-hoc Tukey's pairwise comparison tests were utilized to identify differences when ANOVAs or ANCOVAs produced significant results. Additionally, we used linear regressions to identify a possible relationship between SVL and environmental variables of the habitat (temperature and precipitation).

Reproductive analysis

Adult and sexually mature males were identified by presence of enlarged testes and convoluted epididymides typically associated with sperm production (Lozano 2013). The SVL of the smallest female with enlarged vitellogenic follicles (VF), oviductal eggs or both was used to estimate the minimum adult SVL (Ramírez-Bautista et al. 2008). The largest egg (in each oviduct) was removed and weighed to the nearest 0.0001 g and multiplied by the number of eggs on that side to estimate total egg mass on each side of the body (Ramírez-Bautista et al. 2008). We quantified clutch sizes by counting the VF and eggs of females during the reproductive season (Ramírez-Bautista & Olvera-Becerril 2004).

Clutch frequency, or production of multiple clutches per reproductive season, was inferred from the presence of VF in the ovary and eggs in the oviduct simultaneously (Ramírez-Bautista & Vitt 1997, 1998), or VF and presence of corpora lutea. Because no differences were observed in the mean of VF and eggs, they were pooled to calculate a Pearson's correlation coefficient to test for a possibly significant relationship between clutch size and the SVLs of females (for all years). To identify differences in clutch size, egg mass, and egg volume between years (1980–1983), we performed ANCOVA tests, using SVL as the covariate. We performed linear regressions to identify a possible relationship between clutch size and environmental variables (temperature and precipitation). Results were considered significant if p was ≤ 0.05. In general, data met the conditions for a parametric test, but if they did not, we used nonparametric approaches for testing the hypothesis. All statistical analyses were performed using StatView IV (Abacus Concepts 1992). Means are presented with ± 1 SE.

Results

Body size and sexual dimorphism

Adult males of *S. aeneus* showed a SVL range from 37–55 mm, whereas females were 40–55 mm (Table 1). Males were larger than females in all morphological characteristics (Table 1). There was a difference in mean SVL between years for both females and males, but not per year between sexes (Table 2). Post-hoc Tukey's tests revealed that females from 1982 were different from those in 1980 (p = 0.046), 1981 (p = 0.006), and 1983 (p = 0.0001); and males from 1982 differed from those in 1983 (p = 0.047), but were similar to those collected in 1980 (p = 0.56) and 1981 (p = 0.99). No differences were found in HL, HW, FL, or TL between years for each sex (Table 3). Linear regressions revealed a significant relationship between SVL and temperature (males: r = 0.44, p = 0.008; females: r = 0.47, p < 0.0001) and precipitation (males: r = 0.56, p = 0.0004; females: r = 0.43, p < 0.0001) for both sexes.

Table 2. Variation in body size (SVL mm) of females and males of *Sceloporus aeneus* from Cahuacán, Municipality of Nicolás Romero, State of Mexico, Mexico, between years. Means are presented with ± 1 SE, n – sample size; SVL – snout–vent length, range in parenthesis; * – ANOVA; ** – Mann-Whitney U-test.

Years	SVL Females	n	SVL Males	n	U-value	p-value
1980	45.5±2.5 (41–48)	6	48.0±4.5 (41–52)	5	8	0.23**
1981	46.0±2.7 (41–55)	17	46.0±4.7 (37–50)	6	42	0.55**
1982	48.6±2.7 (43–55)	39	49.5±2.8 (45–55)	17	273	0.30**
1983	45.1±2.8 (40–55)	43	45.4±2.2 (42–48)	7	130.5	0.58**
	$F_{3,101}$=12.25, p<0.001*		$F_{3,31}$=3.27, p=0.034*			

Table 3. ANCOVA tests for morphological characteristics of adult females and males of *Sceloporus aeneus* from Cahuacán, Municipality of Nicolás Romero, State of Mexico, Mexico. Means are complemented with ± 1 SE.

Morphological characteristic	Females						Males					
	1980	1981	1982	1983	F-value	p-value	1980	1981	1982	1983	F-value	p-value
Head length (HL)	11.3±1.0	11.4±0.5	11.7±0.59	11.3±0.55	0.71	0.54	12.3±0.5	11.8±0.57	12.8±0.15	12.3±0.26	2.31	0.09
Head width (HW)	8.6±0.24	8.6±0.11	8.8±0.07	8.4±0.11	0.52	0.67	9.4±0.31	9.4±0.38	9.8±0.15	9.2±0.31	0.57	0.64
Forearm length (FL)	6.5±0.21	6.3±0.11	6.6±0.09	6.3±0.07	0.38	0.77	6.5±0.32	7.1±0.63	7.2±0.14	6.4±0.19	1.59	0.21
Tibia length (TL)	8.6±0.32	8.4±0.15	8.8±0.09	8.5±0.11	0.52	0.67	9.3±0.37	9.0±0.41	9.9±0.16	9.3±0.30	0.8	0.5

Table 4. Female reproductive characteristics of *Sceloporus aeneus* from Cahuacán, Municipality of Nicolás Romero, State of Mexico, Mexico. Significant (*) and non-significant (ns) differences between clutch size/snout–vent length (SVL) of females with eggs and vitellogenic follicles. Means are presented with ± 1 SE.

Characteristics	SVL (mm)	Clutch size	n	Egg mass (g)	n
Total	46.6±0.31 (40–55)	6.4±0.16 (2–10)	99		
Eggs	47.6±0.53 (42–55)*	6.8±0.24 (4–10)^{ns}	40		
Vitellogenic follicles	45.9±0.38 (40–52)*	6.2±0.19 (2–10)^{ns}	59		
Years					
1980		6.33±0.33	6	–	–
1981		6.25±0.32	12	0.93±0.13	7
1982		7.36±0.23	39	1.07±0.08	15
1983		5.57±0.19	42	0.77±0.07	17

Reproduction

A total of 105 females were sexually mature during the period from May through August. The mean SVL of females with non-vitellogenic follicles (SVL = 46.7 ± 1.0 mm, n = 6), vitellogenic follicles (45.9 ± 0.38 mm, n = 59), and oviductal eggs (47.6 ± 0.53 mm, n = 40) were different (ANOVA, F = 3.73, df = 2,103, p = 0.027). The mean VF was similar to that of oviductal eggs (ANCOVA, F = 0.32, df = 1,96, p = 0.57; Table 4). Considering VF and eggs together, the mean clutch size was 6.4 ± 0.15 eggs (range 2–10). Clutch size was significantly related to SVL (r = 0.59, p < 0.0001; Fig. 2) and environmental variables (temperature: r = 0.49, p < 0.0001; precipitation: r = 0.47, p < 0.0001). This oviparous species lays at least two clutches per reproductive season, and 20 females had oviductal eggs and VF simultaneously. Females with eggs were larger in SVL than females with VF (Mann-Whitney U-test, Z = -2.45, p = 0.014; Table 4). The general clutch size varied between years (ANCOVA, F = 3.77, df = 3,94, p = 0.013). Tukey's pairwise tests showed that clutch size data from 1982 were higher than from those of 1981 (p = 0.029) and 1983 (p < 0.001), but similar to those found in 1980 (p = 0.20), whereas all other comparisons produced similar results (p ≥ 0.3, Table 4). Mean egg mass and mean egg volume were similar between years (ANCOVA, F = 0.7, df = 3,35, p = 0.55; F = 0.4, df = 3,35, p = 0.75; respectively).

Discussion

Morphology

Sexual dimorphism may show in many traits of lizard species, such as morphology, colour pattern, behaviour, and niche divergence (Cooper & Vitt 1989, Andrews & Stamps 1994, Olsson et al. 2002, Verrastro 2004, Filogonio et al. 2009, Hierlihy et al. 2013). In spite of

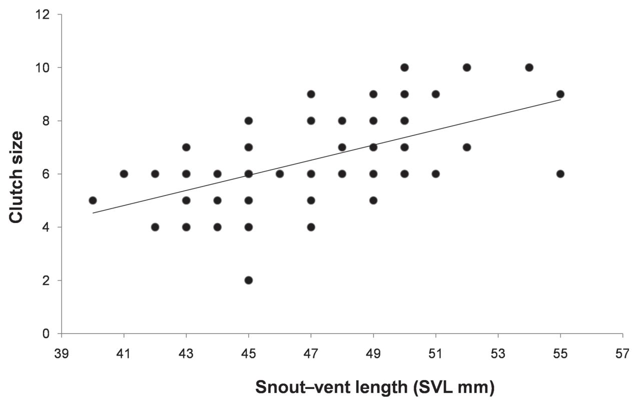

Figure 2. Relationship between female snout–vent length and clutch size for *Sceloporus aeneus* from Cahuacán, State of Mexico, Mexico.

the three patterns of sexual size dimorphism identified by Fitch (1978) in species of *Sceloporus* (male-biased, female-biased, or no such dimorphism), these patterns have been poorly tested for various populations of a single species (Ramírez-Bautista et al. 2013), and information on a single population through several years has been reported to an even lesser extent (Fitch 1978, Hierlihy et al. 2013). Females and males of *S. aeneus* were different from one another in all morphological traits (Table 1). This pattern has likewise been found in other *Sceloporus* studies, such as *S. gadoviae* (Lemos-Espinal et al. 1999), *S. grammicus* (Ramírez-Bautista et al. 2012), *S. siniferus* (Hierlihy et al. 2013), *S. horridus* (Valencia-Limón et al. 2014), as well in other squamate species (Anderson & Vitt 1990). Nonetheless, sexual dimorphism has been noted not only in morphological characteristics, but also in colour patterns between males and females in both oviparous and viviparous species (Fitch 1978). In addition to the sexual size dimorphism in morphological characteristics of this population of *S. aeneus*, we suggest that different colour patterns between males and females play an important role in reproductive behaviour (care and territorial defence) and reproduction (better access to females). Males from this population showed darker blue (bright colour) patches in ventral region than females; therefore, this pattern together with the morphological structures of males and females are important evidence of sexual dimorphism during reproduction (Ramírez-Bautista & Pavón 2009).

Males of viviparous and oviparous *Sceloporus* species are known to be territorial (Fitch 1978), as is suggested by their being larger in many morphological structures and brighter in colour pattern than females (e.g., *S. formosus*: Ramírez-Bautista & Pavón 2009). However, in some species, males and females are similar in morphological structures but different in colour patterns (dorsal and ventral region of the body), such as in oviparous (*S. horridus*: Valdéz-González & Ramírez-Bautista 2002; *S. spinosus*: Valdéz-González & Ramírez-Bautista 2002, Ramírez-Bautista et al. 2013; *S. melanorhinus*: Ramírez-Bautista et al. 2006a; *Urosaurus bicarinatus*: Ramírez-Bautista et al. 1995) and viviparous species (*S. bicanthalis*: Rodríguez-Romero et al. 2004; *S. torquatus*: Feria-Ortíz et al. 2001; *S. jarrovii*: Ramírez-Bautista et al. 2002, Gadsden & Estrada-Rodríguez 2008; *S. minor*: Ramírez-Bautista et al. 2008; *S. formosus*: Ramírez-Bautista & Pavón 2009; *S. grammicus*: Lozano 2013). These patterns (morphology structures and bright colours) of dimorphism between males and females in these species have been favoured by natural selection in the shape of sexual selection (Olsson et al. 2002).

Per year investigated, body size (SVL) did not vary between males and females (Table 2), nor did any morphological characteristic for either sex (Table 3) from all years analysed (1980–1983), but these results should be regarded with caution because our sample size of males could bias data. However, the mean SVL varied between years (1980–1983) in males and females (Table 2) and these variations can be explained in the context of variation in environmental conditions (Fig. 1).

Clutch size

Females of *S. aeneus* from this population showed a similar clutch size (6.4 eggs) to that of other populations of the same species (6.7 eggs: Manríquez-Morán et al. 2013; 7 eggs: Rodríguez-Romero 1999). Large-body-sized oviparous lizards with longer reproductive periods generally have higher clutch frequencies (Dunham et al. 1988, Ramírez-Bautista & Vitt 1997, 1998). Gravid females of *S. aeneus* in our study produced at least two clutches per reproductive season, such as has been documented for other populations of the same species (Rodríguez-Romero 1999, Manríquez-Morán et al. 2013) and various oviparous species (Benabib 1994, Ramírez-Bautista & Vitt 1997, 1998, Ramírez-Bautista et al. 2006b). Variations in clutch size between years could be a response to environmental conditions; such as has been mentioned for other lizard species (Dunham 1982, Benabib 1994, Hamilton et al. 2008, Wang et al. 2011). For example, the clutch size from 1982 (7.36 ± 0.23) was higher than in 1981 (6.25 ± 0.32) and 1983 (5.57 ± 0.19), which could indicate that these lizards respond to changing environmental conditions in their habitat. Precipitation for 1981 (1,035.2 mm) was higher than in 1982 (716.1 mm), but the former could have an influence on next year's insect biomass, and, therefore may have led to larger clutch sizes in 1982, as has been documented in other studies (Ballinger 1977, Dunham 1978). These studies have shown the influence of food availability on growth rate and fecundity (Dunham 1978).

No correlation between female SVL and clutch size has been found for other populations of *S. aeneus* (Rodríguez-Romero 1999, Manríquez-Morán et al. 2013); however, in our population, a significant relationship was found to exist between these variables. Females with greater SVLs (1982 = 48.6 mm) and clutch sizes (1982 = 7.36 eggs) could explain the relationship between these characteristics. These results also would be explained by the environmental conditions of these years, such as has been found in other studies (Ballinger 1977, Benabib 1994, Smith & Ballinger 1994, Ramírez-Bautista & Vitt 1997). Several studies have demonstrated that females with a larger body size had a higher fecundity than females with a smaller SVL, such as found in this population (Horváthová et al. 2013).

In summary, females and males were similar in SVL in different years. All morphological structures were different between sexes, but not between years (only SVL). Larger females in 1982 had larger clutch sizes than during the other years analysed. Studies exploring variations in sexual size dimorphism between populations and years are very scarce; however, our study at least confirms some of the patterns of sexual dimorphism described by Fitch (1978) for the genus *Sceloporus*. Nevertheless, we need to explore other populations of the same species and compare them over several years in order to learn how species respond between populations and years. For that, it is necessary to understand the life history of the species, because we presume that multiple factors may be involved in driving sexual dimorphism and life history variation within and between populations of lizard species, and it is the case for this population of *S. aeneus*. To draw conclusions about proximate and ultimate factors influencing sexual dimorphism and life history variation within a population and between years in *S. aeneus* will require long-term studies and demographic research (longer than ours) to address this context.

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