

Reproductive cycle of the spiny lizard *Sceloporus jarrovi* from the central Chihuahuan Desert, Mexico

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The reproductive cycle of a population of *Sceloporus jarrovi* was determined using monthly samples of both sexes collected between April 2004 and March 2005 at the canyon of Las Piedras Encimadas, located in Gómez Palacio, Durango, Mexico. Reproductive activity of both sexes was synchronous, similar to other lizards inhabiting montane zones. Testicular recrudescence began in mid-summer (August), and maximum testicular volume occurred from September to January, declining in February. Testicular recrudescence in volume was negatively correlated with ambient temperature. Females show fall reproductive activity and the reproductive period extended from November to early May. Vitellogenesis occurred from mid fall (November) to early winter (January), with ovulation occurring in late December. Embryonic growth took place from January to May and neonates were observed from May to July. This fall reproductive pattern is common in females from high elevation populations of other viviparous *Sceloporus*. Mean litter size based on embryos in utero was 6.0 ± 0.32 SE (range 4–8). Litter size was positively correlated with female SVL. Fat body cycles in females and males were similar. Fat bodies in males were largest when maximum reproductive activity occurred, and decreased after the reproductive season. Females contained large fat bodies from October to January, followed by a gradual decrease from late winter to mid-spring. Female fat body mass was not depleted until late May, just prior to parturition. This study adds to our understanding of the reproductive cycle of *S. jarrovi*, and indicates that fall reproductive activity is a common reproductive strategy among viviparous *Sceloporus*.

Key words: ovulation, Phrynosomatidae, Sauria, testicular volume, vitellogenesis

INTRODUCTION

Reproductive cycles are indicative of the reproductive strategy of a species (Guillette & Bearce, 1986). Since the classic work of Fitch (1970), an extended literature has developed indicating that lizard species display a number of different reproductive activity patterns (Guillette & Casas-Andreu, 1981; Guillette, 1982; Andrews & Mathies, 2000). For example, the timing of reproductive activity is an important aspect of a species' reproductive tactics. Data from several early studies examining viviparous *Sceloporus* confirmed that a different pattern of seasonal activity was possible for temperate species, as gametogenesis, courtship, mating and fertilization occurred during the fall months. Embryos then develop throughout the winter months with parturition the following spring (Crisp, 1964; Callard et al., 1972; Goldberg, 1970, 1971; Ballinger, 1973; Guillette, 1982; Guillette & Mendez de la Cruz, 1993; Ramirez-Bautista et al., 2002, 2008; Gadsden et al., 2005).

Fat body cycles can reflect the pattern of reproductive effort in lizards (Derickson, 1976a,b). In females, fat bodies may be used for vitellogenesis and winter nutrition (Hahn & Tinkle, 1965; Goldberg, 1972; Guillette & Casas-Andreu, 1981; Guillette & Bearce, 1986), whereas in males fat bodies may contribute to testicular recrudescence,

courtship behaviour and winter nutrition (Goldberg, 1971; Ruby, 1977; Guillette & Casas-Andreu, 1981; Guillette & Bearce, 1986).

Studies of fall breeding in *Sceloporus* frequently find asynchronous reproduction of males and females. In several species, males begin testicular activity during the spring or summer whereas females are vitellogenic and ovulate in the fall (e.g. *S. grammicus*, Guillette & Casas-Andreu, 1980; *S. mucronatus*, Mendez-de la Cruz et al., 1988; *S. minor*, Ramirez-Bautista et al., 2008), suggesting that different factors may influence the timing of reproductive activity in males and females. Mendez-de la Cruz et al. (1988) suggested that males and females either do not use the same environmental signals or use the same cues but in different ways. In reptiles, three environmental factors have been shown to affect reproductive activity: ambient temperature, photoperiod and precipitation (Duvall et al., 1982; Licht, 1984). The precise way in which these mechanisms influence reproductive timing is still little understood (Duvall et al., 1982; Licht, 1984).

The reproductive biology of *Sceloporus jarrovi* has been studied in the southwestern United States (Goldberg, 1972; Ballinger, 1979; Guillette et al., 1981). However in Mexico the few reproductive studies of this species have been focused on temperate or higher elevation populations (Goldberg, 1997; Ramirez-Bautista et al.,

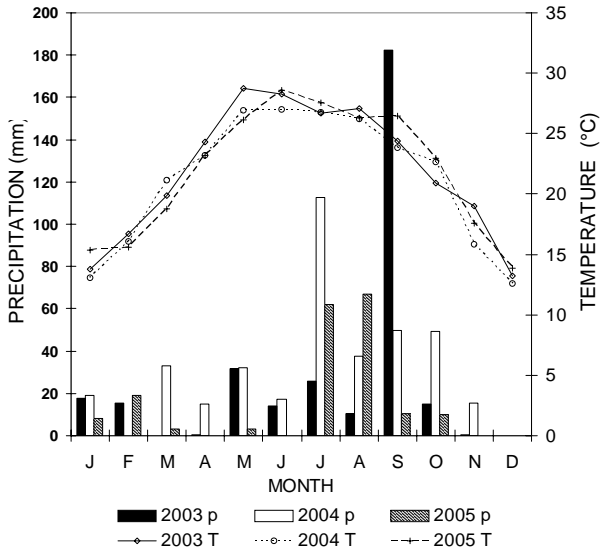


Fig. 1. Monthly mean temperature and precipitation values (2003–2005) for the study area, Estación Lerdo, Durango, Mexico (CONAGUA-SARH, 2006).

2002). Our study examines the annual reproductive and fat body cycles of male and female *S. jarrovi* (*sensu* Wiens et al., 1999) from a population in a low elevation, xeric environment in the central Chihuahua Desert and contrast it with high elevation and temperate populations of *S. jarrovi*.

MATERIALS AND METHODS

Study area

This study was conducted in a location known as the Las Piedras Encimadas canyon (25°38'47"N, 103°38'40"W), 25 km northwest of Gomez Palacio, Durango, Mexico (elevation 1425 m). The climate of the study area is seasonal, with the highest temperature and rainfall occurring in spring and summer, respectively. Mean annual precipitation is 239 mm and mean annual temperature is 21°C (CONAGUA-SARH, 2006; see Fig. 1). Climatic and meteorological data for a three-year period (2003–2005) collected approximately 10 km from the study area were used in this study. Vegetation was dominated by *Agave lechuguilla*, *Acacia greggii*, *Yuca filifera*, *Fouquieria splendens*, *Opuntia rufida*, *Opuntia leptocaulis* and *Jatropha dioica*, and is within the Lechuguilla Scrub (Matorral Xerófilo-Rosetófilo with *Agave lechuguilla*; see Rzedowsky, 1978).

Reproductive analysis

Adult specimens ($n=94$, 51 females and 43 males) of *S. jarrovi* were collected between April 2004 and March 2005. In this study the small sample sizes used may limit our study; however, small sample sizes were intentionally used to minimize the number of lizards sacrificed. Each lizard was measured and weighed, placed on ice, and preserved in 10% formalin. Specimens are deposited in

the collection of the Universidad Juárez del Estado de Durango (voucher specimens – UJED-ESB-SJ-1-94).

Data obtained on each preserved adult included: 1) snout–vent length (SVL, mm); 2) length and width of each testis; 3) fat body mass (to nearest 0.0001 g); 4) number of non-vitellogenic or vitellogenic follicles in each ovary; and 5) number, mass and developmental stage (using Dufaure & Hubert, 1961) of embryos. Testicular volume (V) was calculated by using the formula for the volume of an ellipsoid:

$$V = 4/3 \pi a^2 b$$

where a is half the shortest diameter and b is half the long diameter (Selby, 1965).

Because testicular volume and fat body mass may vary with SVL, we first calculated regressions of \log_{10} -transformed variables with \log_{10} -SVL. For significant regressions (indicating a body-size effect), we used residuals from the relationship to produce SVL-adjusted variables. We used these residuals to describe testicular and fat body cycles (Ramirez-Bautista & Vitt, 1997; Schulte-Hostedde et al., 2005). We performed one-way ANOVA on testicular volume and fat body mass (with month as the factor) to determine whether significant monthly variation exists, including only those months for which $n \geq 3$ (Ramirez-Bautista & Vitt 1997, Ramirez-Bautista et al., 2002). In addition, testicular recrudescence in volume (July throughout November) was correlated with ambient temperature and precipitation.

Male *S. jarrovi* were considered sexually mature if the smallest SVL contained enlarged testes ($\geq 11.3 \text{ mm}^3$) and highly convoluted epididymides, typically associated with sperm production (Goldberg & Lowe, 1966).

The female reproductive cycle was described using the proportion of individuals exhibiting the following conditions: non-vitellogenic follicles (NVF), vitellogenic follicles (VF) and uterine embryos (E). We examined the monthly percentages of these categories throughout the year (see Gadsden & Estrada-Rodriguez, 2008). A

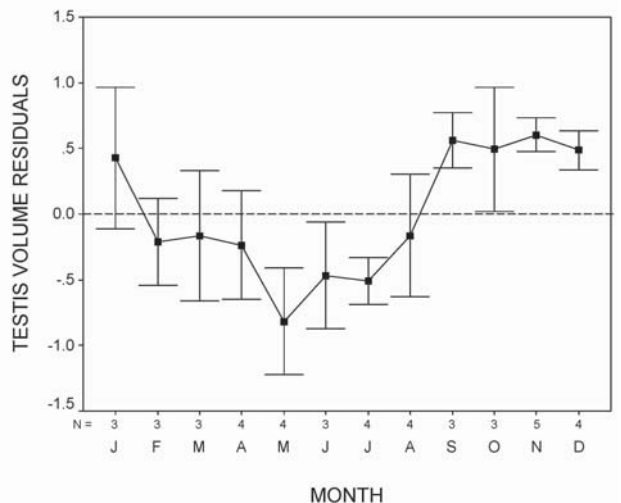


Fig. 2. Male testes cycle of *Sceloporus jarrovi* from the Las Piedras Encimadas canyon, Lerdo, Durango, Mexico. Means are given ± 1 SE. N = sample size.

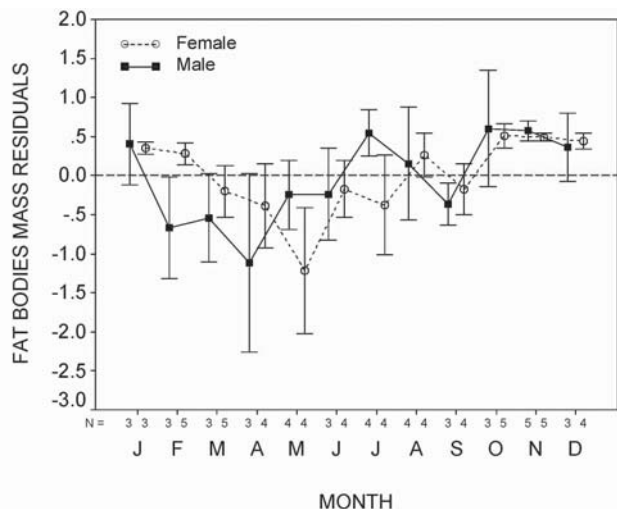


Fig. 3. Male and female fat body cycles of *Sceloporus jarrovi* from Las Piedras Encimadas canyon, Lerdo, Durango, Mexico. Means are given \pm 1 SE. N = sample size.

Pearson’s product-moment correlation coefficient test was used to determine the correlation between SVL of females and litter size (number of embryos in utero) (see Bruning & Kintz, 1977).

RESULTS

Body size (SVL) of reproductively active males averaged 69.6 ± 0.8 mm SVL (mean \pm 1 S.E., 61–83 mm, $n=43$), which was significantly larger than the average SVL of reproductive females (65.3 ± 0.6 mm, 60–81 mm, $n=51$; Mann–Whitney U -test, $Z = -3.7$, $P < 0.0001$).

Male reproductive cycle

There were significant relationships between \log_{10} -SVL of sexually mature males and \log_{10} -testis volume ($r^2=0.12$, $F_{1,41}=5.8$, $P < 0.03$) and \log_{10} -fat body mass ($r^2=0.12$, $F_{1,39}=5.4$, $P < 0.03$). An ANOVA on residuals of the regressions revealed a significant month effect on testis volume ($F_{11,31}=25.13$, $P < 0.001$; Fig. 2). Testicular recrudescence begins in mid-summer (August) with an extended peak from late summer (September) to mid-winter (January). Testes volume decreased from February to May (Fig. 2).

Fat bodies varied in size among months ($F_{11,29}=14.40$, $P < 0.001$; Fig. 3), with a peak in July, a small decrease in August and September, and another peak from October to January, followed by a decline from February to April (see Fig. 3). Testicular recrudescence in volume was negatively correlated with ambient temperature ($r = -0.96$, $P = 0.03$) but not precipitation ($r = -0.49$, $P = 0.5$).

Female reproductive cycle

Females show fall reproductive activity and a reproductive period that extends from mid-fall to mid-spring (Fig. 4), with embryos present from January to May. Nevertheless, females and males have synchronous reproductive activity.

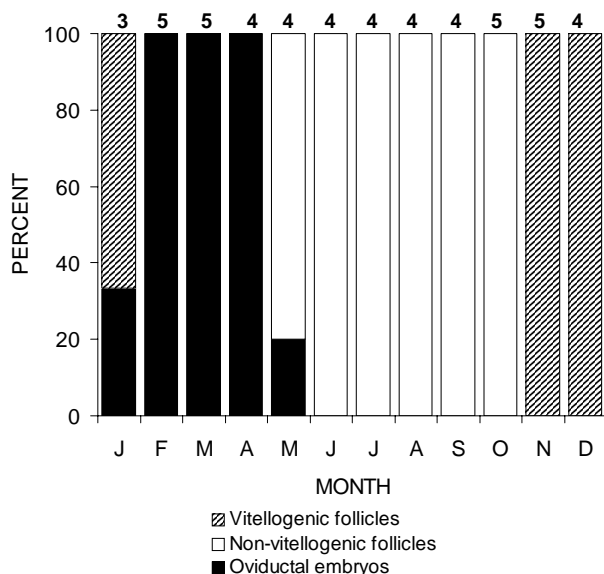


Fig. 4. Percentage of *Sceloporus jarrovi* females in different egg classes at different times of the year. Sample sizes appear above bars.

Vitellogenic follicles were present in females in November (100%, $n=5$), December (100%, $n=4$) and January (66.6%, $n=3$) (see Fig. 4). Ovulation and fertilization occur between December and early January, and females remain pregnant throughout the winter and spring. Mean SVL of gravid females was 68.5 ± 1.3 mm ($n=16$). Gravid females represented 53% of all sexually mature females caught during the reproductive season ($n=30$). The two smallest females with embryos had SVLs of 61 mm. Of 14 females collected from February to April, 100% had embryos in utero.

The embryonic developmental period was estimated from the date at which ovulation and fertilization occurred (December) to the date when the first offspring were seen in the field (late May). These data suggest a gestation period of about 153 days. Embryonic development begins

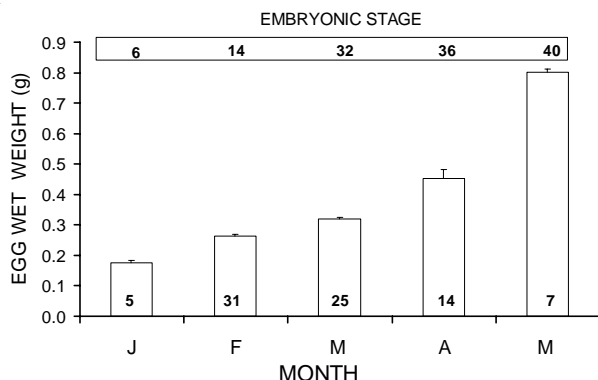


Fig. 5. Mean embryonic stage and egg wet weight (mean \pm 1 SE) in grams during pregnancy in the viviparous lizard *Sceloporus jarrovi*. Sample sizes of embryos appear inside bars.

immediately following ovulation and fertilization and continues for five months (Fig. 5). Rates of embryonic development are relatively slow during the winter (January–March) but increase rapidly during April and May as indicated by the average embryonic stage observed during these months (Fig. 5). Following ovulation eggs increase in wet mass, and during May wet mass increases significantly.

Mean litter size based on the number of in utero embryos was 6.06 ± 0.32 S.E. (range 4–8, $n=15$). Litter size was positively correlated with SVL ($n=16$, $R^2=0.75$, $P<0.0001$). Most births occurred between late May and July, a period when most of the annual precipitation occurred and food was abundant. Neonates averaged 30.19 ± 0.86 mm SVL ($n=13$).

There were significant relationships between \log_{10} -SVL of sexually mature females and \log_{10} -fat body mass ($r^2=0.11$, $F_{1,49}=6.5$, $P<0.02$). An ANOVA on residuals of the regression revealed significant monthly variation in fat body mass ($F_{11,39}=17.73$, $P<0.001$; Fig. 3). Fat body mass peaked from October to February, followed by a gradual decrease from late winter (March) through the spring. Female fat body masses were not depleted until late spring, coinciding with parturition. During fall and winter ingested energy was apparently put into embryonic growth.

DISCUSSION

Male and female *S. jarrovii* from our population are reproductively synchronous, with a fall reproductive pattern, suggesting that both sexes may have similar

responses to environmental cues. Synchronous fall reproductive patterns are similar to other populations of viviparous *Sceloporus* from Durango, Mexico: *Sceloporus grammicus* from high elevations (Ortega & Barbault, 1984) and *Sceloporus poinsetti* from low elevations (Gadsden et al., 2005). However, the fall reproductive pattern we observed shows some variation compared to reproductive cycles of other populations of *S. jarrovii* (see Table 1), and high elevation populations of other viviparous *Sceloporus* (Guillette & Casas-Andreu, 1980; Guillette, 1983; Ramirez-Bautista et al., 2008). All of these species and populations have a fall reproductive season but there are subtle differences among species and among populations of the same species, suggesting that fall reproduction may be adaptive in other habitats than high elevations where it appears so common (Guillette, 1983; Ortega & Barbault, 1984; Guillette & Mendez-de la Cruz, 1993; Goldberg, 1997).

In addition, the fall reproductive cycle in viviparous sceloporine lizards (e.g. the *torquatus* group) could be a phylogenetically conserved trait. Furthermore, fall reproductive activity may be correlated with the evolution of viviparity in these species (Guillette & Mendez-de la Cruz, 1993). In other words, the fall reproductive pattern may have evolved in an ancestral sceloporine in the lineage that had either evolved viviparity or that would evolve viviparity (Guillette, 1982). Nevertheless populations do show differences in SVL at sexual maturity, litter size, vitellogenesis, gestation time and testicular cycles. Females from northern populations tend to be larger and have larger litter sizes and shorter gestation times than females from southern populations (Table 1).

Table 1. Reproductive and fat body characteristics from different populations of *Sceloporus jarrovii* in their distribution range in the United States and Mexico. SVL MMS = snout–vent length minimum and maximum at sexual maturity. Means are presented ± 1 SE. TH: Tinkle and Hadley, 1973; Ba: Ballinger, 1973; Go: Goldberg, 1971, 1997; R-B: Ramirez-Bautista et al., 2002. *Actually *Sceloporus sugillatus* (see Wiens et al., 1999).

Variables	Durango	Arizona	Chiricahua	Baboquivari	Mexico	Morelos
Elevation (m)	1425	1500–2500	1675	1889–1981	2500	3050
Females						
SVL (mm)	65.3 \pm 0.6 (51)	71.8 (52)	64.3 \pm 1.02 (25)	75 (85)	70.7 \pm 0.97 (62)	65.3 \pm 3.2 (4)
SVL MMS	60–81	55–94	–	–	60–86	62–68
Sexual maturity	6–12 months	–	5–17 months	–	–	–
Vitellogenesis	Nov–Jan	Oct–Nov	Oct–Feb	Sep–Nov	Aug–Nov	Aug–Nov
Ovulation	December	November	December	Nov–Dec	December	Nov–Dec
Gestation time	Jan–May	Feb–Apr	Mar–Jun	Dec–May	Jan–Apr	Dec–?
Litter size	6.0 \pm 0.32	6.75 \pm 0.3	7.1 \pm 0.3	6.7 \pm 0.32	6.6 \pm 0.56	3.5 \pm 0.92
Maximum fat body mass	Oct–Feb	–	–	–	Sep	–
Decrease fat body mass	Mar–May	–	–	–	Oct–May	–
Males						
SVL (mm)	69.6 \pm 0.8 (43)	–	–	>60	73.5 \pm 1.3 (98)	81.6 \pm 7.4 (15)
SVL MMS	61–83	–	–	–	60–86	71–93
Testicular recrudescence	Aug–Sep	–	Aug–Dec	Jul–Oct	Aug–Oct	Sep
Decrease testes volume	Feb–May	–	Jan–Apr	Nov–May	Nov–May	–
Maximum fat body mass	Oct–Jan	–	–	–	Sep	–
Decrease fat body mass	Feb–Apr	–	–	–	Nov–Apr	–
Source	This study	TH(1973)	Ba(1973)	Go(1971)	R-B(2002)	Go(1997)*

Our study also indicates that reproductive characteristics of *S. jarrovi* can differ among populations from different altitudes. For example, males from high altitudes are larger in SVL at sexual maturity (Table 1). Females from low altitude populations (e.g. Durango and the Chiricahua Mountains) tend to mature in their first reproductive season (age 5–6 months), whereas no females mature in their first year of activity, instead delaying maturity until 16–17 months of age at high altitude (see Ballinger, 1979). Ballinger (1979) and Ballinger et al. (1996) experimentally demonstrated that high-altitude lizards of *S. jarrovi* do not mature in their first reproductive season if raised in the low-altitude environment, suggesting genetic differences between low- and high-altitude populations.

In our study the reproductive season of female for *S. jarrovi* began after the rains in November–January with embryonic development from January to May. Previous authors have indicated that the primary benefits of a fall reproductive pattern are defence of the embryos from low temperatures by females and producing young at the onset of the spring growing season (Goldberg, 1971; Ballinger, 1973) when food is abundant, as occurs in other species of the *torquatus* group (Ballinger, 1973, 1977; Fitch, 1978; Ramirez-Bautista et al., 2002). This timing would allow maximum growth of neonates before the onset of the next winter and may increase juvenile survivorship (Ballinger, 1973; Ferguson et al., 1982; Mendez-de la Cruz et al., 1988).

The acquisition of food during the winter months may not be necessary as females have lipid stores available to them (Goldberg, 1972; Guillette & Casas-Andreu, 1980, 1981). Pregnancy during winter and early spring would allow the female to use the late spring and summer months to assimilate energy needed for somatic maintenance, growth and reproduction (Guillette & Bearce, 1986). This suggestion is supported by this and other studies demonstrating that just prior to fall reproductive activity in *S. jarrovi* (Goldberg, 1972) and *S. grammicus microlepidotus* (Guillette & Casas-Andreu, 1981), fat body masses increase. Moreover, these lipids appear to be partitioned so that adequate supplies are available for use in reproductive activity (possibly vitellogenesis in females and courtship in males) and somatic maintenance during the winter months. Our results provide further support for this hypothesis.

Average litter size for our population was 6.0, which is smaller than in an Arizona population (Ballinger, 1973) and larger than in a central Mexico population (Ramirez-Bautista et al., 2002). We found a significant relationship between body size and litter size, as has been found in other populations of *S. jarrovi* (Goldberg, 1971; Ballinger, 1973, 1979).

Comparisons of several reproductive characteristics among populations of *S. jarrovi* reveal both similarities and differences. In summary, populations of *S. jarrovi* in Durango, Morelos, and central Mexico show sexual dimorphism in body size (Table 1). However, in the Durango populations, females mature at a smaller body size than in Arizona (see Gadsden & Estrada-Rodriguez, 2008) and have smaller litters than the populations in Arizona. Nev-

ertheless, the Durango population showed larger litter sizes than populations from the central region of Mexico. Thus, each population studied so far differs in some reproductive characteristic from the others, perhaps as a result of local adaptation or geographic differences in the proximate environment. We suggest that the differences in maturity and litter size are probably related to proximate differences in the environment, just as differences in life-history characteristics occur in species such as *Sceloporus undulatus* (Tinkle & Ballinger, 1972; Gillis & Ballinger, 1992; Niewiarowski et al., 2004) or *Urosaurus ornatus* (Dunham, 1982). Much remains to be learned about the reproductive characteristics of at least five evolutionary species previously included in *Sceloporus jarrovi* (Wiens et al., 1999; Martinez-Mendez & Mendez-de la Cruz, 2007; Ramirez-Bautista et al., 2008). Further studies examining the reproductive biology of diverse populations are required so that an understanding of the inherent flexibility in these species can be reached.

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