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Reproduction in the Boulder Spiny Lizard, *Sceloporus pyrocephalus* (Sauria: Phrynosomatidae), from a Tropical Dry Forest of México

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ABSTRACT.—The reproductive cycle and cycle in fat body mass are described for male and female *Sceloporus pyrocephalus* taken from the Municipio de Tejupilco, state of México, México. Males reached sexual maturity at 50.0 mm snout–vent length (SVL); females reached sexual maturity at 47.0 mm SVL. Testis of males began to increase in size in early April, maximum testis mass occurred during May through October, and testis mass decreased abruptly in November and December. Maximum testicular growth was associated with increased temperature, photoperiod, and precipitation. This is an oviparous species. Enlarged vitellogenic follicles first appeared during early May in females. Females contained oviductal eggs from May to September. Vitellogenesis, follicular growth, and egg production were associated with increasing photoperiod and precipitation but not with temperature. From a sample of 21 females with oviductal eggs, 13 (61.9%) had two clutches, and eight (38.1%) had a single clutch. Mean clutch size was not correlated with female SVL.

RESUMEN.—El ciclo reproductivo y el ciclo de la masa del cuerpo graso son descritos para los machos y las hembras de *Sceloporus pyrocephalus* estudiados del Municipio de Tejupilco, estado de México, México. Los machos alcanzaron la madurez sexual a los 50.0 mm de longitud hocico-cloaca (LHC); las hembras alcanzaron la madurez sexual a los 47.0 mm de LHC. Los testículos de los machos comenzaron a incrementar en tamaño a principios de abril, la máxima masa testicular ocurrió de mayo a octubre, y decreció abruptamente en noviembre y diciembre. El máximo crecimiento testicular estuvo asociado con el incremento de la temperatura, fotoperiodo, y precipitación. Esta es una especie ovípara. Los primeros folículos vitelogénicos alargados que presentaron las hembras aparecieron a principios de mayo. Las hembras presentaron huevos oviductales de mayo a septiembre. La vitelogénesis, crecimiento folicular, y producción de huevos estuvieron asociados con el incremento del fotoperiodo y precipitación, pero no con la temperatura. De la muestra de 21 hembras con huevos en el oviducto, 13 (61.9%) presentaron evidencias de dos puestas, y ocho (38.1%) tuvieron una sola puesta. El tamaño medio de la puesta no estuvo correlacionado con la LHC de las hembras.

Many studies have shown that organisms inhabiting tropical regions have different reproductive strategies than those inhabiting temperate zones (Ortega and Barbault, 1984; Ramírez-Bautista and Vitt, 1997, 1998; Lemos-Espinal et al., 1999; Ramírez-Bautista et al., 2000). Lizards from tropical zones tend to reach sexual maturity at a younger age and a smaller snout–vent length (SVL) and to have smaller but more frequent clutches compared to lizards from temperate regions (Tinkle et al., 1970; Ramírez-Bautista and Vitt, 1998). However, most of the data to leading to this generalization are based on lizards from the wet tropics (Tinkle et al., 1970; Benabib, 1994) and tropical dry forest (Ramírez-Bautista and Vitt, 1997, 1998), and few studies have been published on lizards inhabiting the arid tropics of México. Thus, it is presently unclear whether species inhabiting tropical dry forest and arid regions show similar reproductive

strategies. For example, it is possible that the extreme seasonality of the arid tropics could cause different reproductive strategies than in wet and tropical dry forests.

Seasonal and annual fluctuations of environmental variables can induce proximate variation in life-history traits within populations (Ballinger, 1977; Dunham, 1982; Ramírez-Bautista and Vitt, 1997, 1998). Food availability, precipitation, and temperature can affect growth rate and reproductive characteristics, including length of reproductive season, clutch size, clutch frequency, and age and size at sexual maturity (Benabib, 1994; Dunham, 1982; Ramírez-Bautista, 1995). These reproductive characteristics in lizards of the genus *Sceloporus* usually vary with resource availability, temperature, rainfall, and food (Ballinger, 1977; Benabib, 1994; Lemos-Espinal et al., 1999). In México, species of the genus *Sceloporus* inhabit a wide range of environments, ranging from desert to high-elevation temperate zones to wet and dry tropical (seasonal) environments. However, most of the research on reproduction in *Sceloporus* has been focused on desert, temperate,

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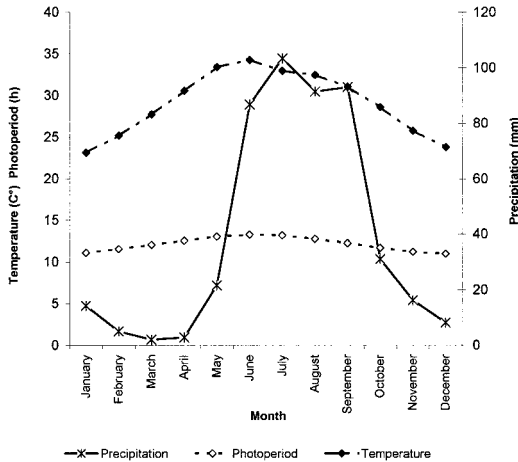


FIG. 1. Monthly temperature and precipitation based on a period of 10-yr means recorded from the study area at Bejucos, México, México (García, 1983). Photoperiod data were acquired elsewhere (Astronomical Almanac, 1984).

and montane species in the United States and México (Sites et al., 1992).

At this time, little is known about reproduction of *Sceloporus pyrocephalus* and other species inhabiting arid tropical forests. In this study, we address the following general questions with respect to reproductive characteristics of *S. pyrocephalus*: (1) Are sexually mature male and females the same size? (2) What is the nature of the annual reproductive cycle in females and males? (3) Is peak reproductive activity associated with environmental factors (temperature, precipitation or photoperiod)? (4) Does clutch size vary with female SVL? (5) Are reproductive characteristics of *S. pyrocephalus* similar to those of other *Sceloporus* species inhabiting seasonal environments?

MATERIALS AND METHODS

This study was conducted in Bejucos (18°46.5'N latitude and 100°25.5'W longitude) at an elevation of 550 m. The site belongs to the Municipio de Tejupilco, state of México, situated in the Rio Balsas Basin. The mean annual temperature is 28°C and the average annual rainfall is 850 mm. The dominant vegetation is subhumid tropical forest (García, 1983; Rzedowski, 1978). Monthly temperature and precipitation over a 10-yr period were taken from García (1983). Data on photoperiod were taken from the Astronomical Almanac (1984). We used these data to construct a climatic profile for the region and consider it representative for the study area (Fig. 1).

A total of 211 (76 adult females, 75 adult males, 45 juveniles, and 15 neonates) individuals were

collected from March 1985 to February 1986. Lizards were humanely killed and fixed in 10% formalin in the laboratory, where gonadal analyses were performed. The following linear measurements were taken to the nearest 1 mm on necropsied females and males: snout-vent length (SVL, mm), head length (HL, mm) and width (HW, mm), forearm length (FL, mm), and tibia length (TL, mm), length and width of right testis in males, and length and width of left and right vitellogenic, and nonvitellogenic follicles and freshly ovulated eggs in females. We removed and weighed (0.0001 g) the fat bodies of both sexes to determine whether fat body size fluctuates with changes in gonadal activity. The number of nonvitellogenic and vitellogenic follicles, and eggs, in each oviduct was also recorded.

Length and width measurements were used to estimate testicular and follicles/eggs volume (V) using the formula for volume of an ellipsoid:

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

where a is one-half the shortest diameter and b is one-half the longest diameter. Testicular and follicular volumes were used as indicators of reproductive activity of males and females and could be defined as female and male reproductive parameters (Guillette, 1983; Ramírez-Bautista et al., 1998). Males were considered sexually mature if they contained enlarged testes and convoluted epididymides typically associated with sperm production (Goldberg and Lowe, 1966). To describe the male and female reproductive cycle, we first tested for a relationship between the log-transformed testis or total follicle/egg volume and log SVL. In both sexes, there was a significant relationship indicating that lizard size influences gonadal volume (see Results), so we calculated the residuals from regressions and performed an ANOVA on these residuals with the month as a factor (Ramírez-Bautista and Vitt, 1997, 1998).

Snout-vent length of the smallest female with enlarged vitellogenic follicles or oviductal eggs was used to estimate minimum SVL at maturity (Ramírez-Bautista and Vitt, 1997, 1998). We determine clutch size by counting vitellogenic follicles and eggs in the oviducts of adult females during the reproductive season, and tested for a correlation between clutch size and SVL of females. Because these variables usually vary with SVL, we first calculated regressions of \log_{10} -transformed of all variables data with \log_{10} of lizards SVL. For significant regressions, we calculated residuals from the relationship of variables on SVL to produce SVL-adjusted variables. We then used these residuals to examine sexual size differences between mature males and females, and performed a Mann-Whitney

TABLE 1. Morphological characteristics (HL = Head length, HW = Head width, FL = Femur length, and TL = Tibia length) of sexual mature females ($N = 76$) and males ($N = 75$) of *Sceloporus pyrocephalus*. The statistical test is Mann-Whitney U -test ($P < 0.01 = *$, $P < 0.001 = **$, $P < 0.0001 = ***$).

Characteristics	Males mean \pm SE	Females mean \pm SE	Test	P
HL (mm)	0.006 \pm 0.004	-0.006 \pm 0.003	$Z = -4.19$	***
HW (mm)	0.009 \pm 0.004	-0.009 \pm 0.003	$Z = -3.8$	**
FL (mm)	0.006 \pm 0.004	-0.006 \pm 0.004	$Z = -2.4$	*
TL (mm)	0.011 \pm 0.003	-0.012 \pm 0.003	$Z = -5.4$	***

U -test on HL, HW, FL, and TL. We used a $P < 0.05$ to assess statistical significance. Results are expressed as mean \pm SE. Statistical analyses were performed with StatView IV (Abacus Concepts, Inc., Berkeley, CA, 1992).

RESULTS

Sexual Dimorphism.—Males of *S. pyrocephalus* reached sexual maturity at a minimum size of 50 mm SVL and females reached sexual maturity at 47 mm SVL. Sexually mature males ranged from 50–75 mm SVL (mean \pm SE = 61.9 \pm 0.69, $N = 75$). Sexually mature females ranged from 47–62 mm SVL (53.4 \pm 0.41, $N = 76$). Males (SVL) were larger than females (Mann-Whitney U -test, $Z = -10.62$, $P < 0.0001$). Males attained a significantly larger HL ($Z = -4.19$, $P < 0.0001$), HW ($Z = -3.8$, $P < 0.001$), FL ($Z = -2.4$, $P < 0.01$), and TL ($Z = -5.4$, $P < 0.0001$) than females (Table 1).

Reproductive Cycles.—The annual reproductive cycle of males is based on 75 sexually mature lizards collected in 1985 and 1986. There was a significant positive relationship between \log_{10} -testis volume and the \log_{10} -SVL ($r^2 = 0.22$, $F_{1,74} = 19.9$, $P < 0.0001$) and \log_{10} -fat body mass ($r^2 = 0.082$, $F_{1,72} = 6.3$, $P < 0.01$). Consequently, we used residuals of the common regression to describe the testis volume and fat body cycles independent of male size. An ANOVA on residuals of the regressions revealed significant variation among months in testis volume ($F_{11,63} = 12.4$, $P < 0.0001$) and fat body mass ($F_{9,66} = 9.2$, $P < 0.0001$). Testis size was smallest during January, February, and March but began to increase in size during April (Fig. 2). Testicular recrudescence began in midspring (May and June) and midsummer (July and August), and testes reached maximal size during September and October, followed by a rapid decrease in size during November. Testicular volume was positively correlated with temperature ($r^2 = 0.46$, $P < 0.05$), photoperiod ($r^2 = 0.79$, $P < 0.001$), and precipitation ($r^2 = 0.72$, $P < 0.005$).

There was a significant relationship between \log_{10} -follicles/eggs volume and \log_{10} of female SVL ($r^2 = 0.180$, $F_{1,74} = 16.3$, $P < 0.005$) and \log_{10} -fat body mass ($r^2 = 0.11$, $F_{1,75} = 9.0$, $P < 0.005$). As with males, we removed the effect of

female size by using the residuals from the regressions to describe the gonadal and fat body cycles. ANOVAs on residuals of the regressions revealed significant effects of month on gonad volume ($F_{9,66} = 8.6$, $P < 0.0001$) and fat body mass ($F_{9,66} = 9.2$, $P < 0.0001$). Follicles were at their minimal size during March and April; vitellogenesis and egg production began in May and continued from June through August, then decreased significantly in September (Fig. 3). Monthly mean vitellogenesis and follicular growth of female were positively correlated with photoperiod ($r^2 = 0.84$, $P < 0.001$) and pre-

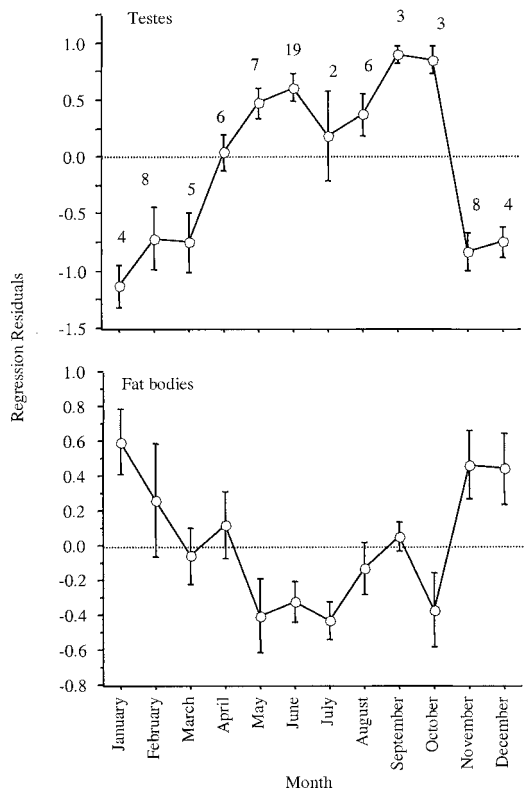


FIG. 2. Males testis and fat body cycles of *Sceloporus pyrocephalus*. Data are mean (± 1 SE) residuals from a regression of \log_{10} -testis volume (mm^3) and fat body mass (g) against \log_{10} -SVL.

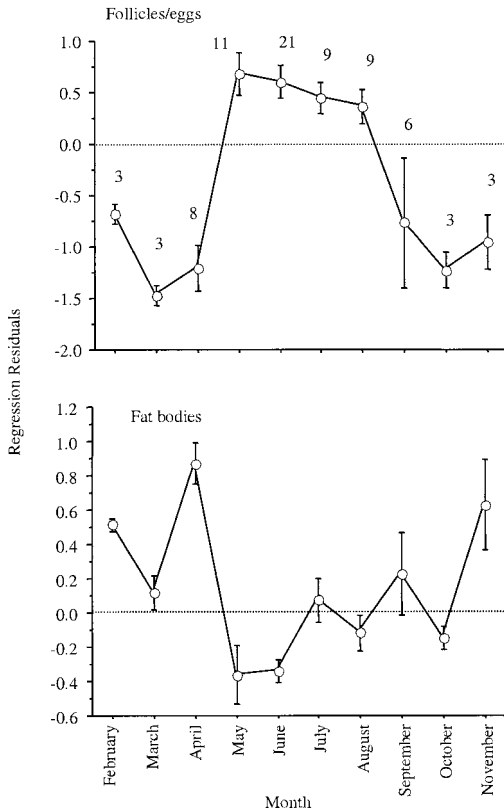


FIG. 3. Female follicles/eggs and fat body cycles of *Sceloporus pyrocephalus*. Data are mean (± 1 SE) residuals from a regression of \log_{10} -follicles/eggs volume (mm^3) and fat body mass (g) against \log_{10} -SVL.

cipitation ($r^2 = 0.84$, $P < 0.001$) but not with temperature ($r^2 = 0.13$, $P > 0.05$).

Females with vitellogenic follicles and oviductal eggs were observed between mid spring and late summer: May (90.9%, $N = 11$), June (100%, $N = 21$), July (100%, $N = 9$), August (100%, $N = 9$), and September (66.7%, $N = 6$). Females from October to March ($N = 3$ each month) had nonvitellogenic follicles. Females began to lay their eggs on 25 May, and the first hatchlings were observed in the field on 15 August. These data suggest an incubation period of 82 days.

Clutch Size.—Females containing oviductal eggs did not differ in size to females containing enlarged vitellogenic follicles (mean SVL = 55.2 ± 0.83 and 54.1 ± 0.51 mm, respectively; Mann-Whitney U -test, $Z = -1.505$, $P = 0.1301$). Mean clutch size based on counts of vitellogenic follicles was 5.5 ± 0.27 (2–10, $N = 32$); mean clutch size on counts of oviductal eggs was 5.8 ± 0.31 (4–9, $N = 21$) which did not differ significantly (Mann-Whitney U -test, $Z = -0.701$, $P = 0.465$). A sample of 22 females (SVL = $55.0 \pm$

0.66 mm) contained a mean of nonvitellogenic follicles of 15.3 ± 1.56 (range 5–37). Clutch size was not correlated with female SVL ($r = 0.23$; $F_{1,51} = 3.0$; $P > 0.05$). Pooling data on counts of vitellogenic follicles and oviductal eggs produced an overall mean clutch size of 5.6 ± 0.20 (2–10, $N = 53$). Oviductal egg mass did not covary with female SVL (\log_{10} -transformed, $r^2 = 0.35$; $F_{1,19} = 2.5$; $P = 0.1305$), and there was no relationship between the number of eggs produced and females mass \log_{10} -transformed ($r^2 = 0.26$; $P = 0.2714$).

Of the sample size of 21 females with oviductal eggs, 13 (SVL = 55.4 ± 1.08 mm) had two clutches (5.6 ± 0.37 ; vitellogenic follicles and oviductal eggs simultaneously), and 8 (SVL = 55.3 ± 1.19 mm) had a single clutch (6.1 ± 0.52 ; oviductal eggs), which were not significantly different in clutch size (Mann-Whitney U -test, $Z = -0.616$; $P = 0.517$).

Juveniles collected between September and June had a mean SVL of 42.4 ± 0.52 mm (34–49 mm; $N = 45$). Mean size of hatchlings was 26.1 ± 0.11 mm (20–32 mm; $N = 15$).

DISCUSSION

Sexual Dimorphism.—As with many lizard species of the genera *Sceloporus* (Fitch, 1978; Lemos-Espinal et al., 1999), *Urosaurus* (Ramírez-Bautista and Vitt, 1998), *Cnemidophorus* (Ramírez-Bautista et al., 2000), and *Anolis* (Ramírez-Bautista and Vitt, 1997), male *S. pyrocephalus* are larger than females in SVL, and other measures of size (Table 1). Male *S. pyrocephalus* reached sexual maturity at a larger size and attained larger maximum size than females, a pattern similar to many other species of *Sceloporus* (Fitch, 1978; Lemos-Espinal et al., 1999; Valdéz-González and Ramírez-Bautista, 2002). Sexual dimorphism in this species may be explained by two non-exclusive hypotheses. First, sexual selection, in which larger males are at an advantage over smaller males in acquiring mates, can maintain large body size in male lizards when large males mate more frequently than smaller ones. During reproduction, a fight between two adult males (SVL = 54 and 61 mm) was observed in the field for approximately 22 min. It occurred over a rock where a pregnant female was perched. The largest male was the winner. Similar results occur in other lizard species (Trivers, 1976; Ruby, 1981, 1984; Dugan, 1982). Second, differential energy allocation causing different growth trajectories between sexes are suggested by the seasonal distributions of mean body size with female growth appearing to slow down relative to that of males during the reproductive season. Sexual dimorphism in body size could result from reduction in growth in females coincident

TABLE 2. Reproductive characteristics of females of various oviparous species of the genus *Sceloporus* from México. Data were gathered from the literature and unpublished data set. Multiple (M) and single (S) clutch.

Species	Body size (mm) mean \pm SE	Range	Clutch size mean \pm SE	Clutch frequency	Reproductive season	Source
<i>S. chrysostictus</i>	51.3 \pm 0.97	44–61	2.5 \pm 0.21	M	April to September	Fitch, 1978
<i>S. gadoviae</i>	55.0 \pm 0.20	47–76	3.6 \pm 0.2	M	April to December	Lemos-Espinal et al., 1999
<i>S. cozumelae</i>	45.5 \pm 0.59	41–57	1.8	M	May to September	Fitch, 1978
<i>S. siniferus</i>	53.7 \pm 0.43	48–61	5.0	M	June to September	Fitch, 1978
<i>S. scalaris</i>	45.5 \pm 0.62	41–53	5.2 \pm 0.43	S	May to August	Fitch, 1978
<i>S. teapensis</i>	52.0 \pm 0.67	47–62	2.33	M	January to September	Fitch, 1978
<i>S. utiformis</i>	63.8 \pm 0.5	56–73	7.1 \pm 0.21	S	June to February	Ramírez-Bautista and Gutiérrez-Mayén, 2003
<i>S. variabilis</i>	53.1 \pm 0.49	44–68	4.6 \pm 0.14	M	November to September	Benabib, 1994
<i>S. pyrocephalus</i>	55.2 \pm 0.83	47–62	5.8 \pm 0.3	M	May to September	this study

with reproduction such as occurs in other species (Dearing and Schall, 1994).

Reproductive Cycle.—Male *S. pyrocephalus* showed a seasonal reproductive pattern with an activity peak from August to October. Reproductive behaviors, such as courtship and mating, began in April and May, coincident with beginning of the rainy season. Testis volume increased as precipitation, temperature, and photoperiod increased. These factors or a combination of them appear to stimulate gonadal activity in males of some other lizard species (Licht and Gorman, 1970; Marion, 1982). To date, several studies of lizards inhabiting tropical dry forests have shown that these three factors can play an important role in reproductive activity (Ramírez-Bautista, 1995; Ramírez-Bautista and Vitt, 1997, 1998; Ramírez-Bautista et al., 2000). However, in this kind of environment, reproductive activity of each species may be influenced by different proximal factors, as occurs in other species inhabiting similar environments. For example, in *Anolis nebulosus* (Ramírez-Bautista and Vitt, 1997) and *Urosaurus bicarinatus* (Ramírez-Bautista and Vitt, 1998), gonadal activity is correlated with temperature and photoperiod, whereas in *Cnemidophorus lineatissimus* (Ramírez-Bautista et al., 2000), precipitation and temperature appear most important.

Male reproductive activity in *S. pyrocephalus* was seasonal as in other species inhabiting tropical dry forests (Ramírez-Bautista and Vitt, 1997, 1998; Lemos-Espinal et al., 1999). A high energetic cost to male reproductive activities is suggested by the negative relationship between testis development and fat body mass from April to September (Fig. 2). This pattern is similar to that of other lizard species that occur in tropical dry forests (Ramírez-Bautista and Vitt, 1997, 1998).

The female reproductive cycle of *S. pyrocephalus* was also seasonal. Follicles increased in size

during May, and most egg production occurred from May to August, coinciding with maximum rainfall. Female reproduction is typically seasonal in other *Sceloporus* species inhabiting tropical dry forests in México: *Sceloporus chrysostictus*, *Sceloporus siniferus*, and *Sceloporus cozumelae* (Table 2). Tropical and subtropical lizards as the sister species *Sceloporus gadoviae* (Lemos-Espinal et al., 1999) and other species such as *Sceloporus utiformis* (Ramírez-Bautista and Gutiérrez-Mayén, 2003), and *Sceloporus variabilis* (Benabib, 1994) have extended breeding seasons. In *S. pyrocephalus*, the reduction in fat body size is associated with egg production (Fig. 3). This suggests that females cannot harvest enough resources to support continued egg production and thus must mobilize some of the energy contained in fat bodies for reproduction, as occurs in other lizard species such as *S. variabilis* (Benabib, 1994).

Vitellogenesis and egg production coincided with increases in rainfall, temperature, and photoperiod. These data suggest a combination of the three factors likely play an important role initiating reproduction (Marion, 1982; Licht, 1984; Ramírez-Bautista and Vitt, 1998). Although all three factors possibly influence reproductive activity of this species, the timing of rainfall may be the ultimate cue for reproduction through its effects on egg and offspring survival (Andrews and Sexton, 1981).

Clutch Size.—Neither clutch size nor egg mass of *S. pyrocephalus* was correlated with female size. This pattern is similar to other species with multiple clutches (Benabib, 1994; Ramírez-Bautista and Vitt, 1998; Lemos-Espinal et al., 1999). Because some females had both vitellogenic follicles and oviductal eggs simultaneously, these data suggest that females potentially could produce at least two clutches during the reproductive season, if so, their annual reproductive potential would be 11.2 eggs on average. Clutch

size of *S. pyrocephalus* was larger (5.6 eggs) than that of species of the genus *Sceloporus* with multiple clutches of similar SVL (Table 2). For example, some species of similar body size have smaller clutch sizes such as *S. gadoviae* (3.6 eggs: Lemos-Espinal et al., 1999), *S. siniferus* (5.0 eggs: Fitch, 1978), *S. variabilis* (4.6 eggs: Benabib, 1994). These data suggest that the differences in clutch size of these species could be explained by the environment these species inhabit (Ballinger, 1977; Dunham, 1982; Benabib, 1994).

In summary, the reproductive cycle of *S. pyrocephalus* in the dry forest of México is similar to those of other species of *Sceloporus* inhabiting seasonal tropical dry forests (Table 2). Females and males have seasonal reproduction, both sexes are active during the wet season, and the females produce multiple clutches within a short period (May through August) of the reproductive season. In most species of the genus *Sceloporus*, clutch size is correlated with SVL; however, in females of *S. pyrocephalus* and its relative *S. gadoviae* (Lemos-Espinal et al., 1999), clutch size is not correlated with SVL. Species from tropical, wetter and warmer environments tend to have smaller SVL at sexual maturity, lay several clutches per year, and have smaller clutch sizes than species from dry tropical dry forest such as *S. pyrocephalus* (Table 2).

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LITERATURE CITED

- ANDREW, R. M., AND O. I. SEXTON. 1981. Water relations of the eggs of *Anolis aeneus* and *Anolis limifrons*. *Ecology* 62:556–562.
- ASTRONOMICAL ALMANAC OF THE WORLD. 1984. United States Government Printing Office and Her Majesty's Stationary Office, London.
- BALLINGER, R. E. 1977. Reproductive strategies: food availability as a source of proximal variation in a lizard. *Ecology* 58:628–635.
- BENABIB, M. 1994. Reproduction and lipid utilization of tropical populations of *Sceloporus variabilis*. *Herpetological Monographs* 8:160–180.
- DEARING, M. D., AND J. J. SCHALL. 1994. Atypical reproduction and sexual dimorphism of the tropical Bonaire Island Whiptail Lizard, *Cnemidophorus murinus*. *Copeia* 1994:760–766.
- DUGAN, B. 1982. The mating behavior of the Green Iguana, *Iguana iguana*. In G. M. Burghardt and A. S. Rand (eds.), *Iguanas of the World: Their Behavior, Ecology, and Conservation*, p. 320–341. Noyes Press, Park Ridge, NJ.
- DUNHAM, A. E. 1982. Demographic and life-history variation among populations of the iguanid lizard *Urosaurus ornatus*: implications for the study of life-history phenomena in lizards. *Herpetologica* 38:208–221.
- FITCH, H. S. 1978. Sexual size differences in the genus *Sceloporus*. *Univ. of Kansas Science Bulletin* 51:441–461.
- GARCÍA, E. 1983. Modificaciones al sistema de clasificación de Köppen. Tercera ed. Instituto de Geografía, Universidad Nacional Autónoma de México, Mexico City.
- GOLDBERG, S. R., AND C. H. LOWE. 1966. The reproductive cycle of the Western Whiptail Lizard (*Cnemidophorus tigris*) in southern Arizona. *Journal of Morphology* 118:543–548.
- GUILLETTE JR., L. J. 1983. Notes concerning reproduction of the Montane Skink, *Eumeces copei*. *Journal of Herpetology* 17:144–148.
- LEMOS-ESPINAL, J. A., G. R. SMITH, AND R. E. BALLINGER. 1999. Reproduction in Gadow's Spiny Lizard, *Sceloporus gadovae* (Phrynosomatidae), from arid tropical México. *Southwestern Naturalist* 44: 57–63.
- LICHT, P. 1984. Reptiles. In G. E. Lamming (ed.), *Marshall's Physiology of Reproduction*. 4th ed. Vol. 1, pp. 206–282. Churchill Livingstone, Edinburgh, Scotland.
- LICHT, P., AND G. C. GORMAN. 1970. Reproductive and fat cycles in Caribbean *Anolis* lizards. *Univ. of California Publications in Zoology* 95:1–52.
- MARION, K. R. 1982. Reproductive cues for gonadal development in temperate reptiles: temperature and photoperiod effects on the testicular cycles of the lizard *Sceloporus undulatus*. *Herpetologica* 38:26–39.
- ORTEGA, A., AND R. BARBAULT. 1984. Reproductive cycles in the Mesquite Lizard *Sceloporus grammicus*. *Journal of Herpetology* 18:168–175.
- RAMÍREZ-BAUTISTA, A. 1995. Demografía y reproducción de la lagartija arbórea *Anolis nebulosus* de la Región de Chamela, Jalisco. Tesis Doctoral, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City.
- RAMÍREZ-BAUTISTA, A., AND G. GUTIÉRREZ-MAYÉN. 2003. Reproductive ecology of *Sceloporus utiformis* (Sauria: Phrynosomatidae) from a tropical dry forest of México. *Journal of Herpetology* 37:1–10.
- RAMÍREZ-BAUTISTA, A., AND L. J. VITT. 1997. Reproduction in the lizard *Anolis nebulosus* (Polychrotidae) from the Pacific coast of México. *Herpetologica* 53:423–431.
- . 1998. Reproductive Biology of *Urosaurus bicarinatus* (Sauria: Phrynosomatidae) from a tropical dry forest of México. *Southwestern Naturalist* 43:381–390.
- RAMÍREZ-BAUTISTA, A., J. BARBA-TORRES, AND L. J. VITT. 1998. Reproductive cycle and brood size of *Eumeces lynx* from Pinal de Amoles, Queretaro, México. *Journal of Herpetology* 32:18–24.
- RAMÍREZ-BAUTISTA, A., C. BALDERAS-VALDIVIA, AND L. J. VITT. 2000. Reproductive ecology of the whiptail lizard *Cnemidophorus lineatissimus* (Squamata: Teiidae) in a tropical dry forest. *Copeia* 2000:712–722.
- RUBY, D. E. 1981. Phenotypic correlates of male reproductive success in the lizard *Sceloporus jarrovi*.

- In R. D. Alexander and D. W. Tinkle (eds.), *Natural Selection and Social Behavior*, p. 96–107. Chiron Press, New York.
- . 1984. Male breeding success and differential access to females in *Anolis carolinensis*. *Herpetologica* 40:272–280.
- RZEDOWSKI, J. 1978. *Vegetación de México*. Limusa Wiley, Mexico City, México.
- SITES JR., J. W., J. W. ARCHIE, C. J. COLE, AND O. FLORES-VILLELA. 1992. A review of phylogenetic hypotheses for lizards of the genus *Sceloporus* (Phrynosomatidae): implications for ecological and evolutionary studies. *Bulletin of the American Museum of Natural History* 213:1–110.
- TINKLE, D. W., H. M. WILBUR, AND S. G. TILLEY. 1970. Evolutionary strategies in lizard reproduction. *Evolution* 24:55–74.
- TRIVERS, R. L. 1976. Sexual selection and resource-accurring abilities in *Anolis garmani*. *Evolution* 30:253–269.
- VALDÉZ-GONZÁLEZ, M. A., AND A. RAMÍREZ-BAUTISTA. 2002. Reproductive characteristics of the spiny lizards, *Sceloporus horridus* and *Sceloporus spinosus* (Squamata: Phrynosomatidae) from México. *Journal of Herpetology* 36:36–43.

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Sexual Dimorphism and Allometric Size Variation in a Population of Grass Snakes (*Natrix natrix*) in Southern England

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ABSTRACT.—Sexual dimorphism is widespread in animals, either because of sexual selection or ecological divergence between the sexes. In natricine snakes, for example, females are usually larger than males and have larger heads and shorter tails relative to body length. Grass Snakes (*Natrix natrix*) near Canterbury, U.K., generally proved to be typical natricines in these respects. Most differences between the sexes were apparent at hatching, rather than being confined to adults, but there was no evidence that the sexes differed in allometry. Despite high r^2 -values, allometry of relationships of body mass, head width, and tail length with body length were not satisfactorily explained by linear regressions (using log-transformed data). Rather, both polynomial and piecewise regressions provided better fits, suggesting that allometric coefficients were not constant but varied with body size. Nonetheless, all analyses were in agreement that small snakes had relatively heavier bodies and wider heads than large snakes. How general such patterns are, and their ecological significance, remain to be determined.

In many animals, the sexes differ in various ways, reflecting sexual selection, ecological differences, or both (e.g., Shine, 1989; Anderson and Vitt, 1990). Such sexual dimorphism is widespread in snakes, especially in size and other morphometric traits (Shine, 1993; Bonnet et al., 1998). Studies of sexual dimorphism in snakes frequently focus on broad interspecific comparisons (e.g., Shine, 1991) or on geographic comparisons within species (e.g., Pearson et al., 2002) but less often on single populations. However, intrapopulation studies can be informative in making inferences or generating hypotheses about ontogenetic patterns of sexual dimorphism. Morphometric traits scale with body size (i.e., they change allometrically with growth),

suggesting possible adaptive differences or ecological consequences at different ages. Equally important is the question of whether sexual differences are seen only in adults or are present early in life (e.g., King et al., 1999).

In this paper, I describe sexually dimorphic and size-based patterns of morphometry in a population of Grass Snakes, *Natrix natrix*, in southern England. *Natrix natrix* is a natricine colubrid. Natricines are speciose, widespread, and include some of the most intensively studied species of snakes (e.g., Rossman et al., 1996). Thus, there is a rich base of literature, also encompassing other populations of *N. natrix* (e.g., Thorpe, 1975, 1984; Madsen, 1983; Madsen and Shine, 1993a), for comparative study.