

RESEARCH ARTICLE

Sexual dimorphism and reproductive cycle in the arboreal spiny lizard *Sceloporus formosus* Wiegmann (Squamata: Phrynosomatidae) from central Oaxaca, Mexico

Dimorfismo sexual y ciclo reproductivo de la lagartija espinosa arbórea *Sceloporus formosus* Wiegmann (Squamata: Phrynosomatidae) de la zona central del estado de Oaxaca, México

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ABSTRACT

It is well known that geographic variation occurs in life history characteristics among populations of lizards. Variations in life histories found in some studies are possibly adaptations to environmental pressures. In southwestern México, the reproductive characteristics of the endemic species *Sceloporus formosus* have been poorly studied throughout its geographic range. We used specimens from scientific collections to describe male and female reproductive cycles and sexual dimorphism of *S. formosus*. Other viviparous *Sceloporus* from high elevations show sexual dimorphism, with males being larger in many morphological characteristics than females. We therefore expected that *S. formosus* would show sexual dimorphism. However, we found no sexual dimorphism. Males reached sexual maturity at a smaller (47 mm) snout-vent length (SVL) than females (50 mm). There were no significant differences between sexes and months in liver mass. However, fat body mass in females was greater than in males. For males, there was significant relationship between \log_{10} -testis volume and \log_{10} -SVL. Testis volume was positively correlated with temperature and was smallest during October, November, and December. For females, there was no significant effect of month on gonad volume. Vitellogenesis occurred from April to November. Vitellogenic follicles and embryonic development were significantly correlated with precipitation (Pearson correlation, $r = 0.80$, $n = 10$, $P = 0.0081$) and photoperiod (Pearson correlation, $r = 0.72$, $n = 10$, $P < 0.0001$). Litter size based on embryos was correlated with SVL (Pearson correlation, $r = 0.82$, $n = 10$, $P = 0.0034$). Relative litter mass was not correlated with female SVL (Pearson correlation, $r = 0.43$, $n = 10$, $P = 0.2110$). The fall reproductive pattern found in this species is typical of viviparous species from high elevation, where temperature is low, and precipitation and relative humidity are high. If so, it would suggest that convergence in reproductive cycle could be associated with a shift to montane habitats in these species.

Key words: litter size, reproductive cycles, reproductive strategy, tropical lizards.

RESUMEN

Es bien conocido que la variación geográfica ocurre en las características de historias de vida entre poblaciones de especies de lagartijas. Las variaciones en las características de historias de vida encontradas en algunos estudios son posiblemente adaptaciones a las presiones del ambiente. En el suroeste de México, habita la especie endémica, *Sceloporus formosus* la cual ha sido poco estudiada en sus características reproductivas a través de su intervalo de distribución geográfica. En este estudio se usaron especímenes provenientes de colecciones científicas para describir el ciclo reproductivo de machos y hembras y dimorfismo sexual de *S. formosus*. En otras especies vivíparas de altitudes elevadas del género *Sceloporus* muestran dimorfismo, donde los machos son más grandes que las hembras en muchas características morfológicas; debido a esto, esperábamos que *S. formosus* mostrara dimorfismo sexual. Sin embargo, no encontramos dimorfismo sexual. Los machos alcanzaron la madurez sexual a menor talla (47 mm) en longitud hocico-cloaca (LHC) que las hembras (50 mm). En cuanto a la masa del hígado no hubo diferencias significativas entre sexos y meses. Sin embargo, los cuerpos grasos en las hembras fueron mayores que en

machos. En los machos, no hubo relaciones significativas entre \log_{10} -volumen testicular y el \log_{10} -LHC. El volumen testicular se correlacionó positivamente con la temperatura y este fue más pequeño durante octubre, noviembre y diciembre. Para las hembras, no hubo efectos significativos del mes sobre el volumen de la gónada. La vitelogenénesis ocurrió de abril a noviembre. Los folículos vitelógenicos y el desarrollo embrionario se correlacionaron significativamente con la precipitación (Correlación de Pearson, $r = 0.80$, $n = 10$, $P = 0.0081$) y el fotoperiodo (Correlación de Pearson, $r = 0.72$, $n = 10$, $P < 0.0001$). El tamaño de la camada basado con el número de embriones, se correlacionó con la LHC (Correlación de Pearson, $r = 0.82$, $n = 10$, $P = 0.0034$). La masa relativa de la camada no se correlacionó con la LHC de las hembras (Correlación de Pearson, $r = 0.43$, $n = 10$, $P = 0.2110$). Este patrón reproductivo otoñal encontrado es típico de especies vivíparas que habitan altitudes elevadas, donde la temperatura es baja, la precipitación y la humedad son altas. Lo que sugiere que la convergencia en los ciclos reproductivos puede estar asociada con un cambio a las condiciones ambientales imperantes en altitudes elevadas.

Palabras clave: ciclos reproductivos, estrategias reproductivas, lagartijas tropicales, tamaño de la camada.

INTRODUCTION

Several studies have documented variation in life histories, population dynamics, and demography both among lizard species (Dunham 1980) and among populations of the same species (Ferguson et al. 1990, Benabib 1994, Ramírez-Bautista et al. 2004). Geographic variation of life history characteristics for some species has been studied. Examples of such species are *Sceloporus variabilis* Wiegmann (Benabib 1994), *S. grammicus* Wiegmann (Lemos-Espinal et al. 1998, Ramírez-Bautista et al. 2004), and *Urosaurus bicarinatus* (Duméril, 1856) (Ramírez-Bautista et al. 1995). Variations in life histories found in these studies are possibly adaptations to different environmental pressures (local environments). These variations in age at maturity, extent of reproductive period, clutch or litter size, offspring size at birth, growth rate among populations of the same species, could reflect plasticity in reproductive traits. Some of these characteristics are fixed at higher taxonomic levels, meaning that there are no variations within and among populations (Stearns 1992). For example, all *Anolis* Daudin have a clutch size of one egg (Ramírez-Bautista & Vitt 1997), or all species of the *torquatus* group are viviparous with a similar litter size. Such traits offer no genetic variation on which microevolution could work (Stearns 1992, Roff 2002).

Many studies of lizard life histories have attempted to obtain empirical data to test current hypotheses of life history evolution (Dunham 1982, Benabib 1994, Ramírez-Bautista et al. 1995, 2004, 2008), but this approach is limited

by the paucity of intraspecific studies. These studies on reproductive patterns have revealed geographic variation in life history characteristics such as clutch (oviparous species) or litter (viviparous species) size, egg size, hatchling size, clutch frequency (oviparous species), fecundity, and age and snout-vent length (SVL) at maturity among populations. Among congeners variation also exists in components of reproductive cycles, such as length of reproductive season, litter size, gestation time, and SVL at sexual maturity (e.g. *S. jarrovii* Cope [Ramírez-Bautista et al. 2002, Gadsden et al. 2008], *S. minor* Cope [Ramírez-Bautista et al. 2008], *S. mucronatus* Cope [Méndez-de la Cruz et al. 1988], *S. torquatus* Wiegmann [Feria-Ortiz et al. 2001]). Variation in these reproductive characteristics might be related to environmental factors such as food availability (Dunham 1982, Benabib 1994), duration of appropriate environmental conditions (Benabib 1994) or phylogenetic history among different taxonomic groups (Dunham & Miles 1985, Stearns 1992, Roff 2002). Formulation and testing of hypotheses explaining the evolution of life history traits of lizards requires descriptive studies on reproduction, especially species from lesser known taxa (Ramírez-Bautista et al. 2008).

A reproductive pattern in which gametogenesis, courtship, copulation, and fertilization occur in the fall was reported for *Sceloporus jarrovii* (Ballinger 1973). This fall reproductive activity is common in viviparous lizards of the genus *Sceloporus* (Guillette & Sullivan 1985), *Plestiodon* Wiegmann (Ramírez-Bautista et al. 1998), and *Barisia* Gray (Guillette & Casas-Andreu 1987) from high elevations.

Sexual dimorphism is common in *Sceloporus* Wiegmann (Fitch 1978, Lemos-Espinal et al. 1999). Males are larger in SVL and other morphological structures than females (Ramírez-Bautista et al. 2002). Sexual dimorphism in *Sceloporus* may be maintained by sexual selection (Fitch 1978, Stamps 1983). Several studies have shown that species with reproductive asynchrony, the advantage of larger male size is presumably the ability to secure more mates, which when coupled with female sperm storage increases male fitness (Ramírez-Bautista et al. 2002).

Sceloporus formosus Wiegmann, is an endemic species of southwestern México, and little is known about reproductive characteristics and sexual dimorphism in populations throughout its geographic range (Guillete & Sullivan 1985). To better understand its reproductive strategy and natural variations, it is necessary to study different populations from different environments, and eventually integrate these studies into a comparative phylogenetic context (e.g., Zamudio & Parra-Olea 2000). Considering the lack of information on reproductive characteristics of *S. formosus* from southwestern of México, the objective of this study was to describe the reproductive cycle of male and female and sexual dimorphism. In addition, we relate the environmental factors with the reproductive characteristics of this lizard species. For this study we use specimens from the scientific collections from Universidad Nacional Autónoma de México.

METHODS

Study area

Reproductive data were obtained from preserved specimens of *S. formosus* (60 females, 55 males and 18 neonates) from the Colección Nacional de Anfibios y Reptiles (CNAR-IBH) of Instituto de Biología and Colección from the Museo de Zoología, Facultad de Ciencias (MZFC), both from Universidad Nacional Autónoma de México. Specimens were from municipalities San Pablo Etla (17°13' N, 96°48' W, 1,641 m), San Andrés Huayapam (17°48' N, 97°47' W, 1,572 m), and Santa Catarina Ixtepeji (17°16' N,

96°32' W, 2,050 m) in the state of Oaxaca, Mexico.

The climate of the area is warm sub-humid with the highest temperature and rainfall occurring in summer. Mean annual precipitation is 800-1,000 mm. Vegetation is coniferous forest and oak-pine (Rzedowski 1978). Climate and meteorological data for a 38-yr period (1934-1972), collected approximately 3 km from the site of the largest collection which is San Andrés Huayapam (García 1981; Fig. 1) were used in this study. Photoperiod data were from the Astronomical Almanac (1984).

Morphological analysis

Morphological descriptions and comparisons were restricted to sexually mature males (n = 55) and females (n = 60). All data were taken from specimens (from both collections) previously fixed (10 % formalin), and deposited in the collections, where gonadal analyses were performed. For all lizards examined, 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). We measured forearm length (FL; to nearest 0.1 mm) and tibia length (TL; to nearest 0.1 mm) from the elbow or knee, respectively, to the pad of the foot (see Sites 1982).

Reproductive analysis

Specimens of *S. formosus* were fixed and preserved in 70 % alcohol by the first author of this study from March to December from 1989-1998 and deposited in the collection (CNAR-IBH), and the same techniques were used for specimens from the collection of MZFC. Because the number of specimens was small among months and years (1989 n = 78; 1992 n = 4; 1993 n = 2; 1994 = 15; 1995 = 5; 1997 = 9; 1998 = 2), data were pooled by month to describe the general annual reproductive cycle for both sexes. The SVL of the smallest female with enlarged vitellogenic follicles (late VF in ovary) or embryos in utero was used to estimate minimum SVL at sexual maturity for females. The SVL of the smallest male with enlarged testes and convoluted epididymes was used to estimate the minimal size at sexual

maturity for males (Goldberg & Lowe 1966). The male reproductive cycle was described by changes in testes mass through the year. Testes, non-vitellogenic follicles (NVF), vitellogenic follicles (early or late VF), embryos, livers, and fat bodies were removed and weighed (to nearest 0.0001 g). In reproductive females, the largest egg (embryos in uterus) or follicular mass (vitellogenic follicles or non-vitellogenic follicles) on each side of the body was weighed to the nearest 0.0001 g and multiplied by the number of eggs (embryos, NVF, FV) on that side to estimate total gonadal mass on each side of the body. Because NVF is too small, the mass of each ovary was used to estimate the mass of NVF. The total mass (embryo, VF, and NVF) for both sides constituted female gonadal mass (Ramírez-Bautista et al. 2002). During the gonadal examination of females, we counted the number of vitellogenic follicles (in ovary) or embryos in the uterus (for litter size) and recorded the length and width of left and right vitellogenic follicles or embryos to the nearest 0.1 mm. Follicle and egg or embryos volumes were obtained using the formula for the volume of an ellipsoid (Selby & Girling 1965): $V = 4/3\pi a^2 b^{-1}$, where a is half the shortest diameter and b is half the longest diameter.

Statistical analysis

Morphological differences between sexes were analyzed using MANOVA (Scheiner 2001), with SVL, HL, HW, FL and TL as dependent variables. We performed analyses of covariance (ANCOVA) with sex and month as a factor in order to determine if these had effect on liver and fat body mass (dependent variables). Other ANCOVAs were conducted to determine the effect of month factor on the changes in testes mass in males and gonad volume in females. Considering that liver mass, fat body and gonad mass could be affected by the size of the individuals, SVL was used as the covariate. If one factor were significant, then a Tukey post hoc test was performed (Zar 1999). Prior to the analyses, all variables were transformed \log_{10} to ensure normality and homogeneity (Zar 1999).

We calculated a Pearson's correlation coefficient to test for a significant relationship between litter size and SVL of females (Ramírez-Bautista et al. 2002). We calculated relative litter mass (RLM; Vitt & Congdon 1978) as litter mass (female mass - litter mass)⁻¹. We determined the stage (1 - 40) of embryonic development according to Dufaure & Hubert (1961). Mean litter size based on vitellogenic

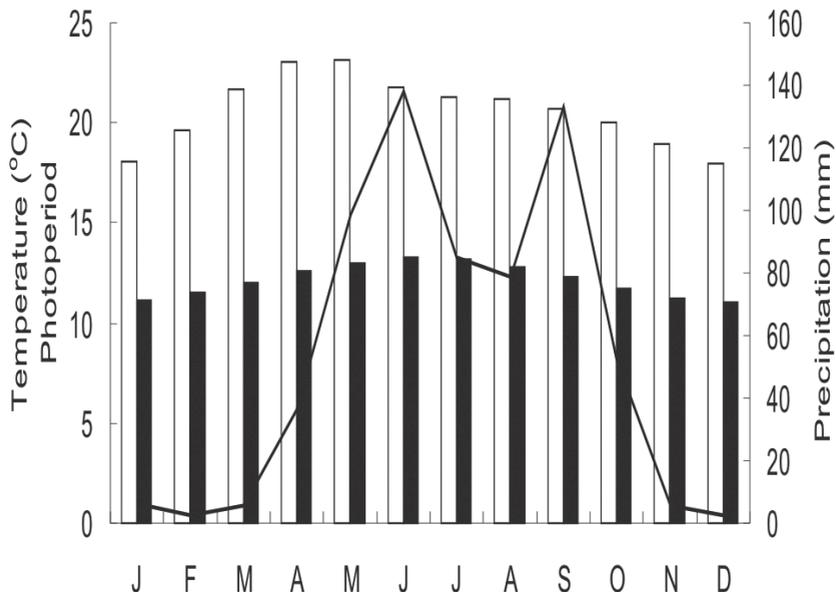


Fig. 1: Mean monthly of temperature (white bars), precipitation (line) and photoperiod (black bars) from de study area.

Promedio mensual de la temperatura (barras blancas), precipitación (línea) y el fotoperiodo (barras negras) del área de estudio.

follicles and oviductal embryos was compared by using a Mann-Whitney test. Testicular volume and vitellogenic follicles were correlated with monthly averages of temperature, precipitation and photoperiod. Statistical analyses were performed using Systat 12.

RESULTS

Sexual dimorphism

Males of *S. formosus* reached sexual maturity at a minimum SVL of 47 mm and females reached sexual maturity at a minimum SVL of 50 mm. Sexually mature males ranged from 47-81 mm SVL (mean = 64.8 ± 1.4 , $n = 55$). Sexually mature females ranged from 50-79 mm SVL (64.8 ± 1.1 , $n = 60$). A MANOVA indicated no sexual dimorphism because there were no significant differences between sexes in any analyzed dependent variables (Table 1).

Reproductive cycles

Analysis of covariance of the liver mass (dependent variable) showed that the major percentage of variance correspond to the SVL (covariate) (ANCOVA, $F_{1,92} = 83.2$, $P < 0.0001$); there was no significant differences between sexes, months and interaction. Fat body mass in females was higher than males (ANCOVA, $F_{1,92} = 24.1$, $P < 0.0001$). Variation between months (ANCOVA, $F_{7,92} = 5.7$, $P = 0.0005$) and the interaction between sex and month (ANCOVA, $F_{7,92} = 5.5$, $P = 0.0005$)

were significant; in addition, the covariate was significant (ANCOVA, $F_{1,92} = 13.1$, $P = 0.0003$). During May and June females had the highest fat bodies mass (Tukey, difference = -3.27 , $n = 8$, $P = 0.7650$), these were different than the other months. In males, there was no significant variation through the year (Fig. 2).

There was a significant positive relationships between \log_{10} - testis volume and \log_{10} -SVL (Spearman correlation, $r^2 = 0.30$, $n = 55$, $P < 0.0001$). Consequently, we used residuals of the linear regression to describe testis volume. An ANCOVA revealed significant variation among months in testis volume ($F_{7,55} = 5.17$, $P = 0.0004$), the covariate effect was significant (ANCOVA, $F_{1,55} = 9.99$, $P = 0.0036$). Testis volume was smallest during October, November, and December (Tukey, difference < -1.06 , $n = 8$, $P < 0.0001$) (Fig. 3; Table 2). Testicular recrudescence began in early spring, and reached maximal volume during mid-spring (from April to May; Fig. 3) and summer (July-September; Fig. 3). Testicular volume was positively correlated with temperature (Pearson correlation, $r = 0.78$, $n = 55$, $P = 0.0085$), photoperiod (Pearson correlation, $r = 0.63$, $n = 55$, $P = 0.0575$) but not with precipitation (Pearson correlation, $r = 0.72$, $n = 55$, $P = 0.1320$).

For females, there were no significant effects of month on gonad volume (ANCOVA, $F_{7,60} = 0.69$, $P = 0.6701$) (Fig. 3); the effect of the covariate was significant (ANCOVA, $F_{7,60} = 23.04$, $P < 0.0001$). Vitellogenic follicles were first detected in April ($n = 2$ females); vitellogenesis took place from April to November ($n = 29$). Two of eight females

TABLE 1

Mean values (\pm SE) of morphological characteristics (SVL = snout-vent length, HL = head length, HW = head width, FL = forearm length, and TL = tibia length) of sexually mature female ($n = 60$) and male ($n = 55$) *Sceloporus formosus*. Results of MANOVA testing differences between sexes.

Valores promedio (\pm ES) de las características morfológicas (SVL = longitud hocico-cloaca, HL = largo de la cabeza, HW = ancho de la cabeza, FL = largo del fémur, y TL = largo de la tibia) de hembras sexualmente maduras ($n = 60$) y machos ($n = 55$) de *Sceloporus formosus*. Se muestra los resultados de la MANOVA de probar diferencias entre sexos.

Characteristics	Males	Females	F	P
SVL	64.8 ± 1.4	64.8 ± 1.1	0.01	0.992
HL (mm)	17.1 ± 0.32	16.6 ± 0.22	1.53	0.218
HW (mm)	14.0 ± 0.30	13.5 ± 0.22	1.78	0.184
FL (mm)	11.2 ± 0.24	10.8 ± 0.17	1.10	0.296
TL (mm)	15.0 ± 0.32	14.4 ± 0.21	1.58	0.211

collected on 28 April had vitellogenic follicles, one female had embryos (stage 6), and five females had non-vitellogenic follicles (3.05 mm³). In October, 12 of 14 females had late vitellogenic follicles (296.7 mm³), and in November; two of three females had vitellogenic follicles (365.3 mm³). Small females (51 - 55 mm SVL) collected between 13 September and 27 October had late vitellogenic follicles. The reproductive cycle of females starts in April-May with maximum

gonad volume from October to November (Fig. 3). The maximum number (n = 7, 50 %) of pregnant females occurred in March. Vitellogenic follicles (n = 29) and embryonic development (n = 10) were positively correlated with precipitation (Pearson correlation, r = 0.80, n = 10, P = 0.0081), photoperiod (Pearson correlation, r = 0.72, n = 10, P < 0.0001), but not with temperature (Pearson correlation, r = 0.52, n = 10, P = 0.1523).

TABLE 2

Reproductive characteristics of male and female *Sceloporus formosus* from Oaxaca, México. We showed mean (\pm SE) and ranges (parenthesis) of RLM (relative litter mass) and SVL (snout-vent length).

Características reproductivas de machos y hembras de *Sceloporus formosus* de Oaxaca, México. Se muestra el promedio (\pm ES) e intervalos (entre paréntesis) de RLM (tamaño relativo de la camada) y SVL (longitud hocico-cloaca).

Characteristics	Male (n = 55)	Female (n = 60)
Reproductive period	March-September	April-November
Vitellogenesis period		April-November
Embryonic development		November-March
Litter size		6.6 \pm 0.62 (4 - 9)
RLM		0.433 \pm 0.06 (0.145 - 0.772)
SVL at hatching (mm)		30.0 \pm 0.63 (25.0 - 33.0)
SVL (range) at sexual maturity (mm)	47.0 - 81.0	50.0 - 79.0

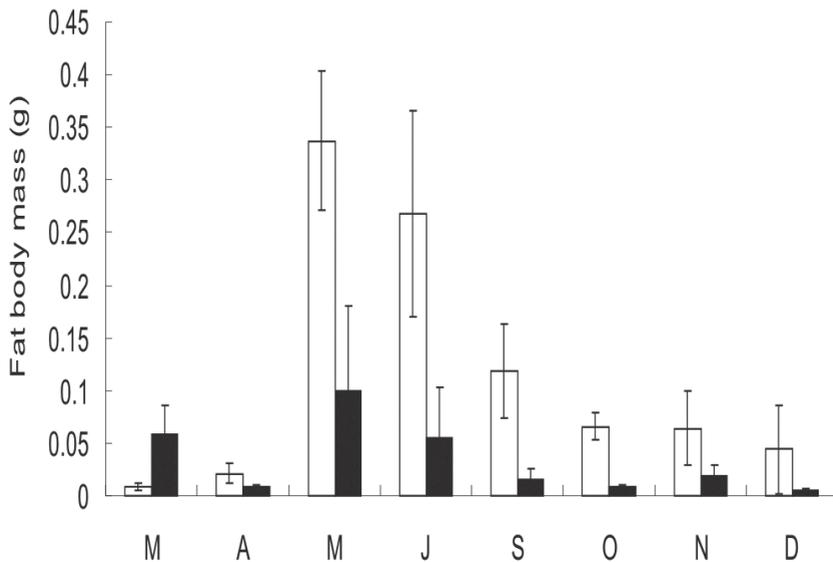


Fig. 2: Annual variation of fat body mass (g) for males (black bars) and females (white bars) of *Sceloporus formosus*. Data are means \pm SE.

Variación anual de los cuerpos grasos (g) de machos (barras llenas) y hembras (barras abiertas) de *Sceloporus formosus*. Los datos son promedios \pm ES.

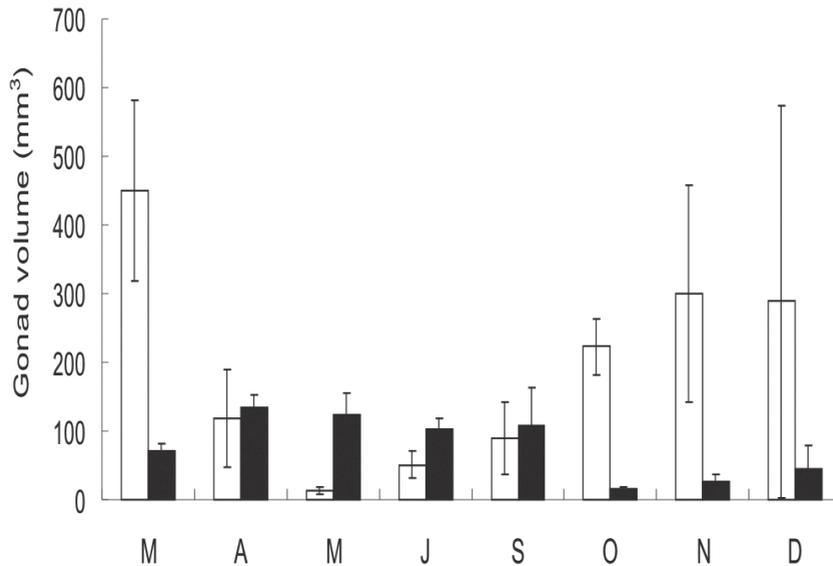


Fig. 3: Annual variation in testis volume (mm^3) (black bars) and females gonads volume (mm^3) (white bars) in reproductive cycles of *Sceloporus formosus*. Data are means \pm SE.

Variación anual en el volumen del testículo (mm^3) (barras llenas) y volumen de las gónadas en hembras (mm^3) (barras abiertas) en el ciclo reproductivo de *Sceloporus formosus*. Los datos son promedios \pm ES.

Litter size and relative litter mass

Mean litter size based on counts of vitellogenic follicles was 8.6 ± 0.59 (3-15, $n = 29$); mean litter size based on counts of oviductal embryos was 6.6 ± 0.62 (4-9, $n = 10$), which were not different (Mann-Whitney, $Z = -1.88$, $n = 10$, $P = 0.0587$). Litter size based on embryos was correlated with SVL (Pearson correlation, $r = 0.82$, $n = 10$, $P = 0.0034$). In November and December, females had embryos ranging from developmental stage 24 to 28, and in March they had embryos in stage 40. Parturition began on 3 March. Mean neonate size was 30.0 ± 0.62 mm (25.0 - 33.0 mm, $n = 18$). Mean relative litter mass (RLM) was 0.433 ± 0.06 (0.145-0.772). Relative litter mass from November and December was 0.145 and 0.413, respectively, and from March was from 0.324 to 0.550. Relative litter mass (RLM) was not correlated with female SVL (Pearson correlation, $r = 0.43$, $n = 10$, $P = 0.2110$).

DISCUSSION

Male *S. formosus* reached sexual maturity at a smaller size than females, which is similar to other populations of *S. formosus* (Guillette &

Sullivan, 1985). Males and females were similar in SVL and other morphological characteristics (HL, HW, FL, and TL). Sexual dimorphism is a very common in *Sceloporus* (Fitch 1978, Ramírez-Bautista et al. 2005). However, in this population we did not find sexual dimorphism, though it could be present in other morphological structures. Males of this species have bright colors on the ventral and ventrolateral body surfaces and the throat are involved in displays to females during courtship and mating during the reproductive season, as occurs in other squamates (Carpenter 1995, Valdez-González & Ramírez-Bautista 2002, Ramírez-Bautista et al. 2006). We suggest that bright color in males could be more important than body size during the reproductive season. Sexual dimorphism has been seen not only in morphological characteristics but also in pattern color between males and females of viviparous species such as *S. jarrovi* (Ramírez-Bautista et al. 2002, Gadsden et al. 2008), *S. minor* (Ramírez-Bautista et al. 2008). Males of viviparous and oviparous species known to be territorial (Fitch 1978), are larger in many morphological structures and brighter in color patterns than females. However, in some species, males and females are similar in morphological structures

but different in color pattern (dorsal and ventral region of the body) such as in *S. torquatus* (Feria-Ortiz et al. 2001), *S. melanorhinus* Bocourt (Ramírez-Bautista et al. 2006), *S. spinosus* Wiegmann and *S. horridus* Wiegmann (Valdez-González & Ramírez-Bautista 2002).

In *S. formosus* vitellogenesis extends from mid-spring (April) to late-autumn (November), and ovulation apparently occurs in mid-fall (October) and early winter (December), and neonates are born in late winter (March) and early spring (March-April). This pattern is similar to other viviparous species from high elevation, such as *S. grammicus* (Guillette & Casas-Andreu 1980, Ramírez-Bautista et al. 2004, 2005), *S. jarrovi* (Ramírez-Bautista et al. 2002), *S. mucronatus* (Méndez-de la Cruz et al. 1988), *S. torquatus* (Feria-Ortiz et al. 2001), *Plestiodon copei* Taylor (Ramírez-Bautista et al. 1996), *P. lynxe* Wiegmann (Ramírez-Bautista et al. 1998), and *Barisia imbricata* Wiegmann (Guillette & Casas-Andreu 1987). The fall reproductive pattern found in this population is typical like above mentioned species and similar to other population of the same species (Guillette & Sullivan 1985). The *formosus* group consists of 14 species (Wiens & Reeder 1997); however there are no studies on reproduction of these species, except a population from southern México (Guillette & Sullivan 1985). It is possible that all of these species could show a fall reproductive pattern (Fitch 1970). If so, it would suggest that this reproductive pattern represents a single evolutionary event in the history of this lineage as it occurs in the *torquatus* group (Ramírez-Bautista et al. 2002, Andrews & Mathies 2000). However, other species of the genus (mentioned above) which inhabit high elevation habitats of México have independently evolved a similar reproductive pattern (Guillette & Casas-Andreu 1987, Méndez-de la Cruz et al. 1988, Ramírez-Bautista et al. 1998). These studies provide compelling evidence that convergence in reproductive cycle is associated with a shift to montane habitats in these species, which has been shown in other species from different environment as well (Boretto et al. 2007, Ibargeüengoytia & Casalins 2007). Several studies have suggested that the primary advantage of this reproductive pattern is protection of the embryos from low temperatures by females and also, to produce

neonates at a time (spring) when resources are abundant (Ballinger 1973, Ramírez-Bautista et al. 1998, 2002, Feria-Ortiz et al. 2001). In addition, another advantage in cooler environments is that gestating females can regulate the temperature of their developing embryos (Andrews & Rose 1994, Andrews et al. 1999).

Male and female *S. formosus* have asynchronous testicular and ovarian cycles, suggesting that mating may occur prior to ovulation, as in viviparous species of the families Scincidae (Ramírez-Bautista et al. 1998), Phrynosomatidae (Guillette 1982, Guillette & Sullivan 1985, Feria-Ortiz et al. 2001, Ramírez-Bautista et al. 2002), Anguidae (Guillette & Casas-Andreu 1987), and Cordylidae (Flemming 1993). This disparity in the onset of reproductive activity in males and females suggests that sexes use different environmental cues, such as in other species inhabiting high elevation (montane) habitats (Guillette & Casas-Andreu 1980, Méndez-de la Cruz et al. 1988, Ramírez-Bautista et al. 1998). An increase of testis size was correlated only with increasing temperature and photoperiod but not with precipitation, even though it is well known that the latter factor plays an important role in the reproductive activity of males in other temperate reptile species (Marion 1982). In contrast, ovarian activity of females was correlated with precipitation and photoperiod but not temperature, suggesting that not all species inhabiting temperate zones respond in the same way to the same environmental cues. Although reproductive activity of males was not correlated with precipitation and that of females was not correlated with temperature, gonad mass starts to increase in both sexes when the highest values of these factors (precipitation and temperature, respectively) occur (Fig. 1), suggesting perhaps a threshold that needs to be reached to start the reproductive cycle. Male and female reproduction in *S. formosus* is correlated with environmental factors in different ways, but experimental studies are needed to determine how environmental factors affect the initiation of gametogenesis.

As with other lizard species, a high energetic cost of reproduction in females is suggested by the negative relationship between gonadal development and fat body and liver

mass during the reproductive season. In contrast, gonad mass of males was positively correlated with both fat body and liver mass. In females, lipids from fat bodies are used for vitellogenesis in some lizard species (Hahn & Tinkle 1965, Derickson 1976); fat bodies in female *S. formosus* increase between May and June, and decrease rapidly between August and December, when ovulation occurs and during embryonic development. A similar pattern occurred with liver mass; it was higher between May and September and decreased between October and March. This pattern is similar to that found in other populations of *S. formosus* (Guillette & Sullivan 1985) and other viviparous *Sceloporus* species (Goldberg 1971, Guillette & Bearce 1986, Feria-Ortiz et al. 2001, Ramírez-Bautista et al. 2002). Reproduction in the fall allows females to give birth in early spring when food begins to be more abundant, as occurs in species from high elevation such as *S. grammicus* (Jiménez-Cruz et al. 2005, Ramírez-Bautista et al. 2005), and species of the *torquatus* group (Fitch 1978, Feria-Ortiz et al. 2001, Ramírez-Bautista et al. 2002). This strategy promotes neonate growth and attainment of minimum SVL for sexual maturity in their first reproductive season as occurs in many lizard species from high elevations (Guillette & Casas-Andreu 1980, Ramírez-Bautista et al. 1996).

Much remains to be learned about reproductive characteristics and cycles of several distinct evolutionary lineages identified within the *formosus* group (Wiens & Reeder 1997) inhabiting a variety of environments across its range of distribution. When we compare the values obtained in this study with Guillette & Sullivan (1985), there were differences in minimum SVL at sexual maturity of males (47.0 mm vs 43.5 mm) and females (50.0 mm vs 42.6). However, there were no differences in mean SVL of sexual maturity in females (64.8 ± 1.1 mm vs 59.8 ± 6.8) and males (64.8 ± 1.4 vs 64.2 ± 6.9 mm). Vitellogenesis (April–November vs May–December) and parturition (March vs April) in this study occurred one month earlier, and litter size was lower (6.6 vs 7.5 young). Litter size was correlated with SVL in females of both studies. Mean RLM was similar to other *Sceloporus* (Vitt & Price 1982). However, our study suggests that there is still much to be

learned about the influence of the environment and phylogeny on life-history characteristics of the species included in the *formosus* group.

In conclusion, we assume multiple factors are involved in life history variation within and among populations of lizard species, and it is the case for this population of *S. formosus*; however, our conclusions could be limited since we used specimens from several years, had small sample sizes for each month, and lacked individuals in some months, and this limits our ability to compare our data with Guillette and Sullivan's study (1985) and use comparative methods (Felsenstein, 1985). To make conclusions about the factors (proximate) influencing life history variation within and among populations of *S. formosus*, requires long-term study, however, this arboreal species has small populations, is restricted to a relatively small area and is very difficult to capture, complicating the continuous capture of individuals. Therefore, the use of specimens from scientific collections permitted us to obtain enough data in order to describe reproductive characteristics.

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