

Reproduction and sexual dimorphism in two populations of *Sceloporus minor* of the Guadalcázar Region, San Luis Potosí, Mexico

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We studied the reproduction and sexual dimorphism of *Sceloporus minor* in two populations, El Oro and Las Lagunas, in the municipality of Guadalcázar, San Luis Potosí, Mexico. Males were larger and had larger heads and tibias than females. Males and females from El Oro were larger than those from Las Lagunas. Reproductive activity of males and females was asynchronous in both populations. Testes of the males from El Oro and Las Lagunas increased in size from July to September, reaching maximum size in October and regressing in November. Vitellogenesis occurred in September in both populations, with ovulation occurring in November–December. Embryonic development was observed from December to March in both populations. Parturition in the El Oro population occurred from late March to early July, whereas in Las Lagunas it occurred from mid-March to late May. Litter size for both populations was similar (El Oro: 6.6, Las Lagunas: 6.2). Litter size was positively related to female SVL in the El Oro population but not in the Las Lagunas population. These two populations show some similarities, but also show differences, possibly due to elevation.

Key words: embryonic development, geographic variation, lizard, Phrynosomatidae, sex differences, Squamata

INTRODUCTION

The genus *Sceloporus* has been the focus of a great deal of research on lizard life histories. In particular, *Sceloporus undulatus* has been a focal point for examining broad geographic variation in life-history traits (e.g. Tinkle & Ballinger, 1972; Ferguson et al., 1980; Niewiarowski, 1994, 2001). However, other *Sceloporus* have proved valuable in understanding life-history variation at a smaller scale, such as elevational variation (e.g. Ballinger, 1979; Grant & Dunham, 1990; Smith et al., 1994; Ballinger et al., 1996; Sears, 2005) and habitat level variation (e.g. Smith, 1998).

In addition to geographic variation in life-history traits, *Sceloporus* have also been used to examine interspecific variation in sexual dimorphism (e.g. Fitch, 1978). However, few studies have examined intraspecific variation in sexual dimorphism, either within *Sceloporus* or in other lizards. One previous study found no differences in sexual dimorphism between two populations of *S. ochoteranae*, even though there were differences in body size and morphometric variables between the two populations (Smith et al., 2003). Studies of other species of lizards suggest that sexual dimorphism can differ among populations (e.g. McCoy et al., 1994; Molina-Borja et al., 1997).

To add to the growing body of literature on geographic variation in life history and sexual dimorphism, we examined variation in life history and sexual dimorphism in two populations of *S. minor* from San Luis Potosí, Mexico that differ in elevation by 630 m. *Sceloporus minor* is a member

of the *torquatus* group (Sites et al., 1992; Martínez-Méndez & Méndez-de la Cruz, 2007) and the “*jarrovii*” complex (Wiens et al., 1999), and occurs from north of Querétaro and Guanajuato, west of Zacatecas, San Luis Potosí and west of Nuevo León (Sites et al., 1992; Wiens et al., 1999; Wiens & Penkrot, 2002).

MATERIALS AND METHODS

Study area

This study was conducted in two localities separated by 20 km, El Oro and Las Lagunas of the municipality of Guadalcázar (22°30'N, 100°23'W, datum: WGS84), at elevations of 1600 and 2230 m, respectively, in San Luis Potosí, Mexico. The vegetation at both localities is mesquite scrub–grassland, oak–juniper woodland and cactus forest dominated by oak forest (*Quercus polymorpha*, *Q. laeta*), mesquite (*Prosopis juliflora*) and juniper (*Juniperus flaccida*). Mean annual temperature at El Oro (25.8 °C) was slightly higher than at Las Lagunas (23.5 °C), whereas mean annual precipitation at El Oro (300 mm) was half of that at Las Lagunas (600 mm; see Fig. 1; García, 1981). Photoperiod data were acquired from the Astronomical Almanac (Nautical Almanac Office & United States Naval Observatory, 1984). To compare climatic variables with gonadal cycling, we performed multiple regressions using monthly means for temperature, photoperiod and precipitation as independent variables and log₁₀-transformed organ masses as the dependent variables.

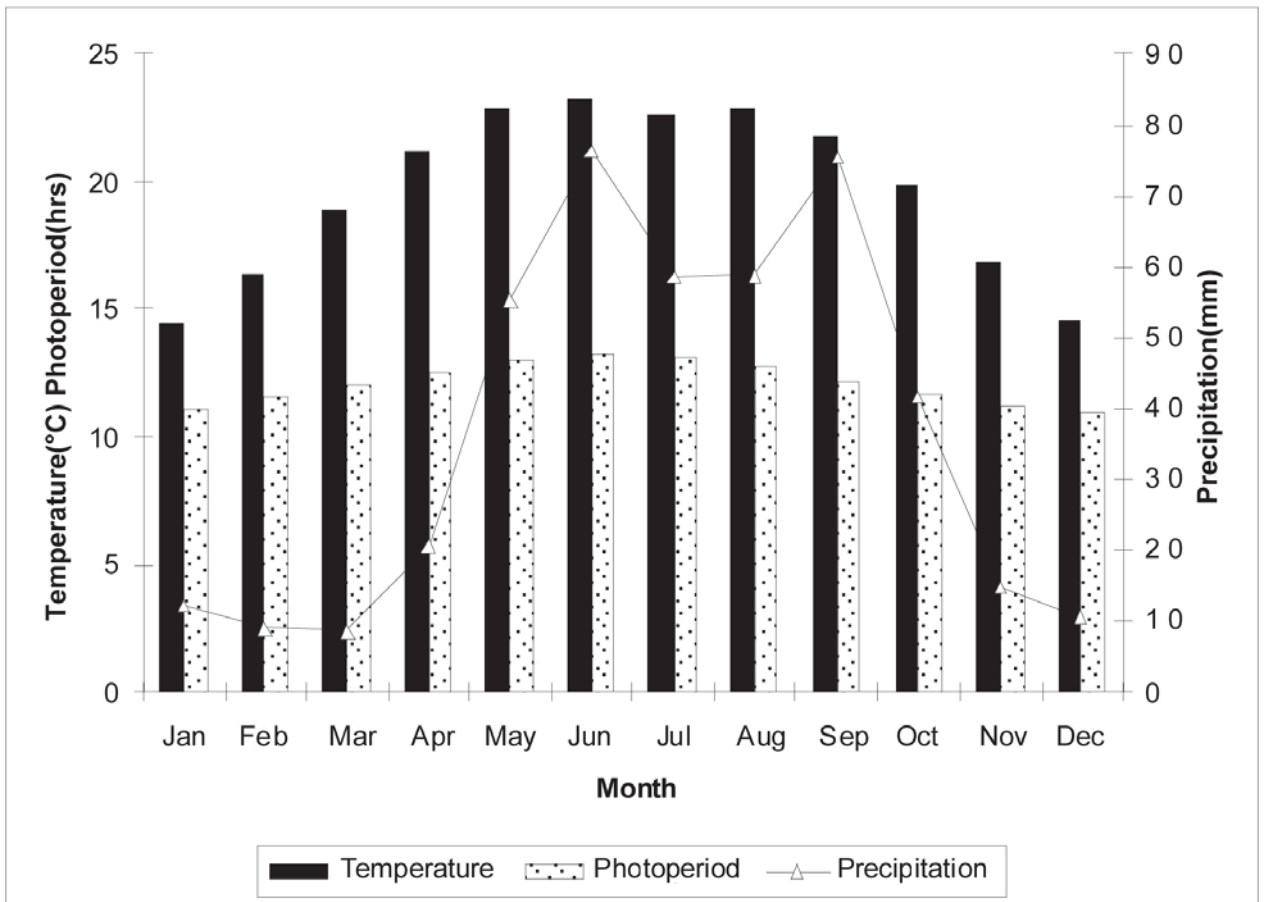


Fig. 1. Annual variation in mean temperature, photoperiod and precipitation for the Guadalcázar region of San Luis Potosí, Mexico.

Morphological analyses

Morphological descriptions and comparisons were restricted to sexually mature males and females. We measured snout–vent length (SVL; to nearest 1.0 mm), mass (to nearest 0.01 g), head length (HL; to nearest 0.1 mm) and head width (HW; to nearest 0.1 mm) on each lizard. Forearm length (FL; to nearest 0.1 mm) and tibia length (TL; to nearest 0.1 mm) were measured from the elbow or knee, respectively, to the pad of the foot. To test for sexual size dimorphism, we compared SVL of adult males and females using an ANOVA and we used ANCOVA with SVL as the covariate to compare HL, HW, FL and TL between males and females (we used untransformed variables because preliminary analyses showed that regressions on untransformed variables fit as good or better than regression using log-log transformed variables). Non-significant interactions involving the covariate were removed from the final model in the ANCOVA analyses.

Reproductive analysis

A total of 206 (106 male and 100 female) *S. minor* was collected from June 1999 to May 2000. Monthly sample size was small, so 1999 and 2000 data were pooled by month to describe the annual reproductive cycle for each population. Lizards were humanely killed and fixed (with 10% formalin) in the laboratory. Testes, non-vitellogenic folli-

cles (NVF), vitellogenic follicles (VF) and embryos were removed and weighed (to the nearest 0.0001 g). In reproductive females, the largest egg (embryos in uterus, VF, or NVF in the ovary) on each side of the body was weighed to the nearest 0.0001 g and multiplied by the number of eggs on that side to estimate total gonadal mass on each side of the body, indicated here as testes mass (TM), ovarian mass (OM) or embryo mass (EM).

In order to control for body-size effects on reproductive variables, we first calculated regressions of \log_{10} transformed organ mass data on \log_{10} male and female SVL. For significant regressions, we calculated residuals from the regression to generate variables adjusted for body size (Schulte-Hostedde et al., 2005). We used these residuals to describe reproductive cycling. This technique retains variation due to extrinsic factors (e.g. season) while minimizing the confounding effect of individual variation in body size. For non-significant regressions (i.e. no body-size effect), we used the \log_{10} -transformed organ mass to describe gonadal cycles. For each variable, we performed single-factor ANOVAs to detect significant monthly variation, but included only those months for which $n \geq 3$.

Litter size was estimated by counting embryos in the oviducts of adult females during the reproductive season. We calculated a Pearson product-moment correlation coefficient to test for a relationship between litter size and

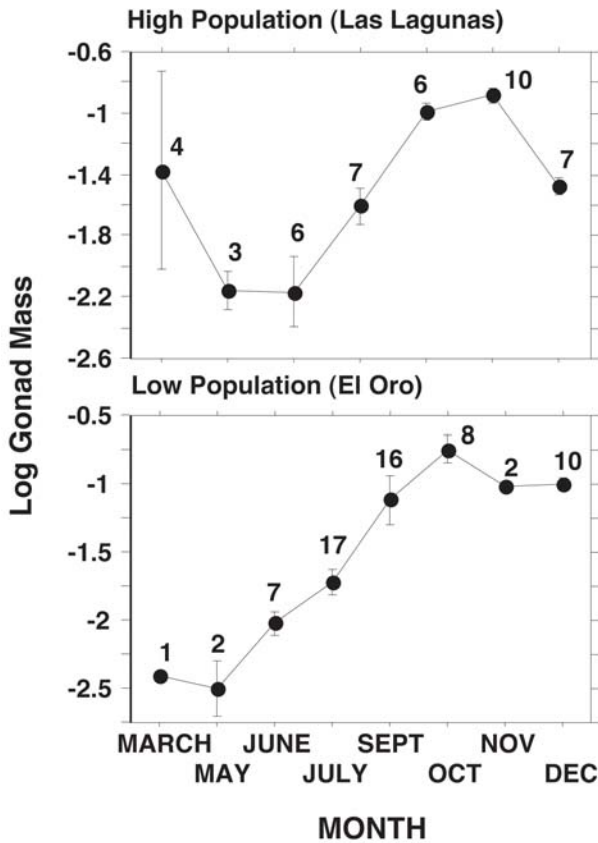


Fig. 2. Annual cycles of testis size for male *Sceloporus minor* from Guadalcázar, San Luis Potosí, Mexico. Means are given ± 1 S.E.

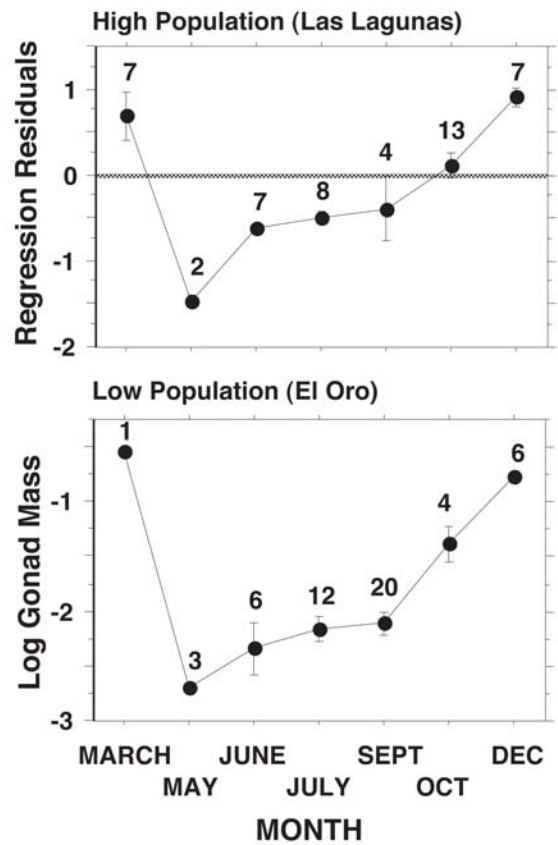


Fig. 3. Annual cycles of follicle/egg size for female *Sceloporus minor* from Guadalcázar, San Luis Potosí, Mexico. Means are given ± 1 S.E.

female SVL. We determined the stage of embryonic development (stages 1 to 40) according to Dufaure & Hubert (1961).

Means are given ± 1 S.E., unless otherwise indicated. Standard parametric statistical tests were used whenever possible; otherwise, we substituted appropriate nonparametric tests.

Table 1. Means of morphological characteristics of adult *Sceloporus minor* from El Oro and Las Lagunas, San Luis Potosí, Mexico. Data for all characteristics are reported in millimetres. Means are given ± 1 S.E.

	El Oro	Las Lagunas
Males		
SVL	72.0 \pm 1.36	64.5 \pm 1.22
Head length (HL)	16.2 \pm 0.27	15.0 \pm 0.24
Head width (HW)	12.6 \pm 0.26	11.6 \pm 0.24
Forearm length (FL)	10.3 \pm 0.21	9.5 \pm 0.19
Tibia length (TL)	13.1 \pm 0.25	12.1 \pm 0.23
Females		
SVL	64.6 \pm 1.1	61.0 \pm 1.1
Head length (HL)	14.2 \pm 0.23	13.8 \pm 0.23
Head width (HW)	11.1 \pm 0.20	10.7 \pm 0.21
Forearm length (FL)	9.4 \pm 0.13	8.9 \pm 0.17
Tibia length (TL)	11.9 \pm 0.17	11.1 \pm 0.17

RESULTS

Body size and sexual dimorphism

Males were larger than females (Table 1; $F_{1,186}=17.2$, $P<0.0001$). Lizards from El Oro were larger than lizards from Las Lagunas (Table 1; $F_{1,186}=18.4$, $P<0.0001$). The interaction between sex and population was not significant ($F_{1,186}=1.77$, $P=0.18$).

Males had longer heads than females (Table 1; $F_{1,184}=29.6$, $P<0.0001$). Head length did not differ between the populations ($F_{1,184}=0.26$, $P=0.61$), nor was the interaction between sex and population significant ($F_{1,184}=0.009$, $P=0.92$). However, the relationship between SVL and HL differed between the two populations ($F_{1,184}=7.65$, $P=0.006$). Head length increased with SVL faster in the El Oro population ($r^2=0.84$, $P<0.0001$; $HL=1.62+0.20*SVL$) than in the Las Lagunas population ($r^2=0.60$, $P<0.0001$; $HL=4.62+0.15*SVL$).

Males had wider heads than females (Table 1; $F_{1,185}=7.11$, $P=0.0083$). Head width did not differ between populations ($F_{1,185}=0.51$, $P=0.48$). The interaction between sex and population was also not significant ($F_{1,185}=0.062$, $P=0.80$). Head width increased with SVL in both populations (El Oro: $n=106$, $r^2=0.67$, $P<0.0001$; $HW=1.44+0.15*SVL$; Las Lagunas: $n=84$, $r^2=0.56$, $P<0.0001$; $HW=2.55+0.14*SVL$).

Forearm length did not differ between sexes ($F_{1,184}=2.64$, $P=0.11$) or populations ($F_{1,184}=2.50$, $P=0.12$).

Table 2. Reproductive characteristics of *Sceloporus minor* from Guadalcázar, San Luis Potosí, México. Mean \pm SE (range, sample size).

Characteristics	El Oro	Las Lagunas
Peak activity males	September–December	September–October
Peak activity females	October–March	December–March
Embryonic development period	December–mid-May	December–early June
Vitellogenic follicles (VFs)	September–December	September–October
Litter size (embryos)	5.7 \pm 0.7 (4–9, $n=6$)	6.0 \pm 0.6 (2–9, $n=11$)
VFs	8.0 \pm 1.3 (2–11, $n=4$)	6.5 \pm 1.0 (2–11, $n=11$)
Embryos plus VFs	6.6 \pm 0.7 (4–11, $n=10$)	6.2 \pm 0.6 (2–11, $n=22$)
Embryo volume (mm ³)	342.1 \pm 170.4 (136.9–1190.9, $n=6$)	338.9 \pm 68.2 (118.6–881.1, $n=11$)
SVL at hatching (mm)	33.5 \pm 0.7 (28.0–35.0, $n=6$)	32.2 \pm 1.3 (28.0–38.0, $n=9$)

(Table 1). The interaction between sex and population was also not significant ($F_{1,184}=0.62$, $P=0.43$). The relationship between SVL and FL differed between males and females ($F_{1,184}=6.66$, $P=0.011$). Forearm length in males grew faster with SVL ($r^2=0.77$, $P<0.0001$; $FL=1.02+0.13*SVL$) than in females ($r^2=0.57$, $P<0.0001$; $FL=2.86+0.099*SVL$).

Males had longer tibias than females (Table 1; $F_{1,184}=7.98$, $P=0.0052$). However, the relationship of SVL and TL differed between the sexes ($F_{1,184}=14.5$, $P=0.0002$), with TL increasing with SVL faster in males ($r^2=0.78$, $P<0.0001$; $TL=1.90+0.16*SVL$) than in females ($r^2=0.50$, $P<0.0001$; $TL=4.28+0.11*SVL$). Populations did not differ in TL ($F_{1,184}=0.26$, $P=0.61$). However, there was a significant interaction between sex and population ($F_{1,184}=7.46$, $P=0.007$). Males and females for El Oro had similar TLs, whereas males had larger TLs than females at Las Lagunas (Table 1).

Male reproductive cycle

No significant relationship existed between \log_{10} SVL and $TM_{\log_{10}}$ in males from either Las Lagunas ($n=43$, $r^2=0.002$, $P=0.76$) or El Oro ($n=63$, $r^2=0.009$, $P=0.46$). At El Oro, TM increased from July through September, reaching a maximum in October, then regressed in November and December (Fig. 2; $F_{7,53}=10.07$, $P<0.0001$). A similar pattern in TM recrudescence occurred in males from Las Lagunas, but maximum TM was from September to October and regression started in December (Fig. 2; $F_{6,37}=21.8$, $P<0.0001$).

Neither population showed a significant relationship between TM and photoperiod (Las Lagunas: $n=7$, $r^2=0.17$, $P=0.36$; El Oro: $n=8$, $r^2=0.35$, $P=0.12$), precipitation (Las Lagunas: $n=7$, $r^2=0.03$, $P=0.72$; El Oro: $n=8$, $r^2=0.12$, $P=0.94$), or temperature (Las Lagunas: $n=7$, $r^2=0.006$, $P=0.87$; El Oro: $n=8$, $r^2=0.11$, $P=0.41$). Using an ANCOVA to examine the interaction of each environmental factor and population, we found no significant interactions (photoperiod: $F_{1,11}=0.47$, $P=0.50$; precipitation: $F_{1,11}=0.08$, $P=0.78$; temperature: $F_{1,11}=0.32$, $P=0.58$).

Female reproductive cycle

A significant relationship existed between $SVL_{\log_{10}}$ and $OM_{\log_{10}}$ and $EM_{\log_{10}}$ of females from Las Lagunas ($n=48$, $r^2=0.22$, $P=0.0007$) but not El Oro ($n=52$, $r^2=0.020$, $P=0.29$). Residual analysis ANOVAs revealed a significant month

effect on OM and EM at Las Lagunas ($F_{6,42}=6.73$, $P<0.0001$) and OM and $EM_{\log_{10}}$ at El Oro ($F_{6,45}=6.33$, $P<0.0001$). EM (*sensu lato*) was largest from December to March and smallest from May to September (Fig. 3).

OM and EM of females from Las Lagunas was positively correlated with precipitation ($n=7$, $r^2=0.84$, $P=0.0035$) and temperature ($n=7$, $r^2=0.69$, $P=0.022$), but not with photoperiod ($n=7$, $r^2=0.44$, $P=0.10$). At El Oro, OM and EM were positively correlated with photoperiod ($n=7$, $r^2=0.71$, $P=0.019$), precipitation ($n=7$, $r^2=0.76$, $P=0.011$) and temperature ($n=7$, $r^2=0.67$, $P=0.024$). Using an ANCOVA to examine the interaction of each environmental factor and population, we found no significant interactions (photoperiod: $F_{1,11}=0.41$, $P=0.84$; precipitation: $F_{1,11}=1.68$, $P=0.22$; temperature: $F_{1,11}=0.63$, $P=0.44$).

Litter size

Mean number of VFs was similar to the mean number of embryos in both females from El Oro (Mann–Whitney U-test, $Z=-149$, $P=0.12$) and females from Las Lagunas (Mann–Whitney U-test, $Z=-0.39$, $P=0.69$; Table 2). Considering VFs and embryos together, mean litter size at El Oro during the reproductive season was 6.6 \pm 0.73 (range 4–11), which did not differ from mean litter size at Las Lagunas (6.2 \pm 0.56, range 2–11; Mann–Whitney U-test, $Z=-0.15$, $P=0.85$; Table 2). Litter size was significantly related to SVL at El Oro ($n=10$, $r^2=0.49$, $P=0.025$), but not at Las Lagunas ($n=22$, $r^2=0.048$, $P=0.33$). Conversely, $EM_{\log_{10}}$ was not related to female $SVL_{\log_{10}}$ ($n=6$, $r^2=0.425$, $P=0.16$) at El Oro but was at Las Lagunas ($n=11$, $r^2=0.62$, $P=0.004$). No relationship existed between the number of embryos produced and female mass (both \log_{10} -transformed) for El Oro ($n=6$, $r^2=0.08$, $P=0.58$), but that relationship was found at Las Lagunas ($n=11$, $r^2=0.52$, $P=0.012$). In December, of seven females from Las Lagunas, four (57.1%) had embryos in the early stages of development (1–6) and three (42.9%) had advanced embryos (stages 20–25). Of five females from El Oro, two (40%) females had embryos in the early stages of development (1–6) and three had advanced embryos (stages 20–25). Females from March ($n=5$) had advanced embryos (stages 20–25, $n=4$; and 30–35, $n=1$).

Embryonic volume was similar for both populations (El Oro: 342 \pm 170 mm³, range 137–1191 mm³; Las Lagunas: 339 \pm 68 mm³, range 119–881 mm³; Mann–Whitney U-test, $Z=-0.85$, $P=0.39$). We estimated the embryonic develop-

ment interval to be approximately 73 days for both El Oro and Las Lagunas. The mean sizes of hatchlings at El Oro (33.5 ± 1.3 mm, range 28.0–38.0 mm, $n=6$) and Las Lagunas (32.2 ± 0.72 mm, range 28.0–35.0 mm, $n=9$) were similar (Mann–Whitney U-test, $Z=-0.65$, $P=0.24$).

DISCUSSION

Sexual dimorphism

Both males and females from El Oro attain a larger body size and have correspondingly larger morphological features (Table 1) than animals from Las Lagunas. This disparity notwithstanding, sexual dimorphism was evident at both sites (Table 1). Sexual dimorphism is common in *Sceloporus* (e.g. Fitch, 1978). In particular, several populations of the closely related *S. jarrovi* show male-biased sexual dimorphism. Male *S. jarrovi* from northern and central temperate regions of Mexico were larger and had larger heads than females (Ramírez-Bautista et al., 2002). Male *S. jarrovi* from the central Chihuahuan desert had larger body size, heads and femurs than females (Gadsden & Estrada-Rodríguez, 2007). Male *S. jarrovi* in southeast Arizona are larger than females (Ruby, 1981; Ruby & Dunham, 1984). In *S. jarrovi*, males engage in aggressive interactions in the months prior to breeding more than females do (Ruby, 1978; Ruby & Baird, 1994). The larger male engaged in an aggressive interaction is generally the winner of the interaction (Ruby, 1978), and larger male *S. jarrovi* have greater reproductive success (Ruby, 1981).

Just as sexual selection may maintain sexual dimorphism within *S. jarrovi* populations, it may, at least partly, explain the sexual dimorphism in *S. minor* at El Oro and Las Lagunas. Proximately, the sexual dimorphism may be explained by differential growth of males and females. Cox & John-Alder (2007) demonstrated that male-biased sexual size dimorphism in *S. jarrovi* arises from males growing faster than females in their first year (see also Cox, 2006). Ruby & Dunham (1984) and Smith & Ballinger (1994) also found that male *S. jarrovi* grow faster than females at all ages.

Reproductive cycles

The testicular cycles for El Oro and Las Lagunas peak in the fall. This is similar to male reproductive cycles in *S. jarrovi* from southeastern Arizona (Goldberg, 1971; Ballinger, 1973).

Except for one female that had VFs (4.2 mm^3) in June, the vitellogenic period for El Oro was apparently longer (September–December) than for Las Lagunas (September–October; Table 2). In contrast, the embryonic development period at El Oro was shorter (December–mid-May) than that of Las Lagunas (December–early June). Although fall ovulation is found in populations of *S. jarrovi* (Goldberg, 1971), Ballinger (1973) noted elevational influences. The earlier timing of parturition at El Oro than at Las Lagunas is consistent with Ballinger's (1973) observations that higher elevation populations give birth later than low-elevation populations. A higher mean annual temperature ($25.8 \text{ }^\circ\text{C}$) at El Oro versus Las Lagunas ($23.5 \text{ }^\circ\text{C}$), a pattern directly influenced by the el-

evation differences between the two sites (1600 m versus 2230 m), may help explain these differences.

As in other species inhabiting montane habitats (Guillette & Casas-Andreu, 1980; Ramírez-Bautista et al., 1996, 1998, 2004), the difference in the onset of reproductive activity (i.e. asynchronous cycles) in males and females suggests that the sexes use different environmental cues. While ovarian activity in females from both Las Lagunas and El Oro increased with precipitation but not temperature, ovarian activity increased with photoperiod only for El Oro females. This suggests that populations of the same species respond differently to differences in the same environmental cues. Intraspecific variation in the timing of male reproductive activity (El Oro: July–December; Las Lagunas: July–October) may reflect intersite differences in the effects of these cues. Mean annual precipitation for El Oro is half of that for Las Lagunas (600 mm), but male reproductive activity was about two months longer at El Oro (July–December) than at Las Lagunas (July–October; Table 2). Several species with fall reproductive activity display a strong inverse correlation between gametogenesis and photoperiod (Ballinger, 1973; Guillette & Bearce, 1986; Ramírez-Bautista et al., 1998, 2002). In contrast, we found no effect of photoperiod on male gonadal growth in either study population, and no effect of photoperiod on female gonadal growth at Las Lagunas. Although a significant effect of temperature and precipitation was found on female gonadal development in both populations, without experimentation we cannot distinguish whether one or both factors are important for initiating gametogenesis. For males, lack of a photoperiod, temperature or precipitation effect at both sites suggests that males do not respond strongly, if at all, to these cues. Other unidentified environmental stimuli may be more important in influencing gonadal development and sexual behaviour in males in these populations.

It should be cautioned that our descriptions of the reproductive cycles are based on small sample sizes in some months. Thus, examination of greater numbers of individuals in those months with low sample sizes would increase our confidence in our interpretations. However, the months when only small sample sizes were examined show patterns similar to what would be expected, and thus we are fairly confident in our conclusions.

Mean litter size for the El Oro and Las Lagunas populations were similar (6.6 and 6.2, respectively). These mean litter sizes fall well within the range of litter sizes observed for the closely related *S. jarrovi* (5.6, Ruby & Dunham, 1984; 5.7, Gadsden & Estrada-Rodríguez, 2007; 6.77, Goldberg, 1971; 4–10.5 depending on age, Ballinger, 1973). At El Oro, but not Las Lagunas, litter size increased with female body size, just as for many populations of *S. jarrovi* (Goldberg, 1971; Ballinger, 1973, 1979; Gadsden & Estrada-Rodríguez, 2007). It is not clear why litter size in Las Lagunas did not vary with female body size. It is particularly interesting that while the relationship between SVL and litter size was significant at El Oro but not Las Lagunas, the relationship between SVL and embryo mass was significant at Las Lagunas but not El Oro. These differences suggest the possibility that the females in these

two populations may engage in alternative life-history or reproductive strategies. In addition, these differences suggest that further examination of this pair of populations might help us understand the determinants of the relationship between female body size, litter size and offspring size in lizards.

In conclusion, the two populations of *S. minor* studied here show some similarities (e.g. litter size, sexual dimorphism), but also several differences (e.g. litter size–female SVL relationship, subtle differences in reproductive cycles, body size). It seems likely that many of these differences can be related to the differences in elevation between the two populations, as has been demonstrated in *S. jarrovi* (Ballinger, 1979). However, further study is necessary to fully understand the source of the similarities and differences.

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