REPRODUCTIVE CYCLE OF MALE AND FEMALE SPINY LIZARDS, *SCELOPORUS MELANORHINUS*, IN A TROPICAL DRY FOREST

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ABSTRACT—Male and female reproductive cycles are described for *Sceloporus melanorhinus* in Chamela, Jalisco, Mexico. Both males and females reached sexual maturity at 62 mm snout–vent length. Testes mass of adult males began to increase in March, reached maximum size in July, and began to decrease in August and September, reaching minimum size in October and November. Testes size was associated with increasing photoperiod, but not with temperature or precipitation. Enlarged vitellogenic follicles first appeared in May, and oviductal eggs were found from June to September. Vitellogenesis, follicular growth, and egg production were correlated with increasing photoperiod, temperature, and precipitation. Females produced a single clutch during the reproductive season. Mean clutch size based on oviductal eggs was 7.7 (range = 5 to 9). Clutch size was not correlated with female snout–vent length.

RESUMEN—Se describen los ciclos reproductivos de machos y hembras de *Sceloporus melanorhinus* en Chamela, Jalisco, México. Los machos y las hembras alcanzaron la madurez sexual a los 62 mm de longitud hocico-cloaca (LHC). La masa de los testículos de los adultos machos comenzó a incrementar en tamaño en marzo, alcanzó el máximo en julio, y comenzó a decrecer en agosto y septiembre, alcanzando el tamaño mínimo en octubre y noviembre. El tamaño testicular estuvo asociado con el incremento del fotoperiodo, pero no con la temperatura o precipitación. Los primeros folículos vitelogénicos alargados aparecieron en mayo, y los huevos oviductales de junio a septiembre. La vitelogénesis, crecimiento folicular, y producción de huevos estuvieron correlacionados con el incremento en el fotoperiodo, temperatura, y precipitación. Las hembras produjeron una sola puesta durante la estación reproductiva. El tamaño medio de la puesta basado en los huevos oviductales fue de 7.7 (intervalo = 5 a 9). El tamaño de la puesta no estuvo correlacionado con la LHC de la hembra.

Lizards exhibit a great diversity of reproductive activity patterns (Fitch, 1970, 1985; Benabib, 1994; Ramírez-Bautista and Vitt, 1997, 1998; Feria-Ortíz et al., 2001). Reproduction in many lizard species inhabiting seasonal tropical environments is cyclical, with courtship, mating, and copulation occurring at the beginning of the wet season, incubation during the wet season, and hatching at the end of the wet season (Ramírez-Bautista and Vitt, 1997, 1998). Other tropical species are aseasonal in reproduction, exhibiting reproductive activity throughout the year (Benabib, 1994).

Considerable variation exists in lizard life-history characteristics, such as clutch, egg size, fecundity, and age at maturity (Tinkle et al., 1970; Benabib, 1994; Ramírez-Bautista and Vitt, 1997, 1998). Large-bodied species generally have larger clutch sizes than small-bodied ones (Fitch, 1970, 1985). Variation in life-history traits among populations and species can be attributed to a combination of historical (phylogenetic), environmental (abiotic), and ecological (biotic) factors (Ballinger, 1983; Dunham and Miles, 1985; Vitt, 1990). Environmental and ecological factors affecting life history variation include photoperiod, rainfall, temperature, and food availability (Dunham, 1982; Marion, 1982). Dunham et al. (1988) showed that variation in reproductive charac-

teristics among major taxa is greater than variation within taxa, thus demonstrating a phylogenetic effect.

Although reproductive cycles of several Mexican species of *Sceloporus* have been studied recently (Benabib, 1994; Feria-Ortíz et al., 2001; Ramírez-Bautista and González-Romero, 2002; Valdéz-González and Ramírez-Bautista, 2002), nothing has been published about reproductive characteristics of the Mexican arboreal, large-bodied lizard *S. melanorhinus* (Ramírez-Bautista, 1994). Previously, this species was assigned to the *S. spinosus* group (Smith, 1939), but Wiens and Reeder (1997) included *S. melanorhinus* in the *S. clarkii* group.

We describe in detail the male and female reproductive cycles of *S. melanorhinus* and address the following questions. Do males and females become sexually mature at the same size? What are the annual reproductive cycles of females and males? Is peak reproductive activity associated with environmental factors (temperature, precipitation, or photoperiod)? Does clutch size vary with female snout–vent length (SVL)? Are reproductive characteristics of *S. melanorhinus* similar to those of other spiny lizards of similar body size?

METHODS—This study was conducted at Chamela, near the Estación de Biología "Chamela" (EBCH, at 19°30′N, 105°03′W), at elevations from 10 to 584 m in Jalisco, México. The dominant vegetation type is tropical dry forest, with rains occurring in late spring and summer. Mean annual temperature is 24.9°C, with average annual rainfall of 748 mm, ranging from 585 to 961 mm (Bullock, 1986). Monthly mean temperature and precipitation over a 10-yr period were recorded at the Estación Metereológica in the region. Data on photoperiod were taken from the Astronomical Almanac (1984).

We collected 30 female and 32 male lizards from January to December 1989. Lizards were humanely killed and fixed in 10% formalin in the laboratory, where gonadal analyses were performed. The following measurements were taken on necropsied lizards: SVL, testes length and width (to nearest 0.1 mm), and diameter of vitellogenic and nonvitellogenic follicles (to nearest 0.1 mm). The SVL of the smallest female with enlarged vitellogenic follicles or oviductal eggs was used to estimate minimum SVL at maturity. Males were considered sexually mature if they contained enlarged testes and convoluted epididymides typically associated with sperm production (Goldberg and Lowe, 1966).

Because organ size (males) and follicles (females)

can vary with SVL, we first calculated regressions of log-transformed organ volume data against log of male and female SVL. For those regressions that were significant (indicating a body size effect), we calculated residuals from the relationship of organ size to SVL (all variables log-transformed) to produce SVL-adjusted variables. We used these residuals to describe the organ sizes and reproductive cycles. We performed one-way ANOVA on the organ volume residuals (with month as the factor) to determine whether significant monthly variation existed.

Length and width of gonads were used to obtain testicular and follicular volume (V), calculated with the formula for the volume of an ellipsoid:

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

where a is one-half the shortest diameter and b one-half the longest diameter. Testicular and follicular volumes were used as indicators of reproductive activity of male and female lizards. Clutch size was determined by counting eggs in the oviducts of adult females.

Means $\pm$ 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, 1992).

RESULTS—Sexually mature males of *S. melanorhinus* varied in size from 62 to 95 mm SVL (mean = 84.6 $\pm$ 1.8 mm, n = 32). Sexually mature females ranged in size from 62 to 98 mm SVL (mean = 87.9 $\pm$ 1.2 mm, n = 30). Males and females were similar in average size (Mann-Whitney *U*-test, $Z = -0.48$, $P = 0.631$).

A significant relationship existed between the $\log_{10}$-transformed testes volume and the $\log_{10}$ of male SVL ($R^2 = 0.13$, $F_{1,30} = 4.5$, $P < 0.05$). Male testes enlarged in March and reached maximum size from May to July (Fig. 1). Testes began to decrease in size during August and September and reached minimum size by November. An ANOVA on the regression residuals indicated significant variation in testicular volume among months ($F_{10,21} = 32.0$, $P < 0.0001$). The increase in testicular volume was positively correlated with photoperiod ($r = 0.81$, $P < 0.001$), but not with temperature ($r = 0.15$, $P = 0.65$) or precipitation ($r = 0.021$, $P = 0.948$).

A significant relationship existed between the $\log_{10}$-transformed volumes of follicles-eggs and the $\log_{10}$ SVL of females ($R^2 = 0.25$, $F_{1,28} = 9.1$, $P = 0.005$). ANOVA on regression resid-
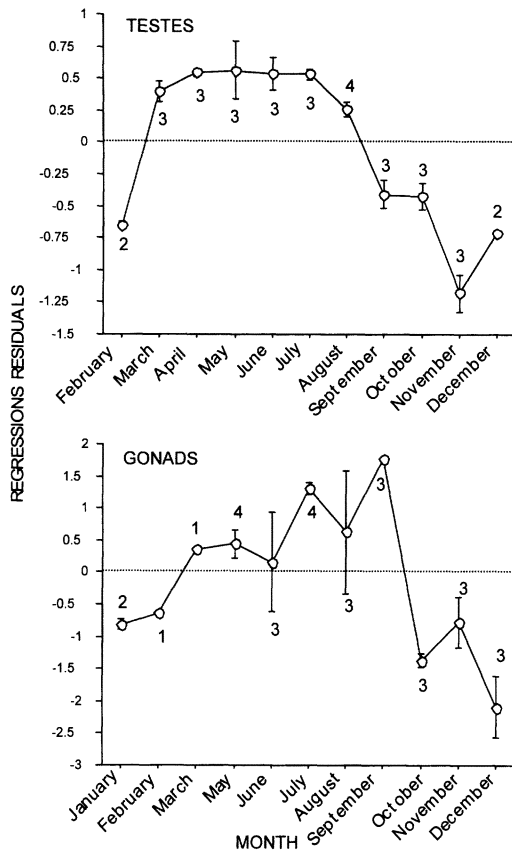
FIG. 1—Seasonal cycle of testes size of males and gonad size of females of *Sceloporus melanorhinus* from Chamela, Jalisco, Mexico. Data are mean (±1 *SE*) residuals from regression of $\log_{10}$ testes and $\log_{10}$ gonad volume (mm^3) against $\log_{10}$ snout–vent length.

uals revealed significant month effects on follicle volume ($F_{10,19} = 6.4$, $P = 0.003$). As with males, the gonadal cycle is represented by plots of regression residuals (Fig. 1). Follicles of females were at their minimal size during late autumn (October) and early winter (January–February) and increased in size from March to September (Fig. 1). Vitellogenesis began in late May, and follicular volume increased significantly between months ($F_{7,16} = 7.46$, $P < 0.005$). Monthly mean volumes of vitellogenic follicles-eggs were positively correlated with photoperiod ($r = 0.56$, $P < 0.05$), temperature ($r = 0.71$, $P < 0.01$), and precipitation ($r = 0.85$, $P < 0.005$). Ovulation began on 25 June and continued throughout July, August, and September. Maximum egg volume at ovulation

was 1,310 mm^3 (July), 885.7 mm^3 (August), and 869.8 mm^3 (September).

Among 30 females, 16 (53.3%) had non-vitellogenic follicles, 2 (6.7%) had vitellogenic follicles, and 12 (40%) had oviductal eggs. Mean number of nonvitellogenic follicles was 14.3 ± 1.1 (range = 2 to 20). Based on counts of the oviductal eggs, mean clutch size was 7.7 ± 0.33 (range = 5 to 9, $n = 12$), and there was no correlation between clutch size and female SVL ($r = 0.39$, $F_{1,10} = 1.9$, $P > 0.05$).

Based on capture-recapture data (A. Ramírez-Bautista, pers. obser.), mean SVL at hatching was 34.2 ± 0.28 mm (range = 29 to 41 mm, $n = 110$). Incubation period was measured between the date that females first had oviductal eggs and the date on which first hatchlings appeared. On 25 June, the first females were found with oviductal eggs. The first hatchlings were seen on the study site on 13 August. Therefore, estimated incubation period was 49 days.

DISCUSSION—Males and females of *S. melanorhinus* reached sexual maturity at a similar size and also attained similar size. No sexual dimorphism was detected in size between sexes of this population. Mature females and males were similar in SVL, as observed in previous studies of the genera *Sceloporus* (Fitch, 1978; Valdéz-González and Ramírez-Bautista, 2002) and *Urosaurus* (Ramírez-Bautista and Vitt, 1998).

Sceloporus melanorhinus males and females showed seasonal reproductive activity. Males attained maximum testes size during May, whereas females attained maximum egg volume from March to September. The reproductive cycle of males and females is slightly offset (asynchronous), but most mating occurred in July and early August (A. Ramírez-Bautista, pers. obser.). Reproductive, territorial, and courtship behavior by males began between late March and early June, during the dry season, before females had oviductal eggs, but the peak of mating was during July, in the wet season, when females began producing oviductal eggs. This reproductive pattern is similar to that of other species from the same region, such as *Anolis nebulosus* (Ramírez-Bautista and Vitt, 1997) and *Urosaurus bicarinatus* (Ramírez-Bautista and Vitt, 1998), and also similar to other species of *Sceloporus* (Table 1). These spe-

TABLE 1—Reproductive characteristics (mean ± 1 *SE*) of females of some large-bodied species of the genus *Sceloporus* from Mexico. Multiple (M) and single (S) clutches.

Species	Body size (mm)	Range	Clutch size	Range	Clutch frequency	Reproductive season	Source
S. clarkii	84.1 ± 1.6	72–120	8.2 ± 1.0	1–10	M	summer	Fitch, 1970, 1978
S. horridus	81.8 ± 1.8	60–100	14.8 ± 0.9	4–27	M	spring–summer	Valdéz-González and Ramírez-Bautista, 2002
S. magister	96.6	80–120	12.4	7–19	S	spring–summer	Fitch, 1978
	—	80–90	6.2	2–9	M	spring–summer	Tinkle, 1976
S. olivaceus	93.0	63–107	14.3	—	M	spring–summer	Fitch, 1978
S. spinosus	87.0 ± 2.5	60–112	18.5 ± 1.5	3–31	M	spring–summer	Valdéz-González and Ramírez-Bautista, 2002
S. melanorhinus	87.9 ± 1.2	75–98	7.7 ± 0.33	5–9	S	spring–summer	This study

cies have a relatively short reproductive season, in contrast to other syntopic species that have extended reproductive activity, such as *Sceloporus utiformis* (May to December; Ramírez-Bautista and Gutiérrez-Mayén, 2003), *Cnemidophorus lineatissimus* (April to January; Ramírez-Bautista et al., 2000), and *C. communis* (April to October; Ramírez-Bautista and Pardo-De la Rosa, 2002). These data suggest that species comprising the lizard community from the Chamela region have different requirements for reproduction. Testes size and vitellogenesis increased as photoperiod increased; temperature and precipitation might have also affected reproductive seasonality, as in some other species (Marion, 1982; Ramírez-Bautista and Vitt, 1997, 1998). Male reproduction ended during August, even though the rainy season does not end until October. Compared with other species of the same region, male reproduction began and ended earlier (March to August). Female reproductive activity began in June and decreased in October, with most egg production from July to September, coinciding with the rainy season. Although the 3 environmental factors influence initiation of reproduction in females, timing of rainfall could be the ultimate cue for reproduction through its effects on egg production and offspring survival (Andrews and Sexton, 1981).

Sceloporus melanorhinus and *S. clarkii* have a similar body size and clutch size (Table 1), and because both lizards belong to the *clarkii* group, the small clutch sizes of both species might reflect historical effects on life-history traits. Large-bodied species in other clades, such as *S. horridus* and *S. spinosus* (*spinosus* group; 14.8 and 18.5 eggs, respectively; Valdéz-González and Ramírez-Bautista, 2002), *S. magister* and *S. orcutti* (*magister* group; 12.4 and 11.0 eggs, respectively; Mayhew, 1963; Fitch, 1978), and *S. olivaceus* (*olivaceus* group; 14.3 eggs; Fitch, 1978), have large clutch sizes (Table 1). Similarity in clutch sizes among closely related species could represent historical effects, and differences among populations could reflect evolved adaptive differences as a result of different environments or proximate effects of abiotic factors in different environments (Dunham and Miles, 1985).

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LITERATURE CITED

ABACUS CONCEPTS. 1992. Statview IV. Abacus Concepts, Inc., Berkeley, California.

ANDREWS, R. M., AND O. I. SEXTON. 1981. Water relations of the eggs of *Anolis auratus* and *Anolis limifrons*. Ecology 62:556–562.

ASTRONOMICAL ALMANAC OF THE WORLD. 1984. United States Government Printing Office and Her Majesty's Stationary Office, Washington, D.C. and London, United Kingdom.

BALLINGER, R. E. 1983. Life-history variations. In: R. B. Huey, E. R. Pianka, and T. W. Schoener, editors. Lizard ecology: studies of a model organism. Harvard University Press, Cambridge, Massachusetts. Pages 241–260.

BENABIB, M. 1994. Reproduction and lipid utilization of tropical populations of *Sceloporus variabilis*. Herpetological Monographs 8:160–180.

BULLOCK, S. H. 1986. Climate of Chamela, Jalisco, and trends in the South Coastal Region of México. Archives for Meteorology, Geophysics, and Bioclimatology, series B 36:297–316.

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.

DUNHAM, A. E., AND D. B. MILES. 1985. Patterns of covariation in life history traits of squamate reptiles: the effects of size and phylogeny reconsidered. American Naturalist 126:231–257.

DUNHAM, A. E., D. B. MILES, AND D. N. RESNICK. 1988. Life history patterns in squamate reptiles. In: C. Gans, editor. Biology of the Reptilia, volume 16. Ecology B: defense and life history. Alan R. Liss, New York. Pages 441–522.

FERIA-ORTÍZ, M., A. NIETO-MONTES DE OCA, AND I. H. SALGADO-UGARTE. 2001. Diet and reproductive biology of the viviparous lizard *Sceloporus torquatus torquatus* (Squamata: Phrynosomatidae). Journal of Herpetology 35:104–112.

FITCH, H. S. 1970. Reproductive cycles in lizards and snakes. University of Kansas Museum of Natural History, Miscellaneous Publications 52:1–247.

FITCH, H. S. 1978. Sexual size differences in the genus *Sceloporus*. University of Kansas Science Bulletin 51:441–461.

FITCH, H. S. 1985. Variation in clutch and litter size in the New World reptiles. University of Kansas Museum of Natural History Publications 76:1–76.

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.

MARION, K. R. 1982. Reproductive cues for gonadal development in temperature and photoperiod effects on the testicular cycles of the lizard *Sceloporus undulatus*. Herpetologica 38:26–39.

MAYHEW, W. W. 1963. Reproduction in the granite spiny lizard, *Sceloporus orcutti*. Copeia 1963:144–152.

RAMÍREZ-BAUTISTA, A. 1994. Manual y claves ilustradas de los anfibios y reptiles de la región de Chamela, Jalisco, México. Cuadernos del Instituto de Biología Numero 23, Universidad Nacional Autónoma de México.

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.

RAMÍREZ-BAUTISTA, A., AND A. GONZALEZ-ROMERO. 2002. Some reproductive and feeding characteristics of the viviparous Mexican lizard *Sceloporus torquatus* (Phrynosomatidae). Southwestern Naturalist 47:98–102.

RAMÍREZ-BAUTISTA, A., AND G. GUTIÉRREZ-MAYÉN. 2003. Reproductive ecology of *Sceloporus utiformis* (Sauria: Phrynosomatidae) from a tropical dry forest of Mexico. Journal of Herpetology 37:1–10.

RAMÍREZ-BAUTISTA, A., AND D. PARDO-DE LA ROSA. 2002. Reproductive cycle and characteristics of the widely-foraging lizard, *Cnemidophorus communis* from Jalisco, México. Southwestern Naturalist 47:205–214.

RAMÍREZ-BAUTISTA, A., AND L. J. VITT. 1997. Reproduction in the lizard *Anolis nebulosus* (Polychrotidae) from the Pacific coast of Mexico. Herpetologica 53:423–431.

RAMÍREZ-BAUTISTA, A., AND L. J. VITT. 1998. Reproductive biology of *Urosaurus bicarinatus* (Sauria: Phrynosomatidae) from a tropical dry forest of México. Southwestern Naturalist 43:381–390.

SMITH, H. M. 1939. The Mexican and Central American lizards of the genus *Sceloporus*. Field Museum of Natural History, Zoology Series 26:1–397.

TINKLE, D. W. 1976. Comparative data on the population ecology of the desert spiny lizard, *Sceloporus magister*. Herpetologica 32:1–6.

TINKLE, D. W., H. M. WILBUR, AND S. G. TILLEY. 1970.

Evolutionary strategies in lizard reproduction. Evolution 24:55–74.

VALDÉS-GONZÁLEZ, M., AND A. RAMÍREZ-BAUTISTA. 2002. Reproductive characteristics of the spiny lizards, *Sceloporus horridus* and *S. spinosus* (Squamata: Phrynosomatidae) from Mexico. Journal of Herpetology 36:36–43.

VITT, L. J. 1990. The influence of foraging mode and phylogeny on seasonality of tropical lizard reproduction. Papéis Avulsos de Zoologia (Sao Paulo) 37:107–123.

WIENS, J. J., AND T. W. REEDER. 1997. Phylogeny of the spiny lizards (*Sceloporus*) based on molecular and morphological evidence. Herpetological Monographs 11:1–101.