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Reproductive strategy of male and female eastern spiny lizards *Sceloporus spinosus* (Squamata: Phrynosomatidae) from a region of the Chihuahuan Desert, México

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Abstract. We examined the reproductive strategy of male (n = 84) and female (n = 62) *S. spinosus* from a single population in San Luis Potosí, México. The male reproductive cycle peaked in March and April and declined from May to September, and was not correlated with fat body mass, but was positively correlated with liver mass. The female reproductive cycle peaked in April and May and declined from June through November, and was not correlated with fat body mass, but was correlated with liver mass. Mean clutch size based on oviductal eggs was 17.5 ± 1.9 (n = 12), and was not correlated with female snout-vent length. Our results for *S. spinosus* are generally similar to those of other populations of the *S. spinosus* species group. However, there are differences in some traits (e.g., timing of the initiation of the female reproductive cycle; clutch size), suggesting that the *S. spinosus* group could serve as another model group within *Sceloporus* to explore ecological and evolutionary causes of among population life history variation.

Keywords. Clutch size, lizard, México, reproductive cycle, *Sceloporus spinosus.*

INTRODUCTION

Studies of lizards in the genus *Sceloporus* have contributed greatly to our understanding of the factors influencing life history variation among populations, especially reproductive characteristics (Ballinger, 1977; Dunham, 1978; Hernández-Salinas et al., 2010). Widespread species such as *S. undulatus* (Lemos-Espinal et al., 2003; Niewiarowski et al.,

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2004), *S. grammicus* (Hernández-Salinas et al., 2010), and *S. variabilis* (Benabib, 1994) have been used in numerous studies to examine reproductive variation among populations. Many of these same species have also been well studied at the level of a single population in the context of reproductive cycles (e.g., *S. grammicus*: Guillette and Bearce, 1986; Jiménez-Cruz et al., 2005) or among multiple populations in the context of life-history variation (*S. grammicus*: Hernández-Salinas et al., 2010; Ramírez-Bautista et al., 2011; *S. jarrovii*: Ballinger, 1973, 1979; Ballinger et al., 1996; Ramírez-Bautista et al., 2002; Gadsden et al., 2008; *S. variabilis*: Benabib, 1994). Collectively this research has provided considerable insights into the factors shaping the evolution of life-history traits in lizards (Benabib, 1994; Hernández-Salinas et al., 2010). However, these well-studied species represent only a small sampling of the more than 90 species that comprise the genus *Sceloporus* [see Wiens and Reeder (1997) and Wiens et al. (2010) for a detailed phylogeny of *Sceloporus* with associated species groups]. All of these studies have documented variations in reproductive timing between females and males within a single population or among populations of the same species, as well as variation in reproductive traits (clutch size, egg size, offspring size at birth, etc.). In addition, studies in *Sceloporus* have shown that fat body and liver mass influence sperm production and vitellogenesis (*S. variabilis*: Benabib, 1994; Ramírez-Bautista et al., 2006; *S. jarrovii*: Ramírez-Bautista et al., 2002; *S. pyrocephalus*: Ramírez-Bautista and Olvera-Becerril, 2004; *S. grammicus*: Jiménez-Cruz et al., 2005; Hernández-Salinas et al., 2010; Ramírez-Bautista et al., 2012; *S. formosus*: Ramírez-Bautista and Pavón, 2009), as well as reproductive characteristics such as snout-vent length (SVL) at sexual maturity, clutch size, and offspring SVL (Ballinger, 1977; Benabib, 1994), but this may not always be the case (e.g., male *S. mucronatus*, Méndez de la Cruz et al., 1988; male *S. utiformis*, Ramírez-Bautista and Gutiérrez-Mayén, 2003) or there may be plasticity in the relationship (e.g., Warne et al., 2012). However, we need additional information about these reproductive characteristics with studies on a single population or multiple populations of the same species to understand better the life history variation among lizard populations (Ramírez-Bautista and Olvera-Becerril, 2004; Ramírez-Bautista et al., 2011). Thus, conclusions drawn about variation in reproductive cycles and life history traits in *Sceloporus* based exclusively on the relatively few well-studied species could be biased by aspects of species-specific ecology or phylogenetic history, obscuring more general patterns characteristic of the genus overall (Dunham and Miles, 1985).

Very little has been published to date on the reproductive characteristics of *Sceloporus spinosus* (Fitch, 1978, 1985; Valdéz-González and Ramírez-Bautista, 2002; Calderón-Espinosa et al., 2006), a relatively large oviparous spiny lizard common in saxicolous habitats in central México. This lizard has a relatively large range, occurring across the states of Durango and western Tamaulipas in the north to northern Jalisco, Michoacán, Hidalgo, and Puebla on the Mexican Plateau in the south (Wiens and Reeder, 1997; Wiens et al., 2010). *Sceloporus spinosus* is part of the *S. spinosus* species group containing three species, all of which are endemic to México (Wiens and Reeder, 1997; Wiens et al., 2010). Here we report the first direct observations on reproduction in males and females of *S. spinosus* in a population from the Chihuahuan Desert, San Luis Potosí, México. We were specifically interested in determining the extent to which this population of *S. spinosus* conforms to the reproductive phenology described for other populations of *S. spinosus*, as well as that of another member of the *S. spinosus* species group, *S. horridus*. For example, previous research indicates that peak male reproductive activity (inferred from testes size) occurs in April and May for *S. spinosus* from Puebla, México and in *S. horridus*; a secondary peak in the fall also occurs for the Puebla population of *S. spinosus* (Valdéz-González and Ramírez-Bautista, 2002). Female reproductive activity in these previously studied populations also exhibits strong seasonality for a variety of traits, including onset and duration of vitellogenesis, clutch size, and the timing and duration of egg deposition (Valdéz-González and Ramírez-Bautista, 2002). In general, vitellogenesis is initiated in the winter or spring, and ovulation occurs in the spring and summer. In *S. spinosus* from Puebla, at least some females were capable of depositing two clutches in a given summer (Valdéz-González and Ramírez-Bautista, 2002). If phylogeny plays a major role in determining the reproductive strategies and life history characteristics of *S. spinosus*, we expected our study population to exhibit similar patterns to those of other populations in the *S. spinosus* species group. Alternatively, if local ecological or evolutionary conditions are more important, we expected to find evidence of different reproductive strategies and other life history traits in our population of *S. spinosus* relative to those observed in other populations of the *S. spinosus* complex.

We were also interested in determining the extent to which indices of energy stores (fat body and liver mass) co-varied with male and female reproductive cycles. Two main strategies for energetic balance during the breeding season have been previously identified in *Sceloporus*. In one strategy, lizards accumulate fat stores only prior to the onset of reproduction, and these reserves are consumed over the course of the primary breeding season due to energetic demands and time constraints imposed by reproductive behaviors and activities (Valdéz-González and Ramírez-Bautista, 2002; Jiménez-Cruz et al., 2005). In the alternative strategy, lizards continue to feed and thus accumulate fat bodies and liver mass until the end of the reproductive period, perhaps by reducing their reproductive activities into a smaller portion of their daily energy and activity budgets (Ramírez-Bautista, 1995; Ramírez-Bautista and Vitt, 1997). Fat body and liver mass influence sperm production in males and vitellogenesis in females in some species of *Sceloporus* (*S. variabilis*: Benabib, 1994; Ramírez-Bautista et al., 2006; *S. jarrovii*: Ballinger, 1977; Ramírez-Bautista et al., 2002; *S. pyrocephalus*: Ramírez-Bautista and Olvera-Becerril, 2004; *S. grammicus*: Jiménez-Cruz et al., 2005; Hernández-Salinas et al., 2010; Ramírez-Bautista et al., 2012; *S. formosus*: Ramírez-Bautista and Pavón, 2009), suggesting an important role for these organs in supporting aspects of reproduction in these species.

MATERIALS AND METHODS

Study area

This study was conducted using specimens collected from June 1999 to May 2000 near the community of Las Lagunas (22°30′N, 100°23′W, datum: WGS84; elevation 2230 m) in the Municipality of Guadalcázar, San Luis Potosí, México. This region consists of characteristic high-elevation Chihuahuan Desert, and common vegetation communities of the study site include mesquite scrub-grassland, oak-juniper woodland, and cactus forest dominated by oaks (*Quercus polymorpha*, *Q. laeta*), mesquite (*Prosopis juliflora*) and juniper (*Juniperus flaccida*) (Rzedowski, 1978). Mean annual temperature and precipitation based on monthly means was 25.8 °C and 600 mm, respectively (García, 1981).

Collection and euthanization techniques

A total of 84 adult male and 62 adult female *S. spinosus* was used in this study. Lizards were captured by hand or noose using standard field techniques (Casas-Andreu et al., 1991). In the laboratory, lizards were anesthetized by freezing and sacrificed by nuchal injection of 10% formalin (Ramírez-Bautista et al., 2012). Specimens were fixed in 10% formalin (Ramírez-Bautista et al., 2008) and deposited in the laboratory of the Centro de Investigaciones Biologicas at Universidad Autónoma del Estado de Hidalgo, Pachuca, Hidalgo, for use in subsequent morphological analyses.

Male reproduction

We removed the testes and weighed them to the nearest 0.0001 g to obtain testes mass (TM). Livers and fat bodies were removed and weighed (to the nearest 0.0001 g) so that seasonal cycles in the mass of organs potentially related to reproduction could be described. The mass or size of the testes is frequently correlated with spermatogenic or breeding activity in lizards (e.g., McKinney and Marion, 1985; Van Sluys, 1993; Ochotorena et al., 2005). We considered males sexually mature if they had enlarged testes and convoluted epididymides consistent with sperm production (Goldberg and Lowe, 1966).

To analyze monthly variation in gonad, fat body, and liver mass, we used the residuals of the regression of each variable ($\log_{10}$ transformed) on $\log_{10}$-transformed SVL in ANOVAs with month as the independent variable. We regressed the residuals of fat body and liver mass on the residuals of gonad mass to examine the relationship between energy storage and testicular size (Ramírez-Bautista and Vitt, 1997). Means are given ± 1 SE unless otherwise indicated.

Female reproduction

Non-vitellogenic follicles (NVF), vitellogenic follicles (VF) in the ovary (= follicular mass [NVF plus VF] = FM), and oviductal eggs were removed and weighed to the nearest 0.0001 g. In reproductive females, the largest egg (of the oviductal eggs, or ovarian VF or NVF) on each side of the body was weighed to the nearest 0.0001 g and multiplied by either the number of eggs (egg mass), or VF or NVF (gonad mass) on the same side of the body as appropriate, in order to estimate total gonad mass, indicated here as either gonad mass (GM) or egg mass (EM). Clutch size was determined by counting the number of eggs in the oviducts (OE) of adult females during the reproductive season (i.e., we only counted shelled eggs for clutch size, not VF or NVF). Livers and fat bodies were removed and weighed (to the nearest 0.0001 g) so that seasonal cycles in the mass of organs potentially related to reproduction could be described. We used the SVL of the smallest female with enlarged vitellogenic follicles or eggs to estimate minimum size at sexual maturity (Ramírez-Bautista and Vitt, 1997, 1998).

There were significant relationships between SVL and gonad mass, fat body mass, and liver mass (all $\log_{10}$ transformed). Thus, we performed ANOVAs on the residuals of gonad mass, liver, and fat body mass ($\log_{10}$ transformed) with month as the independent variable to describe the organ cycles (Ramírez-Bautista and Vitt, 1997, 1998). We calculated a Pearson product-moment correlation coefficient to test for a relationship between clutch size and female SVL. Means are reported ± SE, unless otherwise indicated.

RESULTS

Male Reproduction

All of the 84 males we sampled were sexually mature and their testes ranged in mass from 0.006 – 0.870 g. There was a significant relationship between $\log_{10}$-SVL and $\log_{10}$-gonad mass ($r^2 = 0.42$, $F_{1,83} = 58.6$, $P < 0.0001$), $\log_{10}$-fat body mass ($r^2 = 0.52$, $F_{1,83} = 87.5$, $P < 0.0001$), and $\log_{10}$-liver mass ($r^2 = 0.07$, $F_{1,83} = 6.14$, $P = 0.015$). ANOVAs on the residuals of these regressions revealed significant month effects for testes mass ($F_{8,75} = 5.25$, $P < 0.0001$) and fat body mass ($F_{8,75} = 2.34$, $P = 0.026$), but not liver mass ($F_{8,75} = 1.84$, $P = 0.084$). Residual testes mass in males varied significantly among months, with a peak from March to April, followed by a generally steady decline from May to September. This was followed by a sharp increase in October (Fig. 1A), the latest month in the calendar year for which data were available. Residual fat body mass varied significantly among months, with a steady decline from February through May, followed by a steady increase from May through October (Fig. 1B). Residual liver mass showed no significant monthly variation; however, maximum mass was observed during September and October (Fig. 1C). Residual testicular mass was positively related to residual liver mass ($n = 84$, $r^2 = 0.06$, $P = 0.021$), but not to residual fat body mass ($n = 84$, $r^2 = 0.008$, $P = 0.41$).

Female reproduction

Sixty–two adult females were used to study the reproductive cycle, and these showed a significant relationship between $\log_{10}$-SVL and $\log_{10}$-gonad mass ($r^2 = 0.16$, $F_{1,61} = 11.4$, $P = 0.001$), $\log_{10}$-fat body mass ($r^2 = 0.20$, $F_{1,61} = 14.6$, $P = 0.0003$), and $\log_{10}$-liver mass ($r^2 = 0.46$, $F_{1,61} = 51.2$, $P < 0.0001$). As with males, we removed the effects of female size by using the residuals from these regressions to describe gonad mass, fat body mass, and liver mass cycles (Fig. 2A-C). There was significant monthly variation in residual gonad mass ($F_{1,53} = 5.17$, $P < 0.0001$), but not in residual fat body mass ($F_{8,53} = 1.75$, $P = 0.108$) or residual liver mass ($F_{8,53} = 1.65$, $P = 0.1315$). Residual gonad mass peaked in April and May and declined from June through November (Fig. 2A; $F_{8,53} = 5.13$, $P < 0.0001$, $n = 62$). The visual pattern for residual fat body mass shows a small peak in April followed by a decline in May, and then a gradual increase from June through October (Fig. 2B). Although there was no statistically significant variation across months in residual liver mass, inspection of Fig. 2C suggests that liver mass increased sharply from September to November, as compared with the relatively flat pattern observed from March to August.

Females showed variation in gonad development across months (Table 1). No individual female showed both vitellogenic follicles (in the ovary) and oviductal eggs simultaneously, as would be expected if females can lay multiple clutches during a single reproductive season. Females started to produce oviductal eggs on 15 April, and the first day that hatchlings were observed ($n = 1$) was on 5 July, indicating an incubation period of about 82 days.

Residual gonad mass in females was correlated significantly with residual liver mass ($r = 0.28$, $P = 0.027$, $n = 62$), but not residual fat body mass ($r = 0.061$, $P = 0.64$, $n = 62$). Mean clutch size estimated from oviductal eggs was 17.5 ± 1.9 (range 7-28, $n = 12$). Clutch size showed no significant correlation with female SVL ($r = 0.54$, $P = 0.07$, $n = 12$) or female

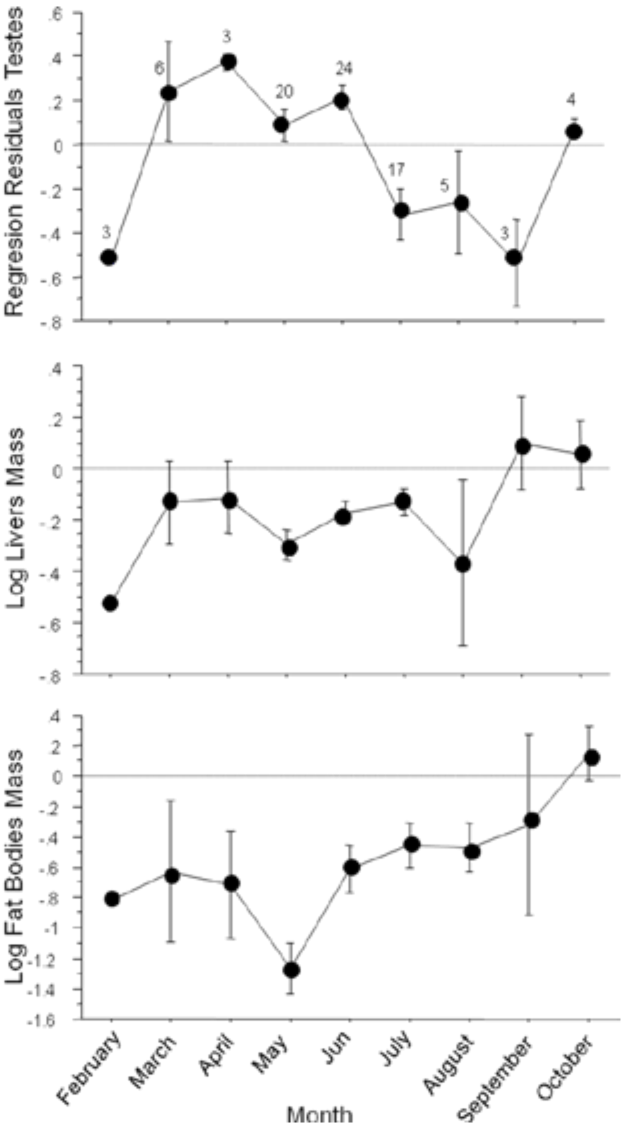

Fig. 1. Annual cycles of residual A) testes mass, B) fat body mass, and C) liver mass for male *Sceloporus spinosus* from Las Lagunas, Municipality of Guadalcázar, San Luis Potosí, México. Means are given ± 1 SE.

mass (both log-transformed, r = 0.08, P = 0.79, n = 12). Total egg mass was also not significantly correlated with female SVL (both log-transformed, r = 0.33, P = 0.290, n = 12).

Mean egg mass was 12.1 ± 1.5 g (range 5.8-24.1 g, n = 12) and was not significantly related to clutch size (n = 10, $r^2 = 0.18$, P = 0.23). Mean hatchling SVL was 34.6 ± 0.8 mm (range 25.7-40.9 mm, n = 33). Hatchlings were observed in the field from July to December.

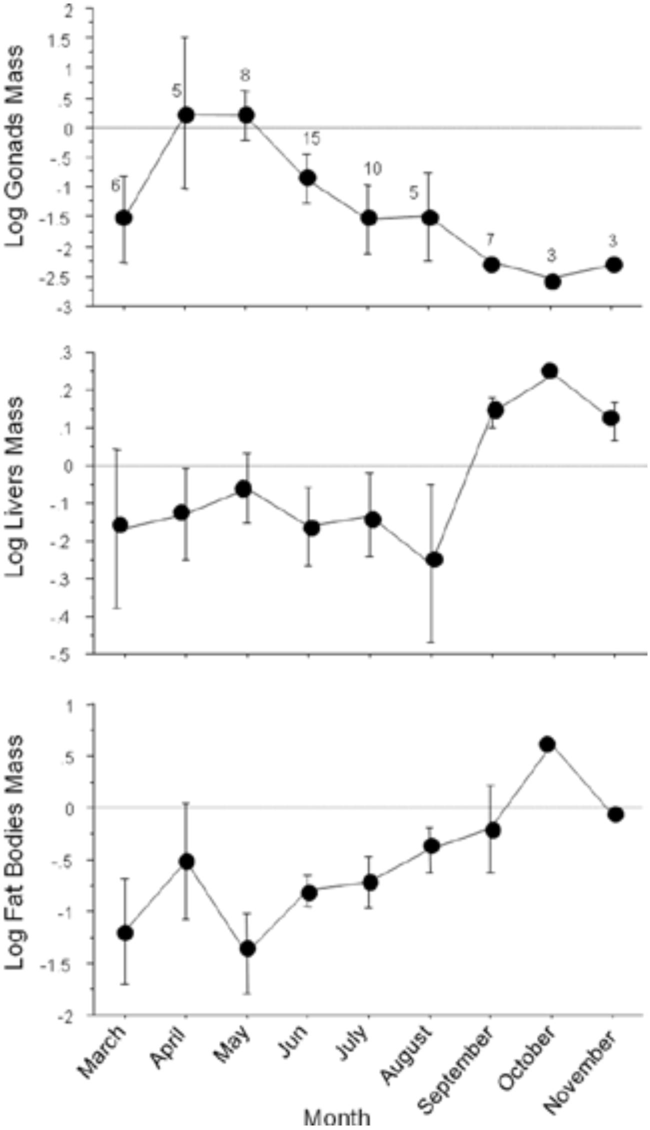

Fig. 2. Annual cycles of residual A) gonad mass, B) fat body mass, and C) liver mass for female *Sceloporus spinosus* from Las Lagunas, Municipality of Guadalcázar, San Luis Potosí, México. Means are given ± 1 SE.

DISCUSSION

Male reproduction

Male *S. spinosus* in Las Lagunas, S.L.P. appear to have a bimodal seasonal reproductive cycle. A peak in testicular mass in April was followed by a gradual decline throughout

Table 1. Number of female *Sceloporus spinosus* with non-vitellogenic follicles (NVF), vitellogenic follicles (VF), and oviductal eggs (OE) in each month of the study.

	March	April	May	June	July	August	September	October	November
NVF	4 (66.7%)	2 (40%)	1 (12.5%)	8 (50%)	7 (70%)	3 (60%)	7 (100%)	3 (100%)	3 (100%)
VF	2 (33.3%)	0	4 (50%)	6 (37.5%)	0	1 (20%)	0	0	0
OE	0	3 (60%)	3 (37.5%)	2 (12.5%)	3 (30%)	1 (20%)	0	0	0

the spring, summer, and early fall, which in turn was followed by a secondary peak in October. The presence of enlarged testes in October suggests that *S. spinosus* may exhibit a second bout of fall breeding activity, although a lack of samples from November to January prevents more definitive conclusions. Although cytological studies are needed to confirm the patterns of seasonality we observed in this study, it is well-established that testicular mass in male lizards is generally greater during the breeding season than before or after (Ramírez-Bautista and Vitt, 1998; Hernández-Salinas et al., 2010). Such a bimodal seasonal pattern of male reproductive activity may be common in *S. spinosus* specifically, and perhaps more generally among members of the *spinosus* group. A previous study of *S. spinosus* from Puebla, México found an initial peak in male testicular size in April and May and a secondary peak in the fall (Valdéz-González and Ramírez-Bautista, 2002). Another member of the *spinosus* group, *S. horridus*, showed an initial peak in testicular size in April and May (Valdéz-González and Ramírez-Bautista, 2002). The onset of the long (March-November) seasonal reproductive cycle of males may be related to one or several environmental factors, such as photoperiod, temperature, or precipitation as has been observed in other lizards (see Marion, 1982). In populations that exhibit two or more breeding seasons within a single year, the onset of each period of reproductive activity may be triggered by different environmental stimuli such as photoperiod or temperature, with the second peak influenced by precipitation, as occurs in many lizards (Marion, 1982; Ramírez-Bautista and Vitt, 1997, 1998). Indeed, a similar pattern showed by males in the population of *S. spinosus* from Puebla, México is related to precipitation (Valdéz-González and Ramírez-Bautista, 2002). Variation in the timing and number of reproductive peaks may indicate the existence of a plastic response to common environmental factors in oviparous species of *Sceloporus* more generally, or it may be that species of the *spinosus* group respond in a similar way to environmental factors as a function of shared evolutionary history (Miles and Dunham, 1992; Wiens and Reeder, 1997).

In male *S. spinosus* from Las Lagunas, testes mass was positively correlated with liver mass, but not with fat body mass. Inspection of Fig. 2B reveals that fat body mass decreased sharply during May, immediately following the peak of the primary reproductive season. Depletion of male fat reserves across the breeding season has been observed in other lizard species, and is consistent with the idea that reproductive activities have a high energetic cost (Ramírez-Bautista and Vitt, 1997; Ramírez-Bautista et al., 2002; Hernández-Salinas et al., 2010). Thus, male *S. spinosus* are apparently unable to maintain a net positive (or neutral) energy balance during the spring reproductive season, despite the relative availability of food resources during this period (Ramírez-Bautista, 1995; Ramírez-Bautista and Vitt, 1997). This pattern has been observed in several other species of *Sce-*

loporus from México, including *S. formosus* (Guillette and Sullivan, 1985), *S. grammicus* (Guillette and Casas-Andreu, 1981; Guillette and Bearce, 1986; Ramírez-Bautista et al., 2009), *S. mucronatus* (Méndez-de la Cruz et al., 1994), *S. pyrocephalus* (Ramírez-Bautista and Olvera-Becerril, 2004), *S. utiformis* (Ramírez-Bautista and Gutierrez-Mayén, 2003), and *S. variabilis* (Benabib, 1994). The alternative strategy, where males maintain stable fat body and liver volumes during the reproductive season, has also been documented in Mexican spiny lizards (e.g., *S. dugesii*: Ramírez-Bautista and Dávila-Ulloa, 2009; *S. gadoviae*: Ramírez-Bautista et al., 2005; *S. jalapae*: Ramírez-Bautista et al., 2005; *S. grammicus*: Hernández-Salinas et al., 2010).

Female reproduction

Female *S. spinosus* also have a seasonal reproductive period, extending from March to August (Table 1). Gonad mass increased sharply in April and May, a finding congruent with an increase in the number of vitellogenic follicles and oviductal eggs during this timeframe (Fig. 2A, Table 1). The onset of the female reproductive period in this population of *S. spinosus* is delayed compared to a population from Puebla, México; at that site, vitellogenesis was initiated in late January, with ovulation occurring in the spring and early summer (Valdéz-González and Ramírez-Bautista, 2002). The female reproductive cycle of *S. horridus* (another member of the *spinosus* group) showed a somewhat similar extension in reproductive activity (Valdéz-González and Ramírez-Bautista, 2002). Male and female *S. spinosus* exhibit synchronous reproduction; thus, as in males, females begin producing vitellogenic follicles in March coincident with increased temperature and photoperiod, and the end of reproduction in August coincides with increased precipitation (see García, 1981). This pattern is similar to that observed in other lizard species (Marion, 1982; Ramírez-Bautista and Olvera-Becerril, 2004), indicating that these three environmental factors can often play an important role in determining the onset and duration of reproductive activity in lizards (Marion, 1982; Hernández-Salinas et al., 2010).

At Las Lagunas, female *S. spinosus* appear to produce only a single clutch per year (Table 1). At Puebla, females can produce up to two clutches per year, each apparently slightly smaller (12.6%) than the single clutch of females from Las Lagunas (Valdéz-González and Ramírez-Bautista, 2002; this study). These results could be explained by variation in predation pressure in the environments that these populations inhabit (Ramírez-Bautista, 1995). All species of the *spinosus* group have a larger clutch size than other species of *Sceloporus* (Valdéz-González and Ramírez-Bautista, 2002; see Ramírez-Bautista and Olvera-Becerril, 2004), which could reflect population or species-specific differences in predation pressure (Ballinger, 1979; Benabib, 1994; Ramírez-Bautista, 1995). The extended reproductive cycle of the Puebla population permits females to have two clutches, perhaps because the wet season at Puebla is longer and results in greater total precipitation than at Las Lagunas (Valdéz-González and Ramírez-Bautista, 2002). However, this interpretation should be considered with caution, since the population studied by Valdéz-González and Ramírez-Bautista (2002) was conducted using individuals from a wide geographic area in México.

Female gonad mass was positively correlated with liver mass, but not fat body mass. As liver mass was relatively high and fat body mass relatively low during the period of peak reproductive activity in females, the energy invested in vitellogenic follicles and eggs probably comes from fat body masses exclusively (or nearly so). These data provide more evidence that reproduction incurs a high energetic cost in female lizards (Ramírez-Bautista and Vitt, 1997, 1998; Ramírez-Bautista and Olvera-Becerril, 2004; Hernández-Salinas et al., 2010), in addition to other costs of reproduction (Ballinger, 1977; Ramírez-Bautista, 1995). Our results suggest that this population of *S. spinosus* could contribute to our understanding of the role of fat body and liver energy reserves in affecting juvenile and adult growth rate, and the onset of sexual maturity in lizards (see Benabib, 1994).

Mean clutch size in our population of *S. spinosus* was 17.5 ± 1.9 eggs, similar to that reported for the Puebla population (15.5 ± 1.2 eggs: Valdéz-González and Ramírez-Bautista, 2002). Clutch size for females from Las Lagunas is greater than that for the populations of the *spinosus* species group reported in Calderón-Espinosa et al. (2006; range of means = 9.2-16.6 eggs), as well as that of a population of *S. spinosus* from Oaxaca (mean = 12.66; Fitch, 1978, 1985). It is also larger than that reported for two populations of another member of the *spinosus* group, *S. horridus* (mean = 14.0, Valdéz-González and Ramírez-Bautista, 2002; mean = 9.3, Ramírez-Bautista, 2003). Thus, there is clearly substantial variation in clutch size among populations of the *spinosus* species group. Further work is needed to examine potential causes of this variation. Obtaining information on additional populations of *S. spinosus* or other members of the *spinosus* species group, as well as data from populations of species groups closely related to the *spinosus* group, will help in elucidating the relative contributions of environmental factors and phylogeny (Ballinger, 1979; Miles and Dunham, 1992; Benabib, 1994).

In lizards, body size usually positively influences clutch size [see Fitch (1985) and Dunham et al. (1988) for reviews]. Interestingly, we did not find a significant relationship between female body size and clutch size, which is an adaptive strategy found in populations of lizards influenced by variation in climate, predation intensity, female size (Vitt and Price, 1982), or variation in rainfall and drought directly affecting food availability and consequently clutch size and offspring size (Abell, 1999). However, at Las Lagunas the trend for larger females (n = 7, females > 100 mm SVL had clutch sizes ranging from 15 – 28 eggs, with the exception of a single female of 108 mm SVL which had 7 eggs) to produce larger clutches was nearly significant ($P = 0.071$). There was also no such relationship in the previously-studied population of *S. spinosus* from Puebla or the population of *S. horridus* (Valdéz-González and Ramírez-Bautista, 2002), suggesting that the relationship between female size and clutch size is non-existent or very weak in the *S. spinosus* species group. This correlation pattern has been documented in both oviparous (Benabib, 1994; Ramírez-Bautista and Olvera-Becerril, 2004; Ramírez-Bautista et al., 2005) and viviparous species (Ramírez-Bautista et al., 2008).

Conclusions

Our results for male and female reproduction in *S. spinosus* suggest that they are generally similar in some reproductive characteristics (see above) to other members of the *S. spinosus* species group. However, we found some evidence of variation in reproductive traits (e.g., timing of the initiation of the female reproductive cycle; clutch size) relative to other populations of *S. spinosus* and other species within the *spinosus* group. These results suggest that the *S. spinosus* group could serve as another model group within *Sceloporus* to explore ecological and evolutionary causes of interpopulational variation in life history traits. Future efforts should target *S. edwardtaylori*, the only member of the *spinosus* group lacking baseline reproductive data. However, studies of additional populations of *S. spinosus* and *S. horridus* will also be crucial in determining both the extent of geographic variation in reproductive traits, as well as assessment of the relative importance of environmental factors and evolutionary history on life history characteristics.

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