

Variation in reproduction and sexual dimorphism in the long-tailed spiny lizard, *Sceloporus siniferus*, from the southern Pacific coast of Mexico

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Manuscript received: 19 February 2014

Accepted: 12 October 2014 by EDGAR LEHR

Abstract. Reproductive cycle and fat body and liver mass variation were described for male and female *Sceloporus siniferus* during four years (1978, 1980, 1983, and 1993) from a population from the southern Pacific coast of Oaxaca, Mexico. These lizards exhibited continuous reproduction, and the degree of sexual dimorphism varied between years. Males were larger than females in snout–vent length (SVL) in 1978, but both sexes were similar in the other sample years examined. In head length (HL), however, males were larger than females in all years, except 1978. Males reached sexual maturity at 39 mm SVL, whereas females did so at 40 mm SVL. Testicular mass (TM) varied between months. Testicular mass began to increase from March to April, with maximum sizes being reached from May to August, and regression occurred in September and October. Testicular mass was positively correlated with increasing precipitation and photoperiod, but not with temperature. Females contained vitellogenic (in ovary) and oviductal eggs throughout the year, although maximal egg production occurred from April to August. Mean clutch size was calculated by counting vitellogenic follicles (5.0 ± 0.37 SE) and oviductal eggs (4.9 ± 0.43 SE), with the combined figure for both vitellogenic follicles and oviductal eggs being 4.9 ± 0.27 eggs. Clutch size was not correlated with female SVL. Differences observed in reproductive characteristics like clutch size between *S. siniferus* and other oviparous species of the same genus with continuous reproduction, indicate *S. siniferus* might be responding to the environment they inhabit.

Key words. Reptilia, Squamata, Phrynosomatidae, *Sceloporus siniferus*, Reproductive cycle, Oaxaca, Mexico.

Introduction

Reproduction in many lizard species from seasonal tropical environments is well documented as usually cyclical, with courtship and mating occurring at the beginning of the rainy season, and incubation during the rainy season (VITT & OHMART 1974, RAMÍREZ-BAUTISTA & VITT 1997, 1998, HUANG 2011). However, reproduction in lizards from tropical habitats such as rainforest is acyclical, with spermatogenesis (RUÍBAL et al. 1972) and reproductive activity of females (egg production) occurring throughout the year (PIANKA & VITT 2003, RAMÍREZ-BAUTISTA et al. 2006). In these environments, females of oviparous species produce three or more clutches during their reproductive seasons (BENABIB 1994, RAMÍREZ-BAUTISTA et al. 2006). Therefore, lizard species inhabiting aseasonal tropical regions would be expected to have longer reproductive seasons than temperate or seasonal

tropical lizards (VITT & OHMART 1974, LEMOS-ESPINAL et al. 1999, MANRÍQUEZ-MORÁN et al. 2005). Thus, different lengths of the reproductive seasons might result in more clutches with fewer eggs and smaller snout–vent lengths (SVL) of the offspring at hatching in the aseasonal tropics, and fewer clutches with more eggs or a larger SVL of newly hatched young in seasonal habitats (BENABIB 1994).

Considering this hypothesis about length of reproductive season and clutch characteristics, seasonal and aseasonal reproductive patterns vary with annual fluctuations of environmental variables that can induce proximal variations in life history traits within a population (EINUM & FLEMING 2000, GLAZIER 2000). In many lizard species, food availability, precipitation, photoperiod, and temperature can affect growth rate, clutch size, and clutch frequency, as well as age and size at sexual maturity (BENABIB 1994, WANG et al. 2011, HORVÁTHOVÁ et al. 2013).

Sceloporus siniferus is a terrestrial species, inhabiting tropical dry and oak forests. Its distribution extends along the Pacific coast from Guerrero to Chiapas in Mexico to extreme western Guatemala (SMITH & TAYLOR 1950). Very few studies of reproduction and sexual dimorphism exist on this species (LEMONS-ESPINAL et al. 2001, HIERLIHY et al. 2013). We studied the reproductive biology of male and female *S. siniferus* from a section of the Pacific coast of Mexico (Pinotepa Nacional, Oaxaca). The environment of this population is seasonal, and the purpose of this study is to compare reproductive traits and the degree of sexual dimorphism of *S. siniferus* with those of other populations of oviparous species and species of the same genus that inhabit seasonal and aseasonal environments in Mexico (BENABIB 1994, RAMÍREZ-BAUTISTA & VITT 1998, RAMÍREZ-BAUTISTA & OLVERA-BECERRIL 2004, RAMÍREZ-BAUTISTA et al. 2006). We address the following general questions: How much do sexually mature males and females vary in morphological features between years? What are the reproductive cycles of males and females? Does clutch size vary with the SVL of females? Is there a correlation between peak reproductive activity and environmental factors (temperature, photoperiod, and precipitation)? Are reproductive characteristics of this population of *S. siniferus* similar to those of other oviparous species with continuous reproduction from tropical environments?

Material and methods

In this study, we examined specimens deposited in the Collection of Amphibians and Reptiles (CNAR) of the National Autonomous University of Mexico (UNAM), which were fixed in 10% formalin and stored in 70% ethanol. These specimens were collected in four years (1978, 1980, 1983, and 1993) from the same region of Pinotepa Nacional, Oaxaca, Mexico (16°21' N, 98°3' W), at an altitude of 190 m above sea level. The total sample size of adults ($n = 307$) had been collected over the four years as follows: 1978 (33 males, 16 females); 1980 (50 males and 25 females); 1983 (66 males and 34 females); and 1993 (51 males and 32 females). An additional 53 hatchlings and 63 juveniles were collected during the same four years.

Over a period of 15 years (1945–1960), the area had a mean annual temperature of 26.9°C and a mean total annual rainfall of 1,699.7 mm. The climate of the region is seasonal, with higher amounts of precipitation between June and October and decreasing in November; the dry season extends from November through May (GARCÍA 1983). Vegetation cover in the area is tropical deciduous forest (TORRES COLÍN 2004).

Morphological analyses

Morphological descriptions and comparisons were limited to sexually mature males and females. We measured the snout–vent length (SVL; to the nearest 1.0 mm), mass

(to the nearest 0.01 g), head length (HL; to the nearest 0.1 mm) and head width (HW; to the nearest 0.1 mm) of each lizard. Forearm length (FL) and tibia length (TL; both to the nearest 0.1 mm) were measured from the elbow or knee, respectively, to the posterior edge of the pad of the foot. To test for sexual size dimorphism present within the whole sample, we compared SVLs using a Mann-Whitney U-test, and between years using ANOVA, and we used a two-way MANCOVA test to assess the effects of years, sex, and the interaction of these on HL, HW, FL, and TL, employing SVL as the covariate. For this latter purpose, we used untransformed variables, because preliminary analyses showed that regressions on these fit as good as or better than regressions using log transformed variables. If test results were significant, we performed a Bonferroni/Dunn Post-hoc test (ZAR 1999).

Reproductive analyses

A total of 307 adults (200 males and 107 females) of *S. siniferus* collected between 1978 and 1993 were analysed. Because sample sizes were small for each month and year, the data from these years were pooled by month to describe the annual reproductive cycle, and reproductive characteristics such as SVL at sexual maturity, clutch size, and egg volume were compared between years by using a one-way ANOVA. The smallest female containing enlarged vitellogenic follicles (in ovary) or oviductal eggs (in oviduct) was used as an estimate of minimum SVL at maturity. Males were considered sexually mature if they contained enlarged testes and highly convoluted epididymides, which are typically associated with sperm production (LOZANO 2013). Testes (testicular mass, TM), non-vitellogenic follicles (previtellogenic follicles, NVF), vitellogenic follicles (VF), and eggs (E) were removed and weighed (to the nearest 0.0001 g); these classes of follicles are also referred to as the gonad mass. In reproducing females, the largest ovarian follicles (NVF or VF) and eggs in the oviduct on either side of the body, were weighed to the nearest 0.0001 g and multiplied by the number of follicles or eggs on that side to estimate the total gonad mass, indicated here as ovarian mass (OM) or egg mass (EM). It is important to point out that the preservative used might affect, at least to a small degree, the masses estimated here.

In order to check for body-size effects on reproductive variables, we first calculated regressions of log-transformed organ mass (gonad mass, liver, and fat body mass) on log-male and -female SVL. For regressions that were significant (indicating a body size effect), we calculated the residuals from the relationship of organ mass to SVL (all variables were log-transformed) to produce SVL-adjusted variables (SCHULTE-HOSTEDDE et al. 2005) and to ensure the normality and homogeneity of variances (ZAR 1999). We used these residuals to describe organ and/or reproductive cycles. This technique maintains the variation that is due to extrinsic factors (e.g., season) while minimizing the compounding effect of individual variation in SVL. For

Table 1. Mean values (± 1 SE) of morphological characteristics of adult males ($n = 200$) and females ($n = 107$) of *Sceloporus siniferus* from Pinotepa Nacional, Oaxaca, Mexico, collected from 1978 to 1993. SVL – snout–vent length; HL – head length; HW – head width; FL – forearm length; TL – tibia length. Results of ANOVA, testing differences between years.

Characteristics	Males						Females					
	1978	1980	1983	1993	F	p	1978	1980	1983	1993	F	p
SVL (mm)	54.0 $\pm$ 0.99	51.4 $\pm$ 0.89	49.0 $\pm$ 0.79	52.0 $\pm$ 0.76	6.78	0.0002	49.0 $\pm$ 1.0	52.0 $\pm$ 1.0	46.4 $\pm$ 0.89	50.3 $\pm$ 1.1	4.95	0.003
HL (mm)	14.6 $\pm$ 0.25	14.2 $\pm$ 0.22	13.5 $\pm$ 0.21	14.2 $\pm$ 0.19	4.4	0.005	12.9 $\pm$ 0.28	13.7 $\pm$ 0.23	12.5 $\pm$ 0.19	13.2 $\pm$ 0.23	4.9	0.003
HW (mm)	9.9 $\pm$ 0.17	9.6 $\pm$ 0.16	9.1 $\pm$ 0.16	10.0 $\pm$ 0.24	9.93	0.003	8.7 $\pm$ 0.15	9.4 $\pm$ 0.17	8.6 $\pm$ 0.18	9.0 $\pm$ 0.17	4.23	0.007
FL (mm)	8.9 $\pm$ 0.19	8.4 $\pm$ 0.17	8.2 $\pm$ 0.14	8.7 $\pm$ 0.14	3.7	0.012	7.9 $\pm$ 0.28	8.3 $\pm$ 0.15	7.9 $\pm$ 0.16	8.1 $\pm$ 0.19	1	0.372
TL (mm)	14.3 $\pm$ 0.33	14.2 $\pm$ 0.28	13.3 $\pm$ 0.25	14.2 $\pm$ 0.22	3.39	0.019	12.6 $\pm$ 0.41	13.7 $\pm$ 0.26	12.5 $\pm$ 0.23	13.0 $\pm$ 0.28	3.9	0.01

Table 2. Sexual dimorphism in morphological structures of *Sceloporus siniferus* from Pinotepa Nacional, Oaxaca, Mexico. * – $p < 0.05$; ns – not significant.

Characteristics	1978		1980		1983		1993	
	Males (33)	Females (16)	Males (50)	Females (25)	Males (66)	Females (34)	Males (51)	Females (32)
SVL (mm)	54.0 $\pm$ 0.99	49.0 $\pm$ 1.0*	51.4 $\pm$ 0.9	51.5 $\pm$ 1.0 ^{ns}	48.5 $\pm$ 0.8	46.4 $\pm$ 0.9 ^{ns}	52.0 $\pm$ 0.8	50.3 $\pm$ 1.1 ^{ns}
HL (mm)	14.6 $\pm$ 0.3	13.0 $\pm$ 0.3 ^{ns}	14.2 $\pm$ 0.2	13.7 $\pm$ 0.2*	13.5 $\pm$ 0.2	12.5 $\pm$ 0.2*	14.2 $\pm$ 0.2	13.2 $\pm$ 0.2*
HW (mm)	9.9 $\pm$ 0.2	8.7 $\pm$ 0.2 ^{ns}	9.6 $\pm$ 0.2	9.4 $\pm$ 0.2 ^{ns}	9.1 $\pm$ 0.16	8.6 $\pm$ 0.18 ^{ns}	10.0 $\pm$ 0.24	9.0 $\pm$ 0.17*
FL (mm)	8.9 $\pm$ 0.19	7.9 $\pm$ 0.28 ^{ns}	8.4 $\pm$ 0.17	8.3 $\pm$ 0.15 ^{ns}	8.2 $\pm$ 0.14	7.9 $\pm$ 0.16 ^{ns}	8.7 $\pm$ 0.14	8.1 $\pm$ 0.19*
TL (mm)	14.3 $\pm$ 0.33	12.6 $\pm$ 0.41 ^{ns}	14.2 $\pm$ 0.28	13.7 $\pm$ 0.26 ^{ns}	13.3 $\pm$ 0.25	12.5 $\pm$ 0.23 ^{ns}	14.2 $\pm$ 0.22	13.0 $\pm$ 0.28*

regressions that were not significant (i.e., no body size effect), we used logs of organ mass to describe reproductive and/or organ mass cycles. We performed ANOVAs on values with month as the factor to find out, if significant variation existed, including only those months for which $n \geq 3$.

Clutch size was quantified by counting the eggs in the oviducts of adult females during the reproductive season. Females with oviductal eggs and vitellogenic follicles simultaneously were considered to have had at least two clutches. Mean clutch size based on the counts of vitellogenic follicles and oviductal eggs, as well as SVL of females containing them, were compared using Mann-Whitney U-tests. We calculated a Pearson's correlation to test for a possible relationship between clutch size and the SVL of females. Gonad masses of males and females were correlated with monthly averages of temperature, precipitation, and photoperiod (RAMÍREZ-BAUTISTA & VITT 1997). For these analyses, data were pooled across years. We assessed significance at $p < 0.05$. Results are expressed as untransformed mean $\pm$ SE. Statistical analyses were performed using StatView IV (ABACUS CONCEPTS 1992) and SYSTAT version 13.

Results

Males of *S. siniferus* reached sexual maturity at similar SVLs in all years: 39 mm in 1978 and 1983, 40 mm in 1980, and 41 mm in 1993. The SVL of the smallest female with vitellogenic follicles, which are indicative of sexual maturity, was the same in 1978 and 1980 (41 mm) and in 1983

and 1993 (40 mm). The variation of SVL in sexually mature individuals is shown in Table 1. In general, males were larger (SVL = 51 mm) than females (SVL = 49 mm; Mann-Whitney, $Z = -2.41$, $p = 0.01$). Significant differences in SVL were found between years in males ($F = 6.78$, $df = 3,196$, $p = 0.0002$), and females ($F = 4.95$, $df = 3,103$, $p = 0.003$; Tab. 1). Sexes were similar in SVL in 1980, 1983, and 1993, but were different in 1978, with males being larger than females (Tab. 2). There were significant effects of year (Wilk's $\lambda = 0.9$, $p < 0.01$), sex (Wilk's $\lambda = 0.85$, $p < 0.01$), but not their interaction (Wilk's $\lambda = 0.95$, $p = 0.29$) on other morphological characteristics, independent of SVL (Tabs 1 + 2).

Male reproductive cycles

There was a significant relationship between log SVL and log mass of the testes ($r^2 = 0.26$, $F = 70.9$, $df = 1,199$, $p < 0.0001$), log liver mass ($r^2 = 0.16$, $F = 36.3$, $df = 1,199$, $p < 0.0001$), but not with log fat body mass ($r^2 = 0.004$, $F = 0.0008$, $df = 1,198$, $p = 0.999$). Consequently, we used the residuals of the common regressions to describe the testes and liver cycles independently of male size, whereas the fat body was best represented by log-transformed fat body mass (Fig. 1). An ANOVA on residuals of the regressions revealed significant effects of month on TM ($F = 8.7$, $df = 10,188$, $p < 0.0001$), liver mass ($F = 2.5$, $df = 10,188$, $p = 0.005$), and log fat body mass ($F = 4.6$, $df = 10,187$, $p < 0.0001$). The TM varied between months; it was small during January and February, and testicular recrudescence began in March and April, when it increased in size, with

a maximal size from May through August, followed by a decrease from September to October; minimal sizes were noted during November and December (Fig. 1A). The reproductive activity of males was correlated with liver mass ($r = 0.28$, $p < 0.0001$), but not with fat body mass ($r = 0.12$, $p = 0.090$). The increase in TM was positively correlated with the mean monthly precipitation ($r^2 = 0.60$, $p = 0.003$) and photoperiod ($r^2 = 0.65$, $p = 0.002$), but not with the mean monthly temperature ($r^2 = 0.28$, $p = 0.079$).

Female reproductive cycles

There was a significant relationship between log SVL of sexually mature females and log gonad mass ($r^2 = 0.27$, $F =$

37.9, $df = 1,106$, $p < 0.0001$), log liver mass ($r^2 = 0.46$, $F = 90.5$, $df = 1,106$, $p < 0.0001$), but not with log fat body mass ($r^2 = 0.005$, $F = 0.49$, $df = 1,106$, $p = 0.484$). As with males, we removed the effect of female size by using the residuals from the common regressions to describe the gonad and liver cycles, whereas the fat body was best represented by log-transformed fat body mass (Fig. 2). The ANOVAs on residuals of the regressions revealed a significant effect of month on gonad mass ($F = 3.04$, $df = 11,95$, $p = 0.002$), but not liver mass ($F = 0.83$, $df = 11,95$, $p = 0.612$) and fat body mass ($F = 1.24$, $df = 11,95$, $p = 0.272$; Fig. 2). Vitellogenesis and egg production began in March and April, with maximal vitellogenesis and egg production from June through August. Egg production decreased in September, but vitellogenesis again increased from October to Novem-

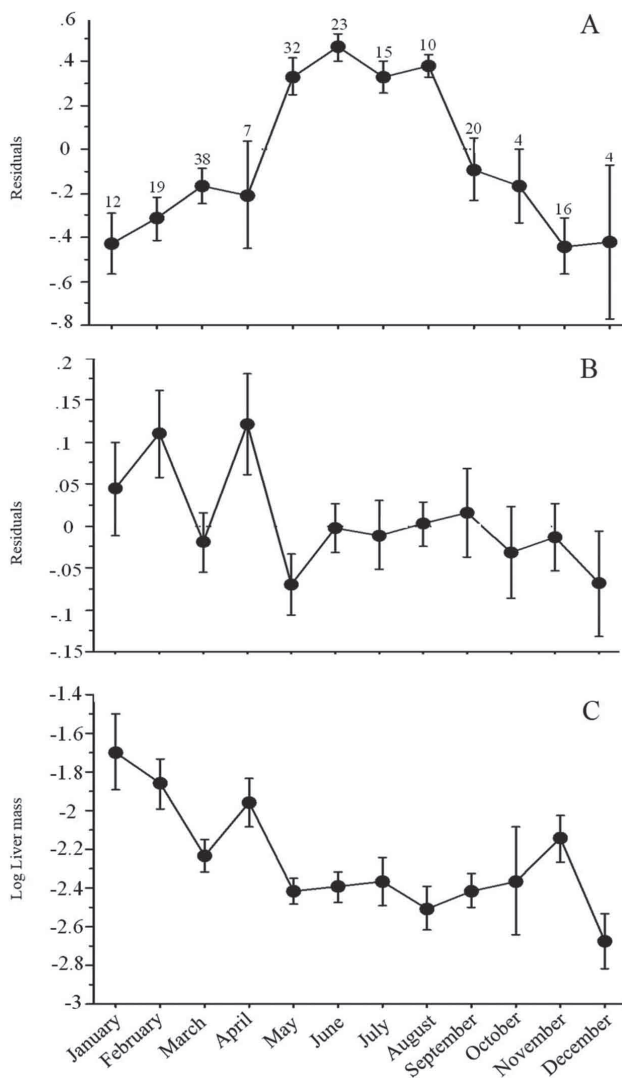


Figure 1. Monthly variation in gonads (A), liver (B), and fat body mass (C) in males of *Sceloporus siniferus* from Pinotepa Nacional, Oaxaca, Mexico. Means are given as $\pm$ SE. Sample sizes are shown above error bars.

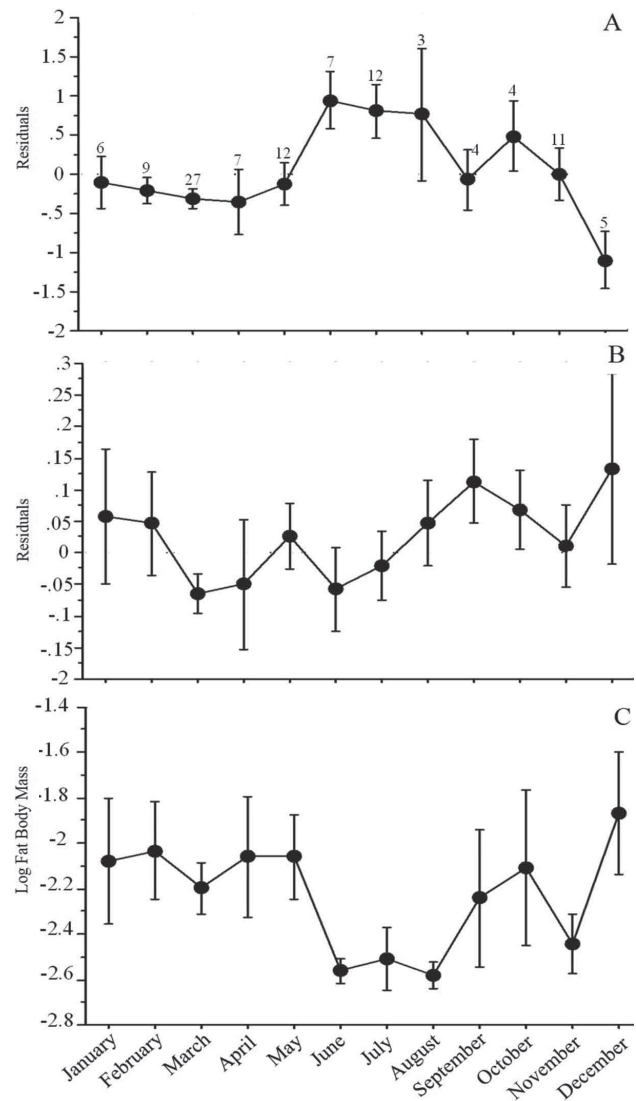


Figure 2. Monthly variation in mass of gonads (A), liver (B), and fat bodies (C) in females of *Sceloporus siniferus* from Pinotepa Nacional, Oaxaca, Mexico. Means are given as $\pm$ SE. Sample sizes are shown above error bars.

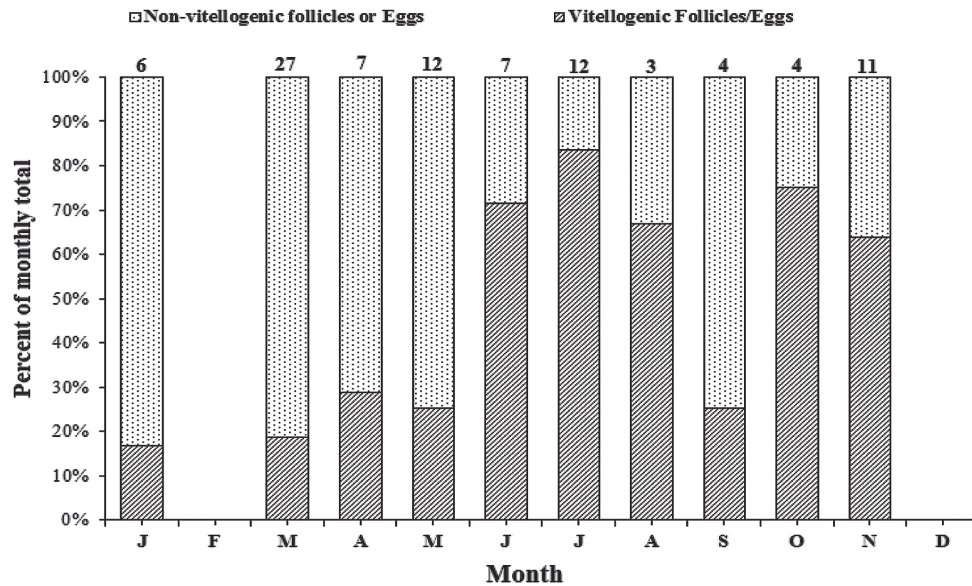


Figure 3. Seasonal distribution (percent) of female *Sceloporus siniferus* in either of the two reproductive states; sample sizes are shown above bars.

ber (Fig. 2A). The reproductive activity was correlated with fat body mass ($r^2 = 0.27$, $p = 0.005$) and liver mass ($r^2 = 0.35$, $p = 0.0003$). Monthly mean gonad mass was positively correlated with precipitation ($r^2 = 0.46$, $p = 0.015$), and photoperiod ($r^2 = 0.39$, $p = 0.031$), but not with temperature ($r^2 = 0.11$, $p = 0.293$).

Vitellogenic ovarian follicles or oviductal eggs were present in January (1/6, 16.7%), March (5/27, 18.5%), April (2/7, 28%), May (3/12, 25%), June (5/7, 71.4%), July (10/12, 83.3%), August (2/3, 66.7%), September (1/4, 25%), October (3/4, 75%), and November (7/11, 64%; Fig. 3).

Clutch size

Of 107 sexually mature females, 71 (66.4%) contained non-vitellogenic follicles, 20 (18.7%) vitellogenic follicles, and 16 (14.9%) oviductal eggs. From the two latter groups, nine females contained both eggs and vitellogenic follicles. Females with NVF varied between years ($F = 2.89$, $df = 3,67$, $p = 0.04$), but not females with VF ($F = 1.99$, $df = 3,16$, $p = 0.157$) or eggs (E) ($F = 0.287$, $df = 3,12$, $p = 0.834$). The mean clutch size based on the count of vitellogenic follicles was similar (5.0 ± 0.37 , $n = 20$) to that derived from counting oviductal eggs (4.9 ± 0.43 , $n = 16$; Mann-Whitney, $Z = -0.015$, $p = 0.988$). The mean clutch size based on counts of both vitellogenic follicles and oviductal eggs was 4.9 ± 0.27 (range = 2–9, $n = 36$). Females with vitellogenic follicles were similar in SVL (52.4 ± 0.87 mm $\pm$ SE, $n = 20$) to females with oviductal eggs (53.2 ± 1.3 mm $\pm$ SE, $n = 16$; Mann-Whitney U-test, $Z = -0.88$, $p = 0.379$). Clutch size was not correlated with female SVL ($r^2 = 0.004$, $p = 0.978$; Fig. 4). No variation between years was found in SVL at hatching ($F = 0.069$, $df = 3,48$, $p = 0.976$). The snout-vent

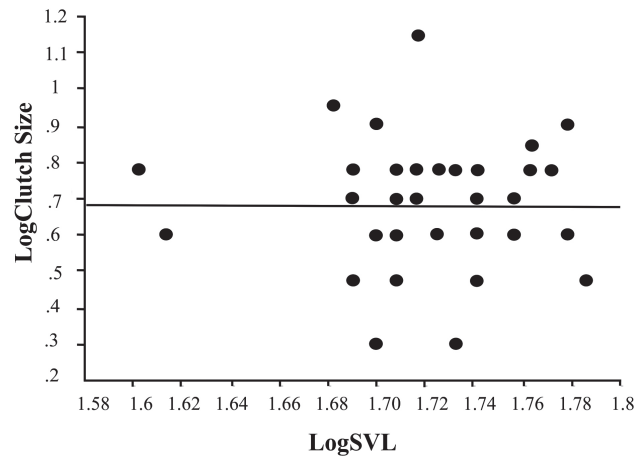


Figure 4. Relationship between log clutch size and log SVL of females *Sceloporus siniferus* from Pinotepa Nacional, Oaxaca, Mexico.

length of hatchlings was 26.9 ± 0.46 mm ($\pm$ SE, range = 21–31 mm, $n = 52$), and that of juveniles 35.0 ± 0.27 mm ($\pm$ SE, range = 32–39 mm, $n = 62$). Hatchlings and juveniles were found in the field almost throughout the year (Fig. 5).

Discussion

Sexual dimorphism

Sexual dimorphism in the genus *Sceloporus* has been relatively well studied in many species (FITCH 1970, 1978, Cox et al. 2003), although there are actually very few studies about its proximate and ultimate causation (Cox et al.

2008). In 1978, FITCH provided data on sexual size dimorphism and tried to identify the potential drivers of this phenomenon in this genus. Among the potential explanations, FITCH identified one in which phylogeny tended to create particular patterns of sexual dimorphism in groups (e.g., male-biased, female-biased, or no dimorphism), and suggested that many species of the genus *Sceloporus* belonged to a group in which “males are relatively larger than females.” However, FITCH’s generalizations were based on single populations of each species he analysed, and nothing has been added for different populations of the same species in recent decades (RAMÍREZ-BAUTISTA et al. 2008, HERNÁNDEZ-SALINAS et al. 2010). In this respect, *S. siniferus* shows the male-biased pattern in different populations of its distribution range (LEMOS-ESPINAL et al. 2001, HIERLIHY et al. 2013, this study). Males of *S. siniferus* were significantly larger than females in SVL and other morphological structures (HL; Tab. 2).

Variations in these morphological characteristics were found to exist between years. For example, in 1978, males and females were similar in these traits, whereas at least one structure was larger in males in the other sample years. Although we do not have sufficient information to identify the cause of sexual dimorphism in *S. siniferus*, it could be explained via the same hypothesis as for other species of the genus (FITCH 1978, LEMOS-ESPINAL et al. 2001). Environmental variables, like temperature and humidity, can influence resource availability and thus the expression of sexual dimorphism, for example in *S. jarrovi* (COX et al. 2006) and *S. spinosus* (RAMÍREZ-BAUTISTA et al. 2013). Differences in morphology between populations might result from different selection pressures that might lead to the evolution of different patterns of sexual dimorphism between populations of the same species. Sexual dimor-

phism in SVL in *S. siniferus* also has been explained by intraspecific niche divergence, which promotes the evolution of trophic sexual size dimorphism (HIERLIHY et al. 2013). Therefore, if males feed on greater quantities of food and their stomachs are larger than those of females, then morphological structures would be expected to be male-biased (VITT & ZANI 1998, McBRAYER & CORBIN 2007, HIERLIHY et al. 2013). Sexual size dimorphism in *S. siniferus* also might be a response to sexual selection, with larger males having an advantage over smaller ones in attracting mates. This phenomenon also could be maintained by differential energy allocation causing different growth trajectories between sexes (RAMÍREZ-BAUTISTA & VITT 1997).

Sexual selection could help to maintain large body size in male lizards if larger males mated more frequently than smaller ones. This hypothesis makes sense, if the male portion of the population is larger than the female one, with males competing for females during the reproductive season, as is the case in *S. variabilis* (RAMÍREZ-BAUTISTA et al. 2006), *S. spinosus* (VALDÉZ-GONZÁLEZ & RAMÍREZ-BAUTISTA 2002), and *S. pyrocephalus* (RAMÍREZ-BAUTISTA & OLVERA-BECERRIL 2004). Similar patterns have been observed in other lizard species (CAROTHERS 1984, BAIRD et al. 1997). Differences in growth rates between sexes are suggested by the seasonal distribution on mean body size, with female growth apparently slowing down relative to that of males before and during reproductive season (BENABIB 1994, RAMÍREZ-BAUTISTA & VITT 1997). Sexual dimorphism in body size could result from a reduction in growth in females coincident with reproduction, as occurs in other lizard species (DEARING & SCHALL 1994, HORVÁTHOVÁ et al. 2013).

Similarities in all morphological structures analysed for 1978 (with the exception of the SVL) in this population

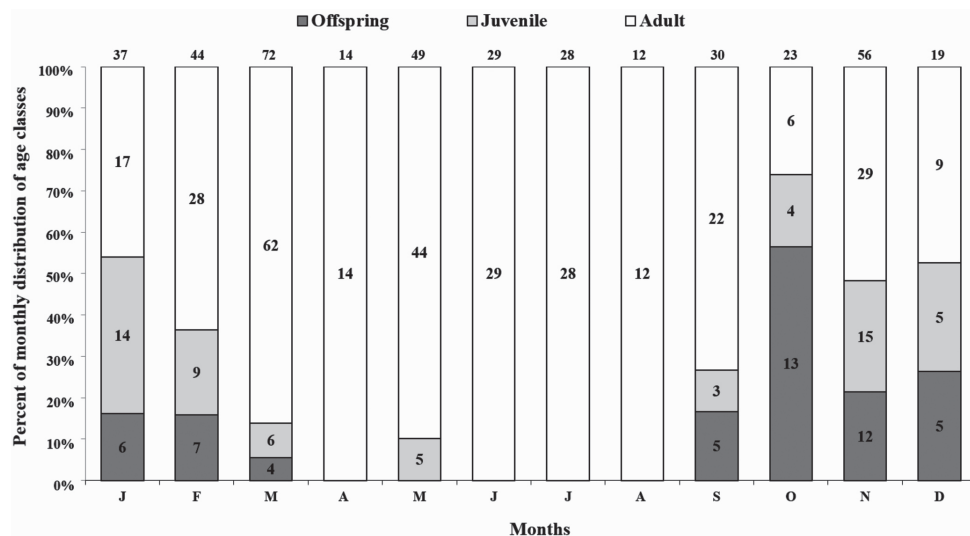


Figure 5. Monthly distribution of age classes (%) of *Sceloporus siniferus* in the study area, Pinotepa Nacional, Oaxaca, Mexico. Sample sizes of each age class are placed in the bars, and total sample sizes are shown above bars.

could be explained by a low degree of polygyny (HIERLIHY et al. 2013), and the high degree of sexual dimorphism that occurred in this population in the years analysed could be explained on the basis of the comments made above. In this study, adult individuals had a smaller SVL (male = 51 mm, female = 49 mm) than those of the Zihuatanejo (male = 53 mm, female = 47 mm; LEMOS-ESPINAL et al. 2001) and Parque Nacional Huatulco populations (male = 57 mm, female = 55 mm; HIERLIHY et al. 2013). These differences between populations and years could be explained by different ecological conditions and their variation between years in male and female *S. siniferus* (LEMOS-ESPINAL et al. 2001, HIERLIHY et al. 2013), as also occurs in other lizard species (AGUILAR-MORENO et al. 2010).

Reproductive cycle

Male *S. siniferus* exhibited seasonal reproductive activity, which occurred from March to October, the extent of which varied between months during the reproductive period. TM began to increase in March and April, maximum TM was from May through August, and a decrease in size occurred during September and October. However, during these latter two months, males probably still have sperm in the ducts epididymis, since there are several histological studies that indicate that males contained masses of sperm in this structure during early regression (McKINNEY & MARION 1985, HERNÁNDEZ-FRANYUTTI & URIBE 2012).

This pattern of reproductive activity is somewhat like that of other lizard species of the genus that inhabit similar environments (*S. variabilis*: GARCÍA-COLLAZO et al. 1993, BENABIB 1994, RAMÍREZ-BAUTISTA et al. 2006; *S. utiformis*: RAMÍREZ-BAUTISTA & GUTIÉRREZ-MAYÉN 2003), and others species (*Sphenomorphus incognitus*: HUANG 2010). The reproductive cycle of male *S. siniferus* was synchronous with the reproductive cycle of the female, primarily in maximum TM with gonad mass (Figs 1A + 2A). The TM was correlated with precipitation and photoperiod, indicating that daylight hours and precipitation are important role players in the activity of males (maximum TM) of this species. No significant correlation was found between TM and temperature; however, the increase in temperature coincided with the increase in TM. Therefore, although it is possible that these three environmental factors play an important role in the reproductive cycle of *S. siniferus*, these may also be correlated with each other. Studies of lizard species inhabiting tropical dry forest have shown that any one or a combination of these factors plays an important role in reproductive cyclicity (MARQUIS et al. 2008, BRANDT & NAVAS 2011). The pattern found in *S. siniferus* is similar to that of other tropical forest species (e.g., *S. variabilis*: GARCÍA-COLLAZO et al. 1993, BENABIB 1994) and other lizard species from tropical rainforests or temperate environments (MARION 1982, LEE et al. 1989).

Reproduction means a high energetic cost to males, as was suggested by the negative relationship between testicular development and fat body masses during the reproduc-

tive season. This pattern is similar to that of lizard species from tropical dry forests with seasonal (RAMÍREZ-BAUTISTA & VITT 1997, 1998) and aseasonal reproduction modes (RAMÍREZ-BAUTISTA et al. 2006). Even though food in this kind of environment is likely to be available at all times, foraging decreases during the mating period because males will spend more time engaging in mating behaviour (HUANG 2010). Male fat body mass decreased during the period of maximum TM (May–August; Figs 1A, C), which might indicate the use of energy for copulation as well as territory acquisition and maintenance during reproduction. In contrast, the liver mass cycle was positively correlated with TM and it only had a maximum peak in April and decreased from May through December; the variation between months was minor (Fig. 1B).

The reproductive activity of females was different from that of males of *S. siniferus*, exhibiting continuous reproduction, despite the fact that maximum VF and egg production were synchronous with maximum sperm production. Females produced VF and eggs almost throughout the year (Fig. 3). Peak reproductive activity (maximum VF and egg production) occurred from March through November, which coincided with increasing (March–May), maximum (June–October), and decreasing (November) activity as well as temperature, precipitation, and photoperiod. This extensive reproductive period could indicate that there is sufficient food available in the environment for females to produce eggs throughout the year (Figs 3 + 5). This pattern has been seen in other oviparous species with continuous reproduction from non-seasonal tropical environments (BENABIB 1994, RAMÍREZ-BAUTISTA et al. 2006), and also in viviparous species from temperate environments (LOZANO 2013).

Clutch size

In this population of *S. siniferus*, clutch size was calculated from the number of enlarged vitellogenic follicles or oviductal eggs. Both parameters yielded similar mean clutch sizes, so that they were summed in order to ascertain clutch size. The small clutch size (5.2 eggs) was larger than that of other species known to have continuous reproduction (3.4–4.6 eggs; *S. variabilis*: BENABIB 1994, RAMÍREZ-BAUTISTA et al. 2006). Female *S. siniferus* did not show any variation in clutch size and egg volume between years even though variation in SVL occurred (Tab. 3).

Variation in clutch size between years has been demonstrated to exist in many lizard species. In smaller ones, this variation could be a reflection of limited food in years of drought (low production of food; BALLINGER 1977). However, small clutches in species with continuous reproduction is an advantage in that females produce several clutches of fewer eggs during reproduction, which spreads the reproductive effort over time and space and in this manner increases the chances for survivorship of the eggs and offspring (ANGUILLETTA et al. 2001, DU et al. 2005). In many lizard species with multiple clutches, clutch size is not cor-

Table 3. Mean values (± 1 SE, followed by sample size and range) of SVL and reproductive traits of adult females ($n = 107$) of *Sceloporus siniferus* from Pinotepa Nacional, Oaxaca, Mexico. Clutch size (Follicles = VF, eggs). Significant statistical differences between years are marked (*) and their p-values shown.

Year	Female SVL (mm)	p	Follicles	p	Eggs	Egg volume (mm ³)
1978	49.1 $\pm$ 1.0 (16) (41–54)		5.2 $\pm$ 1.0 (5) (3–9)		5.0 $\pm$ 0.45 (5) (4–6)	263.1 $\pm$ 48.8 (5) (137–419)
1980	51.5 $\pm$ 1.1 (25)* (41–59)	0.0006	4.3 $\pm$ 0.67 (3) (3–5)		3–6 (2)	202–294 (2)
1983	46.4 $\pm$ 0.89 (34)* (40–55)	0.0006	6.2 $\pm$ 0.49 (5)* (5–8)	0.03	2–6 (2)	199–289 (2)
1993	50.3 $\pm$ 1.1 (32)* (40–61)	0.004	4.1 $\pm$ 0.40 (7)* (3–8)		5.3 $\pm$ 0.78 (7) (2–8)	256 $\pm$ 29.1 (7) (131–350)

related with female SVL (*Urosaurus bicarinatus*: RAMÍREZ-BAUTISTA et al. 1995, RAMÍREZ-BAUTISTA & VITT 1998). A similar pattern occurred in the population of *S. siniferus* studied herein; however, it is not a pattern that occurs in all species with multiple clutches; for example, clutch size is correlated with female SVL in females of several populations of *S. variabilis* (BENABIB 1994, RAMÍREZ-BAUTISTA et al. 2006).

Out of 36 females with VF and eggs, nine (25%) contained both vitellogenic follicles and oviductal eggs. These data suggest that a quarter of the females in this population would have at least two clutches in a given year. This is supported by the number of hatchlings ($n = 53$) and juveniles ($n = 63$) found in almost every month of a year (Fig. 5). These data from this small, oviparous lizard with continuous reproduction could explain the lack of variation in clutch size of the type seen in other tropical lizard species (BENABIB 1994). Another explanation could be the lack of variation of SVL at hatching between years. However, variation in clutch size between years has been reported for many lizard species as a result of years with increased precipitation that favours the abundance of arthropods (BALLINGER 1977, DUNHAM 1982, ZNARI et al. 2002).

Life history characteristics of *S. siniferus* from this population differ from those of closely related congeneric species with continuous or seasonal reproduction and multiple clutches. Small-bodied lizards show variation in life history features, such as female SVL at sexual maturity (range 41–53 mm: RAMÍREZ-BAUTISTA & OLVERA-BECERRIL 2004, RAMÍREZ-BAUTISTA et al. 2006; 40 mm: this study), clutch size (1–4 eggs: RAMÍREZ-BAUTISTA et al. 2006; 2–8 eggs in this study), and reproductive period (seasonal vs. aseasonal: HUANG 2010).

The reproductive period of male and female *S. siniferus* is the longest of species with continuous reproduction in the same genus (*S. siniferus* from Oaxaca: FITCH 1978; *S. variabilis*: BENABIB 1994, RAMÍREZ-BAUTISTA et al. 2006). SVL at hatching was longer (26.9 mm) than that of other lizard species with multiples clutches, such as *U. bicarinatus* (20.0–23.0 mm: RAMÍREZ-BAUTISTA et al. 1995, RAMÍREZ-BAUTISTA & VITT 1998) and *S. pyrocephalus* (26.0 mm: RAMÍREZ-BAUTISTA & OLVERA-BECERRIL 2004). If clutch size is related to the SVL of offspring at birth, then we would expect a larger clutch size and smaller SVL at hatching, but this was not the case in our study, as opposed to other species with continuous reproduction

and multiple clutches (BENABIB 1994, RAMÍREZ-BAUTISTA & VITT 1998). The differences found in these reproductive characteristics among *S. siniferus* and other oviparous species with continuous reproduction (BENABIB 1994, RAMÍREZ-BAUTISTA & OLVERA-BECERRIL 2004) and populations of the same species (FITCH 1978, DU et al. 2014) are likely explained by variation in the environment and the selective pressures on the species (or populations) occupying them (ANGUILLETTA et al. 2001, DU et al. 2005). However, these explanations should be considered with caution at this point of time, because more studies of the same kind are needed for other populations of *S. siniferus*.

Acknowledgements

We thank V. H. REYNOSO and A. BORGONIO (CNAR) for allowing us to examine specimens in the collections under their care. We also thank A. LOZANO for reading a first draft of the manuscript and two anonymous reviewers, who greatly improved it. This study was supported by the project CONABIO Ro45, JM001, and 191908 –Diversidad Biológica del Estado de Hidalgo– 3a Etapa.

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