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Reproductive Characteristics of the Spiny Lizards, *Sceloporus horridus* and *Sceloporus spinosus* (Squamata: Phrynosomatidae) from México

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ABSTRACT.—We studied the reproductive characteristics of the spiny lizards, *Sceloporus horridus* and *Sceloporus spinosus* (Phrynosomatidae). The specimens ($N = 102$) of *S. horridus* came from the state of Morelos and Guerrero, and individuals of *S. spinosus* ($N = 87$) came from Puebla, México. Male *S. horridus* exhibited a peak of reproductive activity during early spring and early summer and male *S. spinosus* during spring and autumn. Females of both species showed a reproductive peak during the summer. Vitellogenesis of *S. horridus* began in late March and of *S. spinosus* in late January, and ovulation in both species occurred during spring and early summer. Mean snout–vent length (SVL) of sexually mature females (based on the largest 50%) was higher in *S. spinosus* ($\bar{x} \pm SE = 98.6 \pm 1.85$) than in *S. horridus* (91.4 ± 1.32 , $P < 0.05$). Mean clutch size (vitellogenic follicles + oviductal eggs) for *S. spinosus* was higher (18.5 ± 1.5 , $N = 18$) than for *S. horridus* (14.8 ± 0.91 , $N = 30$, $P < 0.05$). There was no significant correlation between snout–vent length of females and clutch size of *S. spinosus* ($r = 0.51$, $P > 0.05$) or *S. horridus* ($r = 0.06$, $P > 0.05$).

RESUMEN.—Estudiamos las características reproductivas de las lagartijas espinosas, *Sceloporus horridus* y *Sceloporus spinosus* (Phrynosomatidae). Los especímenes ($N = 102$) de *S. horridus* provinieron de los estados de Morelos y Guerrero, y los individuos de *S. spinosus* ($N = 87$) de Puebla, México. Los machos de *S. horridus* exhibieron un pico de actividad reproductiva al inicio de la primavera y del verano, y los machos de *S. spinosus* durante la primavera y el otoño. Las hembras de ambas especies mostraron el pico reproductivo durante el verano. La vitelogénesis de *S. horridus* comenzó a fines de marzo y de *S. spinosus* a fines de enero, y la ovulación en ambas especies ocurrió durante la primavera y al principio del verano. La media de la longitud hoco-cloaca (LHC) de las hembras sexualmente maduras (basado sobre el 50% más grandes) fue mayor en *S. spinosus* ($\bar{x} \pm SE = 98.6 \pm 1.85$) que en *S. horridus* (91.4 ± 1.32 , $P < 0.05$). La media del tamaño de la puesta (folículos vitelogénicos + huevos oviductales) de *S. spinosus* fue mayor (18.5 ± 1.5 , $N = 18$) que para *S. horridus* (14.8 ± 0.91 , $N = 30$, $P < 0.05$). El tamaño de la puesta no estuvo correlacionada con la LHC ni en las hembras de *S. spinosus* ($r = 0.51$, $P > 0.05$) ni en las de *S. horridus* ($r = 0.06$, $P > 0.05$).

Reproduction in many lizard species from seasonal tropical environments is cyclical, with courtship, mating, and copulations occurring at the beginning of the rainy season (Ramírez-Bautista, 1995; Ramírez-Bautista and Vitt, 1997). Egg production and incubation usually occurs during the wet season, with hatchlings emerging at the end of the rainy season (Ramírez-Bautista and Vitt, 1998). Several studies have associated the seasonal reproductive activity with rainfall, temperature, and photoperiod (Marion, 1982; Ramírez-Bautista et al., 1995, 1996, 1998).

Variation in reproductive characteristics within and among populations also is associated with seasonal and annual fluctuations of the environment (Ballinger, 1977; Dunham, 1982; Smith et al., 1995). Environmental factors such as food, precipitation, and temperature can affect growth rates, survivorship, clutch size,

clutch frequency, and age and size at maturity (Ballinger, 1977; Dunham, 1982; Van Loben Sels and Vitt, 1984; Benabib, 1994). Variation in life history can also depend on phylogeny (Dunham and Miles, 1985; Vitt, 1990, 1992). Life-history variation among higher taxa is often greater than variation among populations of the same species (Grant and Dunham, 1990; Miles and Dunham, 1992; Ramírez-Bautista et al., 1995).

Lizards in temperate regions often have different reproductive patterns from those in tropical regions. For example, lizards from temperate zones tend to have late maturity, larger clutch sizes, and shorter reproductive periods than lizards from tropical regions (Tinkle et al., 1970; Ramírez-Bautista et al., 1995; Ramírez-Bautista and Vitt, 1998). However, many of the data used for these conclusions were based on lizards of small body size from the wet tropics. At the present, few studies exist on reproductive patterns of lizards from tropical arid zones. Thus, one might suspect that the often extreme seasonality of temperate regions could result in

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different reproductive cycles and patterns than in tropical arid environments (Tinkle et al., 1970).

Although the life histories of several species of *Sceloporus* lizards have been studied intensively (Fitch, 1978; Ferguson et al., 1990; Patterson, 1991; Ramírez-Bautista et al., 1995), little has been published on reproductive characteristics of the Mexican lizards *Sceloporus horridus* and *Sceloporus spinosus* (Fitch, 1970, 1978, 1985). Both species belong to the *spinosus* group (Sites et al., 1992). *Sceloporus horridus* occurs in southern Morelos, Guerrero, and Oaxaca in the Balsas Basin, and Puebla. *Sceloporus spinosus* occurs from Durango and western Tamaulipas to northern Jalisco, Michoacán, Hidalgo, and Puebla on the Mexican Plateau (Smith and Taylor, 1950).

In this study, we focused on the male and female reproductive characteristics and cycles of *S. horridus* and *S. spinosus*. We addressed the following questions: (1) Do males and females become sexually mature at the same size? (2) What are the annual reproductive cycles of females and males? (3) How large are the clutches? (4) Is clutch size related to female size?

MATERIALS AND METHODS

We collected reproductive data on preserved specimens of *S. horridus* (37 females and 65 males) and of *S. spinosus* (40 female and 47 males) from the Colección Nacional de Anfibios y Reptiles (CNAR) from Instituto de Biología, Universidad Nacional Autónoma de México. Individuals of *S. horridus* were collected in Morelos state: Cuautla (18°18'N, 99°20'W; elevation 900 m), Cuernavaca (18°55'N, 99°14'W; 1529 m), and El Rodeo (18°46'N, 99°21'W; 1200 m), and Guerrero state: Alcozauca (17°21'N, 98°29'W; 1200 m), Huitzucó (18°18'N, 99°20'W; 900 m), and Zumpango (17°40'N, 99°31'W; 970 m). Specimens of *S. spinosus* came from Acajete (19°7'N, 97°57'W; 2254 m) and Las Minas (19°58'N, 97°23'W; 537 m) in Puebla state. Specimens were collected from 1976 to 1983.

Reproductive Analysis.—The following measurements were taken on necropsied lizards: snout–vent length (SVL), length and width of testes, diameter of oviductal eggs, and the diameter of vitellogenic and nonvitellogenic follicles (all to ± 0.1 mm). The smallest females of *S. horridus* (SVL = 67.0 mm) and *S. spinosus* (SVL = 64.0 mm) with enlarged vitellogenic follicles or oviductal eggs were used to estimate minimum SVL at maturity. Males of *S. horridus* (SVL ≥ 55.0 mm) and *S. spinosus* (SVL ≥ 65.7 mm) were considered sexually mature if they contained enlarged testes (≥ 10.39 and 14.5 mm³, respectively) and epididymides typically associated with sperm production (Goldberg

and Lowe, 1966). Gonads of both sexes were removed and weighed (to ± 0.0001 g). The largest egg (oviductal, vitellogenic follicle, or nonvitellogenic follicle) on each side of the body was weighed to ± 0.0001 g and multiplied by the number of eggs on that side. The calculated total weight for both sides was used as an estimate of female gonadal mass. Because organ mass may vary with SVL, we first calculated regressions of \log_{10} -transformed organ mass data against \log_{10} of female SVL. For those regressions that were significant (indicating a body size effect), we calculated residuals from the relationship of organ mass to SVL (all variables \log_{10} -transformed) to produce SVL-adjusted variables. We used these residuals to describe the organ sizes and reproductive cycles. This technique maintains variation because of extrinsic factors while minimizing the confounding effect of individual variation in SVL (Ramírez-Bautista and Vitt, 1997). We performed one-way ANOVA on the organ masses (with month as the factor) to determine whether significant monthly variation exists, including only those months for which $N \geq 3$ (Ramírez-Bautista and Vitt, 1997).

To estimate the volume of oviductal eggs, we measured length and width of the largest egg in each oviduct, calculated a mean for the two parameters, and estimated volume as:

$$V = \pi LW^2(3c^2 + 14c + 35)/210$$

where L is egg length, W is egg width, and $c = \lambda(\sqrt{E} - 1)$. E was estimated as 2.0 and λ as 0.50 (for both species) by comparing the shape of eggs of *S. horridus* and *S. spinosus* with models in Maritz and Douglas (1994).

The number of nonvitellogenic and vitellogenic follicles and/or oviductal eggs was recorded for females. Clutch size was determined by counting eggs in the oviduct or vitellogenic follicles of adult females during the reproductive season (Ramírez-Bautista et al., 1998).

Morphological descriptions were restricted to sexually mature males and females. To examine sexual size differences between males and females, we restricted the dataset to the upper 50% of the sample of sexually mature lizards to reduce bias due to sampling error (Ramírez-Bautista and Vitt, 1997).

Means ± 1 SE are presented unless otherwise indicated. Parametric statistical tests were used when possible. Otherwise, appropriate nonparametric tests were substituted. Statistical analyses were performed with the Macintosh version of Statview 4.01 (Abacus Concepts, Inc., Berkeley, CA, 1992).

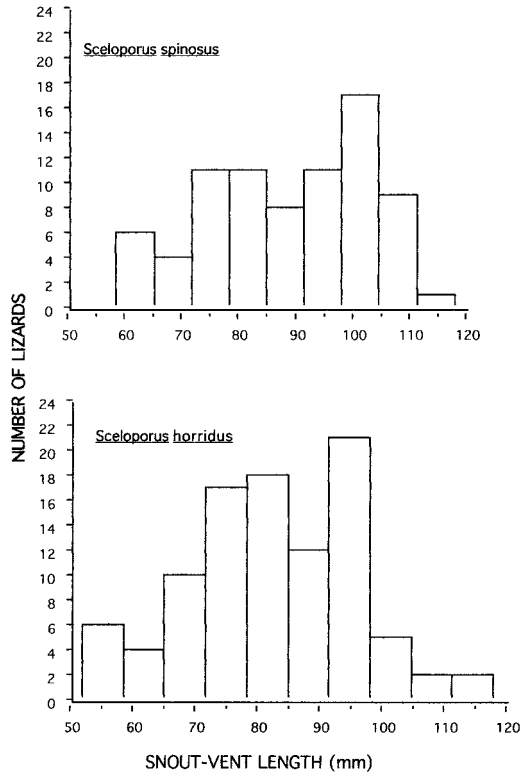


FIG. 1. Size (SVL) distributions of *Sceloporus spinosus* and *Sceloporus horridus* (sexually mature males and females combined).

RESULTS

Body Size and Sexual Maturity.—In *S. horridus*, sexually mature males ranged in size from 52.0–118.0 mm SVL (83.2 ± 2.0 ; $N = 62$) and sexually mature females ranged from 60.0–100.0 mm SVL (81.8 ± 1.8 ; $N = 34$; Fig. 1). In *S. spinosus*, sexually mature males ranged in size from 65.7–110.5 mm SVL (90.4 ± 2.7 ; $N = 40$) and females ranged from 60.0–112.0 (87.0 ± 2.5 , $N = 38$; Fig. 1). Based on comparisons of the largest 50% of sexually mature males and females, there were no differences between sexes in mean SVL of *S. horridus* (Mann-Whitney *U*-test, $Z = -1.354$, $P > 0.05$) or *S. spinosus* (Mann-Whitney *U*-test, $Z = -0.415$, $P > 0.05$). Mean SVL of females was higher in *S. spinosus* (98.6 ± 1.85 , $N = 21$) than *S. horridus* (91.4 ± 1.32 , $N = 16$, Mann-Whitney *U*-test, $Z = -2.74$, $P < 0.05$), but male SVL was similar in both species ($P > 0.05$).

Male Reproductive Cycle.—There were significant positive linear relationships between male SVL and testis volume of *S. horridus* ($r^2 = 0.601$, $F_{1,63} = 94.88$, $P < 0.001$, $N = 65$), and *S. spinosus* ($r^2 = 0.708$, $F_{1,45} = 109.14$, $P < 0.005$, $N = 47$; all data \log_{10} -transformed). An ANOVA on residuals of the regressions revealed significant

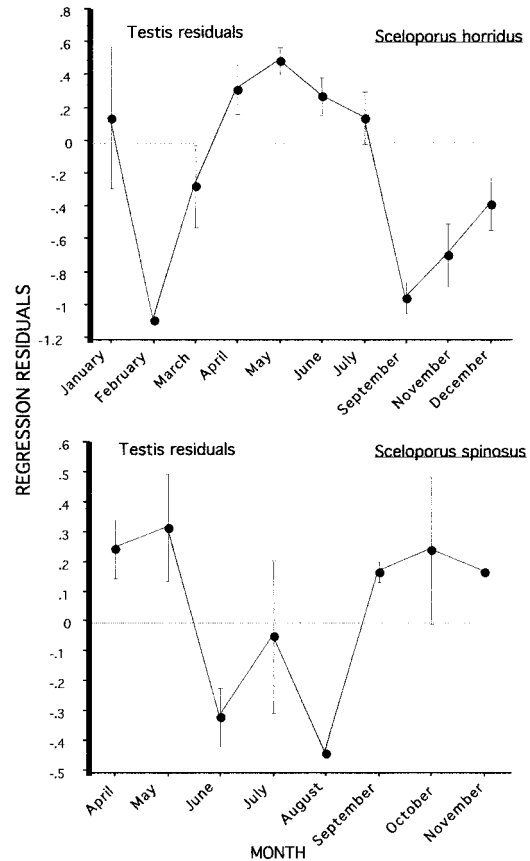


FIG. 2. Seasonal cycle of testis size of male *Sceloporus horridus* and *Sceloporus spinosus*. Data are mean (± 1 SE) residuals from a regression of \log_{10} [testis volume (mm^3)] against \log_{10} (SVL).

variation among months in *S. horridus* ($F_{9,55} = 9.46$, $P < 0.001$; Fig. 2) and *S. spinosus* ($F_{7,39} = 2.37$, $P < 0.05$; Fig. 2). In *S. horridus*, testicular volume increased from February through April, May, June, and July (Fig. 2). In contrast, testicular volume in *S. spinosus* showed two peaks, first during April and May, and the second one between September and November (Fig. 2).

Female Reproductive Cycle.—There were significant linear relationships between female SVL and gonadal mass in *S. horridus* ($r^2 = 0.405$, $F_{1,35} = 23.79$, $P < 0.001$, $N = 37$) and *S. spinosus* ($r^2 = 0.253$, $F_{1,38} = 12.87$, $P < 0.005$, $N = 40$; both variables transformed \log_{10}). An ANOVA on residuals of the regression revealed significant variation among months ($F_{7,32} = 2.31$, $P < 0.05$; Fig. 3) on gonadal mass of females of *S. spinosus* but not in *S. horridus* ($F_{4,32} = 0.625$, $P > 0.05$; Fig. 3).

In *S. horridus*, average female gonadal mass increased from March to July (when females began to ovulate) and possibly decreased from

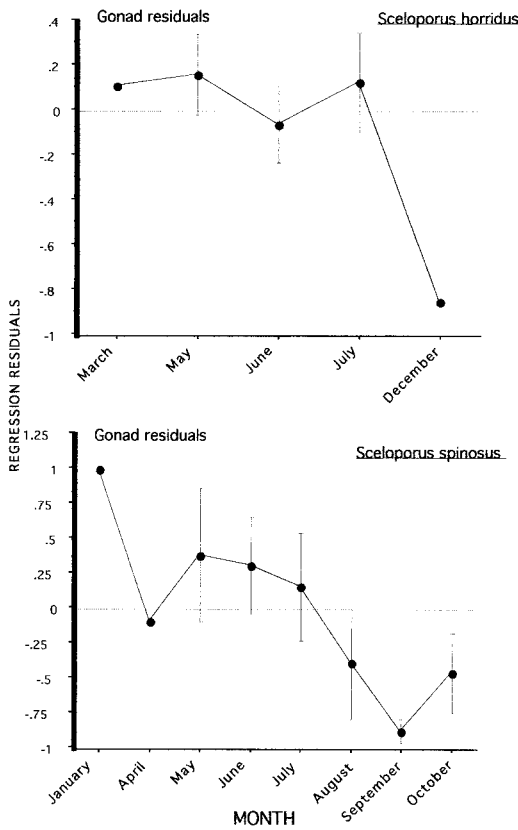


FIG. 3. Seasonal cycle of gonad size for female *Sceloporus horridus* and *Sceloporus spinosus*. Data are mean (\pm SE) residuals from a regression of \log_{10} [gonad mass (g)] against \log_{10} (SVL).

October to November. In contrast, gonadal mass in *S. spinosus* increased from January to July and decreased from August to October. Females of *S. horridus* were found with oviductal eggs from March to July and with three classes of eggs (oviductal eggs, vitellogenic and nonvitellogenic ovarian follicles) from May to July. In contrast,

females of *S. spinosus* were found with all three classes of eggs from January to October.

Clutch Size.—The diameter of vitellogenic follicles of *S. horridus* was similar (15.8 ± 1.7 , $N = 14$) to that of oviductal eggs (14.0 ± 0.82 , $N = 16$; Mann-Whitney U -test, $Z = -0.520$, $P > 0.05$). Considering both egg classes, mean clutch size was 14.8 ± 0.91 eggs (range 4–27; $N = 30$; Table 1) during the reproductive season. Likewise, in female *S. spinosus* the size of vitellogenic follicles was similar (20.5 ± 2.2 , $N = 11$) to that of oviductal eggs (15.3 ± 1.2 , $N = 7$; Mann-Whitney U -test, $Z = -1.50$, $P > 0.05$); mean clutch size (combining egg classes) was 18.5 ± 1.54 eggs (range 8–31, $N = 18$) during the reproductive season. Clutch size was higher in *S. spinosus* than *S. horridus* (Mann-Whitney U -test, $Z = -1.98$, $P < 0.05$). Clutch size was not related to female SVL in *S. spinosus* ($r = 0.51$, $F_{1,16} = 5.51$, $P > 0.05$) or in *S. horridus* ($r = 0.06$, $F_{1,28} = 0.084$, $P > 0.05$). However, total egg mass (eggs and vitellogenic follicles) in females was significantly correlated with female SVL of *S. horridus* ($r = 0.560$, $F_{1,28} = 12.77$, $P < 0.001$) and *S. spinosus* ($r = 0.468$, $F_{1,61} = 4.50$, $P < 0.05$). Four females of *S. horridus* (13.3%) and *S. spinosus* (22.2%) had both vitellogenic follicles and oviductal eggs at the same time, suggesting that females of both species might lay two or more clutches during the reproductive season. Egg production for both species occurred during late June, and hatchlings of *S. horridus* were caught in the field from 20–26 September, and 26 July, 27 August, and 6 October for *S. spinosus*. These data suggest that the egg incubation period is approximately 80–86 days for *S. horridus* and 30 days for *S. spinosus*.

Oviductal eggs from 16 *S. spinosus* averaged 15.1 ± 0.65 mm in length (range = 12.0–17.0 mm), 8.8 ± 0.33 mm in width (range = 7.5–9.8 mm), and 679.2 ± 73.4 mm³ in estimated volume (range = 384.0–928.9 mm³). Oviductal eggs from seven *S. horridus* averaged 14.2 ± 0.23 mm

TABLE 1. Reproductive characteristics of *Sceloporus spinosus* and *Sceloporus horridus*. Mean \pm SE (range, sample size).

Characteristics	<i>S. spinosus</i>	<i>S. horridus</i>
Peak activity of males	spring and autumn	spring-summer
Peak activity of females	spring-summer	spring-summer
Incubation	summer-autumn	summer-autumn
Vitellogenic follicles	20.5 ± 2.2 (8–31, $N = 11$)	15.7 ± 1.7 (4–27, $N = 14$)
Oviductal eggs	15.3 ± 1.2 (12–22, $N = 7$)	14.0 ± 0.8 (7–18, $N = 16$)
Eggs plus vit. fol.	18.5 ± 1.5 (8–31, $N = 18$)	14.8 ± 0.9 (4–27, $N = 30$)
Oviductal eggs volume (mm ³)	679 ± 73 (384–929, $N = 7$)	504 ± 26 (342–769, $N = 16$)
SVL adult males (mm)	90.4 ± 2.1 (65.7–111, $N = 40$)	83.2 ± 2.0 (52–118, $N = 62$)
SVL adult females (mm)	87.0 ± 2.5 (60–112, $N = 38$)	81.8 ± 1.8 (60–100, $N = 35$)
SVL sexually mature female*	98.6 ± 1.9 ($N = 21$)	91.4 ± 1.3 ($N = 16$)

* Largest females with vitellogenic follicles or oviductal eggs.

in length (range, 11.8–15.3 mm), 7.9 ± 0.19 mm in width (range = 6.6–9.4 mm), and 503.6 ± 26.2 mm³ in estimated volume (range = 342.0–769.2 mm³). Egg volume was higher in *S. spinosus* than in *S. horridus* (Mann-Whitney *U*-test, tied $Z = -1.94$, $P < 0.05$).

DISCUSSION

Male *S. horridus* reached sexual maturity at a smaller size than females, but in *S. spinosus*, both sexes reached sexual maturity at the same size. Sexual dimorphism was not found in either species. Mature female and male *S. horridus* and *S. spinosus* are similar in SVL, as has been observed in other species of the genus *Urosaurus* (Ramírez-Bautista et al., 1995; Ramírez-Bautista and Vitt, 1998) and unlike some sexually dimorphic species of the genus *Sceloporus* (Fitch, 1978).

Sexual dimorphism in these species may be present in other morphological characteristics. In males, 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, which is typical of many squamates (Cooper and Greenberg, 1992; Carpenter, 1995). In species with more than one clutch of several eggs per reproductive season as in the genus *Urosaurus* (Van Loben Sels and Vitt, 1984; Ramírez-Bautista et al., 1995; Ramírez-Bautista and Vitt, 1998), the advantage for relatively large male size is presumably the ability to secure disproportionately more mates (Ramírez-Bautista and Vitt, 1997), but apparently this is not the case for *S. horridus* and *S. spinosus*. We suggest that bright color in males could be more important than body size during the reproductive season.

The reproductive cycles of *S. horridus* and *S. spinosus* differ in timing and duration. Both species reproduce seasonally, but *S. spinosus* has a longer reproductive season. The reproductive period for both sexes of *S. horridus* is from March to July, whereas female *S. spinosus* reproduce from January to October. However, males apparently have two reproductive peaks. In *S. spinosus*, the longer reproductive season, larger clutch size, and larger mean SVL of sexually mature adult females may be influenced by the higher annual precipitation level they experience (Puebla, Acajete: 951.1 mm, and Las Minas: 3908.9 mm) and the greater range of elevations (537–2454 m) occupied by this species versus precipitation (Guerrero: Zumpango: 770.3 mm and Huitzuco: 1127.2 mm) and elevation (900–1529 m) of the area inhabited by *S. horridus*. The reproductive activity of *S. spinosus* females is similar to that of another population of *S. spinosus* from a similar altitude (2400 m; Martínez-Loya, 1998). The differences found in the repro-

ductive characteristics between both species, such as the period of reproductive activity, SVL adult, clutch size, and volume of oviductal eggs, could be responses to the different environments inhabited by each species (Table 1). Food abundance is strongly correlated with precipitation in many environments, and variation in resource abundance in turn is related to variation in reproductive characteristics in many lizard species (Ballinger, 1977; Dunham, 1982; Ramírez-Bautista et al., 1995; Ramírez-Bautista and Vitt, 1997, 1998). This could be the case for the population of *S. spinosus*, because both females and males are larger at sexual maturity than *S. horridus* of either sex. *Sceloporus spinosus* had a greater stomach content mass than did *S. horridus* (unpubl. data). This pattern could suggest that the environment of *S. spinosus* is richer in food than that of *S. horridus*. The variation in body size of females of both species could be a demographic response that may influence clutch size and egg size or volume as occurs in other species (Dunham, 1982; Ramírez-Bautista et al., 1995; Ramírez-Bautista and Vitt 1997, 1998) and congeners (Table 2).

Female *S. horridus* and *S. spinosus* have somewhat different reproductive seasons but are similar overall to other species of the same group (Table 2). Small-bodied species of *Sceloporus* inhabiting temperate, arid, desert, or wet tropics have longer reproductive seasons than species of larger body size (Table 2; e.g., *S. chrysostrictus*, *S. olivaceus*, *S. teapensis*, Fitch, 1978; *S. gadocae*, Lemos-Espinal et al., 1999; *S. variabilis*, Ramírez-Bautista and González-Romero, 1991; Benabib, 1994). The variations in reproductive seasons between small-bodied and large-bodied species depend also on duration of appropriate environmental conditions and resource availability (Lemos-Espinal et al., 1999).

The larger number of vitellogenic follicles, clutch size (oviductal eggs), and egg volume for *S. spinosus* compared to *S. horridus* might be considered a reproductive strategy, because production of large clutches might be subject to selective pressures to increase body size of the females to increase clutch size, as has been reported in other species (Dunham 1982; Ramírez-Bautista et al., 1995). Because both lizards belong to the spinosus group, the large clutch sizes of both species might reflect their phylogeny. All species of this group have large clutch sizes, including *S. clarki* (Table 2; 8.2 eggs: Fitch, 1985), *S. magister* (12.4 eggs: Fitch, 1978), *S. olivaceus* (14.3 eggs: Fitch, 1978), *S. orcutti* (11.0 eggs: Mayhew, 1963), *S. spinosus* (12.7 eggs: Fitch, 1978; 11.4 eggs: Martínez-Loya, 1998; 18.5 eggs: this study), and *S. horridus* (14.8 eggs: this study). These data suggest that similarity in the large clutch size of both species is explained by

TABLE 2. Reproductive characteristics (mean \pm SE) of females of various oviparous species of the genus *Sceloporus* from across its range in Mexico. Data were gathered from the literature and unpublished data. Multiple (M) and single (S) clutch.

Species	Body size (mm)	Range	Clutch size	Range	Clutch frequency	Reproductive season	Source
<i>S. chrysostictus</i>	51.3 \pm 0.97	44–61	2.5 \pm 0.21	1–4	M	spring-summer	Fitch, 1978
<i>S. clarkii</i>	84.1 \pm 1.6	72–120	8.2 \pm 1.0	1–10	M	summer	Fitch, 1970, 1978
<i>S. gadoxae</i>	55.0 \pm 0.20	47–76	3.6 \pm 0.2	1–5	M	spring-winter	Lemos-Espinal et al., 1999
<i>S. cozumelae</i>	45.5 \pm 0.59	41–57	1.8	—	M	spring-summer	Fitch, 1978
<i>S. graciosus</i>	53.9 \pm 0.34	48–63	4.24	—	S-M	spring-summer	Fitch, 1970, 1978
<i>S. horridus</i>	—	—	12.0	8–15	M	summer	Fitch, 1970
<i>S. magister</i>	96.6	80–120	12.4	7–19	S	spring-summer	Fitch, 1970, 1978
<i>S. melanorhinus</i>	87.2 \pm 1.6	80–98	7.7 \pm 0.33	5–9	S	spring-summer	A. Ramirez-Bautista, unpubl. data
<i>S. olivaceus</i>	93.0	63–107	14.3	—	M	spring-summer	Fitch, 1978
<i>S. orcutti</i>	—	—	11.0	—	S	spring-summer	Mayhew, 1963
<i>S. pyrocephalus</i>	53.7 \pm 0.43	47–62	5.8	4–9	M	spring-summer	A. Ramirez-Bautista, unpubl. data
<i>S. siniferus</i>	52.3 \pm 0.42	48–61	5.0	4–6	M	spring-summer	Davis and Dixon, 1961
<i>S. scalaris</i>	45.5 \pm 0.62	41–53	5.2 \pm 0.43	4–7	S	summer	Fitch, 1978
<i>S. spinosus</i>	87.2 \pm 1.6	77–96	12.7	8–16	M	spring-summer	Fitch, 1978
<i>S. teapensis</i>	52.0 \pm 0.67	47–62	2.33	—	M	winter-summer	Fitch, 1978
<i>S. utiformis</i>	63.8 \pm 0.5	56–73	7.1 \pm 0.21	2–11	S	summer-fall	A. Ramirez-Bautista, unpubl. data
<i>S. variabilis</i>	53.1 \pm 0.49	44–68	4.6 \pm 0.14	3–7	M	winter-summer	Fitch, 1978; Benabib, 1994
	55.4 \pm 0.82	53–61	3.3 \pm 0.9	2–4	M	spring–	Ramirez-Bautista and González-Romero, 1991

phylogeny, and the variation among populations of the same or different species of this group could reflect either adaptive evolved differences as a result of different environments or proximate effects of different environments (Dunham and Miles 1985; Vitt, 1990, 1992).

Female *S. horridus* and *S. spinosus* are able to lay two clutches during the reproductive season. Like most species of the *spinosus* group, some females (13.3–22.2%) of both species are capable of laying two clutches within a single reproductive season, since vitellogenic follicles and oviductal eggs were present at the same time. This pattern is similar to other lizard species with small body sizes found in temperate or tropical dry forest (Dunham, 1982; Van Loben Sels and Vitt, 1984; Ramírez-Bautista et al., 1995; Smith et al., 1995; Ramírez-Bautista and Vitt, 1998).

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Egg Components and Utilization of Yolk Lipids during Development of the Flatback Turtle *Natator depressus*

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ABSTRACT.—The materials and energy invested in each egg by most oviparous reptiles represent the majority of total parental investment in offspring. For *Natator depressus* from eastern Queensland, Australia, the shell contributed approximately 5%, the albumin 45%, and the yolk 50% to the total egg mass (74 g). Water averaged 79% of the total egg mass. Lipids averaged 29% of the total dry mass of the egg and 35% of the yolk dry mass. Eggs of *N. depressus* contained a high proportion of yolk lipids and water, with greater “parental investment” than those of nonmarine turtles. Approximately 26–27% of lipids in the egg was used for embryogenesis, whereas 73–74% was transferred to the entire hatchling. Initial yolk lipid in the residual yolk was approximately 30–37% but varied with incubation environment. Residual yolk lipids are likely to be used as the immediate energy source for the hatchlings.

Factors such as egg size (Gutzke and Packard, 1985) and quality (e.g., maternal and/or genetic effects) play a significant role in the survival and growth of embryos and hatchlings of turtles (Brooks et al., 1991; Packard et al., 1993; Janzen et al., 1995). Larger eggs have greater hatching success (Gutzke and Packard, 1985) and produce larger hatchlings that may grow faster and survive better than the smaller ones (Brooks et al., 1991; Roosenburg and Kelley, 1996). The

quality of eggs may depend on maternal body size, condition (Congdon et al., 1983b), or heritable factors (Bobyn and Brooks, 1994).

The material and energy in an egg are initially used for embryonic development and then secondarily for hatchling maintenance and possibly initial growth (Congdon et al., 1983b). Egg yolk is the primary nutritional source for a developing turtle embryo (Ewert, 1979). Contents include all the lipid and most (or all) of the protein required to sustain embryonic metabolism, growth (Congdon et al., 1983b), and also part of the calcium required for osteogenesis (Packard

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