

REPRODUCTIVE CYCLE OF THE LIZARD *SCELOPORUS MUCRONATUS* WITH COMMENTS ON INTRASPECIFIC GEOGRAPHIC VARIATION

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ABSTRACT.—*Sceloporus mucronatus* is a viviparous lizard that inhabits high altitudes in central México. Lizards from Tecocomulco, Hidalgo, México, were collected monthly at 2500 m throughout one year. Macro- and microscopic evidence of gonads showed that both sexes reproduce synchronously during the fall. In males, after a short testicular quiescence in December, the recrudescence begins in winter (January) and continues through spring and summer (July), with maximum activity occurring from late summer to early fall (August–September). Regression takes place simultaneously with copulation during the fall (October–November). In females, vitellogenesis occurs during summer and fall (August–November), with ovulation in the fall (November–December). Gravid females were found throughout the winter, and parturition occurs during spring (May). Litter size was correlated with female snout–vent length. Female reproductive phenology of viviparous *Sceloporus* species seems to be highly conservative at different altitudes, but male reproductive phenology shifts between spring–summer (in populations higher than 2500 m) and summer–fall (in populations 2500 m or lower), as in the present study. The longer period of testicular recrudescence (January–July) in the studied population from Tecocomulco suggests plasticity in testicular activity.

Key words: reproduction, geographic variation, *Sceloporus mucronatus*, synchronous cycles, reproductive phenologies.

RESUMEN.—*Sceloporus mucronatus* es una lagartija vivípara que ocurre en altas elevaciones en el Centro de México. Mensualmente fueron colectados ejemplares de Tecocomulco, Hidalgo, México a 2500 m durante un año. La evidencia macro y microscópica de las gónadas mostró que se ambos sexos reproducen sincrónicamente durante el otoño. En los machos, después de un corto periodo de quiescencia testicular en diciembre, inicia la recrudescencia en invierno (enero) y continúa durante la primavera y verano (julio) con máxima actividad durante fines de verano y principios de otoño (agosto–septiembre). Finalmente, la regresión ocurre simultáneamente con las cópulas durante el otoño (octubre–noviembre). En las hembras la vitelogénesis ocurre durante el verano y otoño (agosto a noviembre) con ovulación en el otoño (noviembre–diciembre). Las hembras se encuentran grávidas durante el invierno y el parto ocurre en la primavera (mayo). El tamaño de la camada fue correlacionado con la longitud hocico-cloaca. La fenología reproductora de las hembras de los *Sceloporus* vivíparos parece ser altamente conservativa en diferentes altitudes, pero en los machos puede cambiar de primavera-verano (en poblaciones habitantes de altitudes mayores de 2500 m) a verano – otoño (en poblaciones de altitudes de 2500 m o menores), como en la población del presente estudio. El largo periodo de recrudescencia testicular (enero–julio) de la población estudiada de Tecocomulco sugiere plasticidad en la actividad testicular.

Reptiles have different patterns of reproductive activity, as indicated by seasonal and gonadal changes. Reproductive phenology is an important aspect of a species' reproductive strategy (Fitch 1970). Oviparous and viviparous lizard species of the genus *Sceloporus* exhibit different seasonal reproduction patterns. Reproductive activity of oviparous species in temperate areas is restricted to spring and summer, as in *S. aeneus*, *S. scalaris*, *S. occidentalis*, *S. graciosus*, and *S. spinosus*. In these species, vitellogenesis begins in spring, and oviposition of one or more clutches occurs by

late spring and summer; hatchlings emerge in late summer and fall (Goldberg 1974, Newlin 1976, Guillette 1981, 1982, López-Ortíz 2001). Therefore, reproductive activity is associated with the rainy season (Levings and Windsor 1982, Méndez–de la Cruz et al. 1992, 1998). However, reproductive variation was observed intraspecifically when species occupied different habitats, altitudes, or latitudes (*S. undulatus*, Tinkle and Ballinger 1972; *S. virgatus*, Vinegar 1975; and *S. grammicus*, Guillette and Casas-Andreu 1980, Ortega and Barbault 1984, Guillette and Bearce 1986).

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In viviparous species of the genus *Sceloporus*, vitellogenesis starts toward the end of summer or during fall, ovulation occurs during late summer or early fall, pregnancy occurs during the fall and continues throughout the winter, and births occur the following spring (Guillette and Méndez-de la Cruz 1993, Méndez-de la Cruz et al. 1998). This pattern describes the females as fall breeders, regardless of the altitude. On the other hand, males could be either spring-summer (in areas higher than 2500 m) or fall (in areas lower than 2500 m) breeders (Méndez-de la Cruz et al. 1994). These patterns determine asynchronous or synchronous reproductive activity between both sexes. Asynchronous reproductive activity between males and females may promote protandry (Olsson et al. 1999).

Sceloporus mucronatus is a lizard species native to temperate areas along the Trans-Mexican Volcanic Belt, from Veracruz to the Estado de México in México (Martínez-Méndez and Méndez-de la Cruz 2007). The reproductive cycle of a mountain population (3300 m) was described by Méndez-de la Cruz et al. (1988) and Estrada-Flores et al. (1990). This cycle is seasonal, with recrudescence and maximum testicular activity occurring during spring and summer (April–August) and maximum gonadal activity of females occurring during late summer and early fall (August–September); ovulation occurs in October. Females remain pregnant during the winter months and give birth the following spring. Previous work found differences in populations inhabiting lower elevations (Méndez-de la Cruz et al. 1998). Considering that *S. mucronatus* occupies a wide geographical range with different habitats, the objective of this study was to determine the reproductive cycle and mating season in the low-elevation population from Tecocomulco, Hidalgo.

METHODS

We collected 10–16 male and female specimens of *S. mucronatus* monthly between March 1990 and April 1991 in the Tecocomulco area (19°4'0"N, 98°21'24"W), state of Hidalgo, México, at 2500 m. Dominant vegetation was xeric and composed of abundant *Opuntia*, *Agave*, and *Mammillaria* and sporadic *Prosopis* and *Cupressus* trees. The animals were euthanized by chloroform and fixed in 10% buffered

formalin. We measured snout-vent length (SVL, mm), wet body mass (g), and wet gonadal mass (g) for each animal. Females were categorized according to their reproductive condition: pre-vitellogenetic with ovocytes in ovary <2 mm across, vitellogenetic with ovocytes in ovary undergoing vitellogenesis, or pregnant with eggs in the oviduct. We also recorded the number of eggs in the uterus and the stage of embryonic development, according to Dufaure and Hubert (1961).

In order to confirm correspondence between macroscopic changes in gonadal cycles and gametogenetic activity, the left gonads and conducts (oviducts and epididymides) from each animal of both sexes were fixed in Bouin's solution and prepared for a conventional histological study (dehydrated in alcohol graduals, cleared in xylene, and embedded in paraplast). Tissues were sectioned at 7 μ m and stained with hematoxylin-eosin and Masson's trichrome (Presnell and Schreiber 1997). The presence of spermatozoa in the seminiferous tubules, epididymides, and oviducts was also registered. Male reproductive maturity was established microscopically by the presence of spermatozoa in seminiferous tubules. Female reproductive condition was assessed by the appearance of developing ovarian follicles (vitellogenic) and by the presence of embryos in the oviducts.

To macroscopically determine the reproductive cycle, we conducted a regression analysis with wet gonadal mass (testis or ovary) as the dependent variable and total weight as the independent variable; monthly variation of residuals was analyzed to determine the reproductive cycle (Ibargüengoytía and Casalins 2007). Relative litter mass (RLM) from females during the final stages of embryonic development was determined following Rodríguez-Romero et al. (2004). We determined statistical differences in monthly gonadal changes using an ANOVA of gonadal residuals followed by a post hoc test (Statistica 6.0). Litter size was regressed on body size; a Pearson correlation coefficient was also calculated. Specimens were deposited in the Herpetological Collection of the Instituto de Biología, Universidad Nacional Autónoma de México.

Results were compared with previous studies on a high-altitude population of *S. mucronatus* located in the Ajusco Mountains, near Mexico City, at 3200–3400 m (Méndez-de la

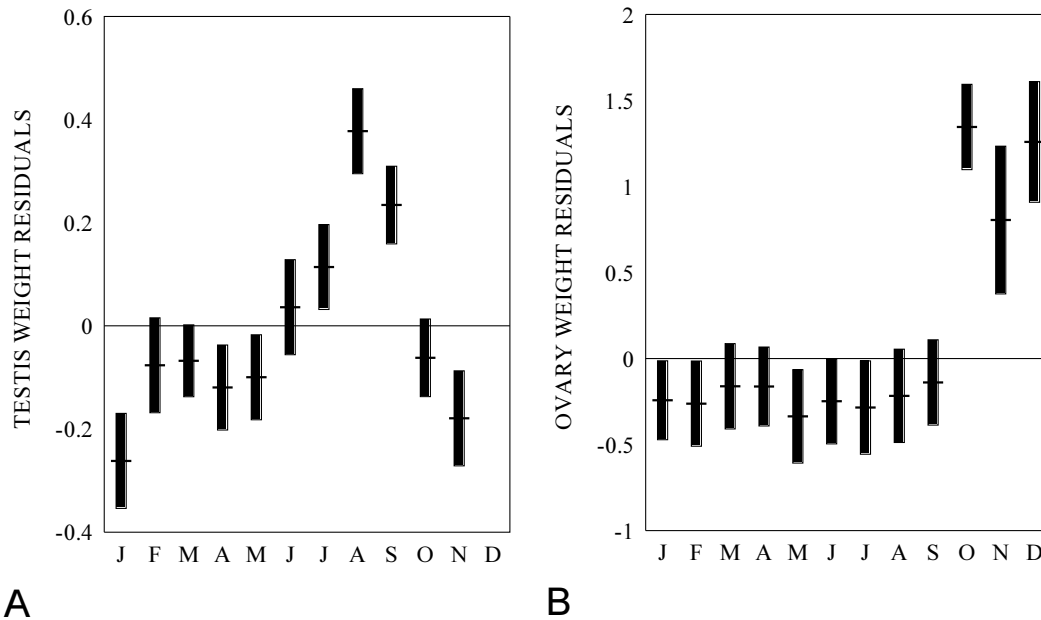


Fig. 1. Monthly changes in testicular (A) and ovarian (B) activity throughout the reproductive cycle of *Sceloporus mucronatus* from the Tecocomulco population. Means and standard errors are represented.

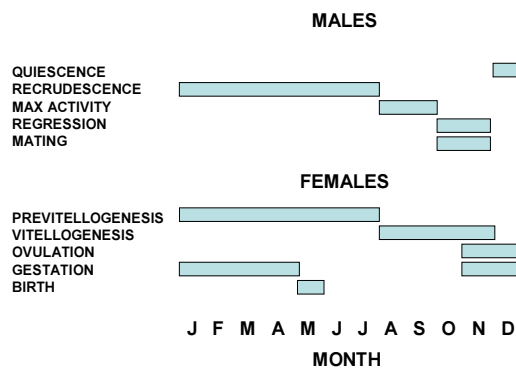


Fig. 2. Diagrammatic representation of the reproductive cycle of *Sceloporus mucronatus* from the Tecocomulco population.

Cruz et al. 1988, Estrada-Flores et al. 1990, Méndez-de la Cruz et al. 1993, 1994).

RESULTS

Both male and female *S. mucronatus* exhibited fall reproductive activity (Fig. 1). Significant changes occurred in the gonadal residuals throughout the reproductive cycle in both males ($F_{10,44} = 10.25, P < 0.001$) and females ($F_{11,52} = 9.80, P < 0.001$). The average SVL ($s_{\bar{x}}$) was

85.4 (1.46; range 66.0–101.0 mm) in adult males and 79.4 (1.24; range 56.5–102.0 mm) in adult females.

Testicular quiescence was observed in December, recrudescence occurred from January to July, and the highest activity occurred from August to September. Regression began in October and continued into November (Figs. 2, 3). Spermatozoa were observed in the interior of the seminiferous tubules and epididymides from August to November, being most abundant in August and September in seminiferous tubules and from August to November in epididymides (Fig. 3).

Females exhibited vitellogenesis during summer-fall (August–November); preovulatory follicles were present in October and November. Ovulation occurred in some females (60%) toward the end of November and in the remaining females during December (40%). Sperm was found in the vagina from October to December but not in the previous months (Figs. 2, 4). Females remained pregnant during the winter and gave birth by May (Fig. 2). Litter size ($s_{\bar{x}}$) averaged 6.46 (0.59; range 2–13), and number of embryos was positively correlated with female body size ($y = 0.243x - 12.831, r^2 = 0.828, df = 24, P < 0.001$; Fig. 5).

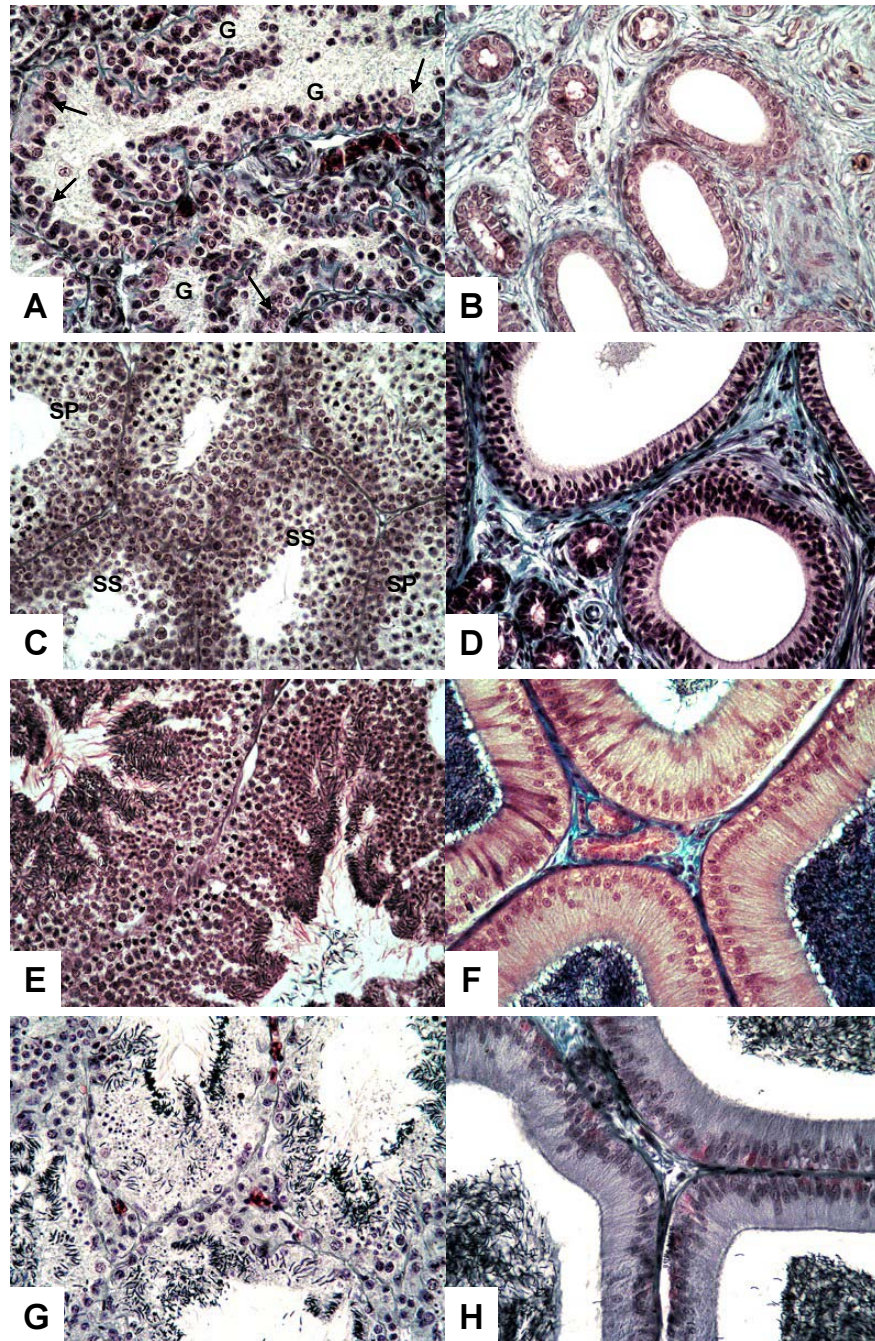


Fig. 3. Gonadal and epididymal changes throughout the reproductive cycle of *Sceloporus mucronatus*. A and B, quiescence (from December): A, seminiferous tubules only with spermatogonia (G) and Sertoli cells (arrows) present; B, epididymis with small ducts and lumen empty. C and D, recrudescence (from June): C, the germinal epithelium with a thickness of 3–4 cells and an increasing number of primary (SP) and secondary spermatocytes (SS) observed close to the lumen; D, epididymis without sperm. E and F, maximal testicular activity (from September): E, spermiogenesis in seminiferous tubules, numerous mature sperm in the lumen or around the periphery of the tubule lumen; F, ducts epididymis showing increased epithelial height and secretory activity and the lumen filled with mature sperm. G and H, regression (from October): G, seminiferous tubules with germinal epithelium reduced; H, epididymal ducts partially filled with sperm. Masson trichrome stain, 400X.

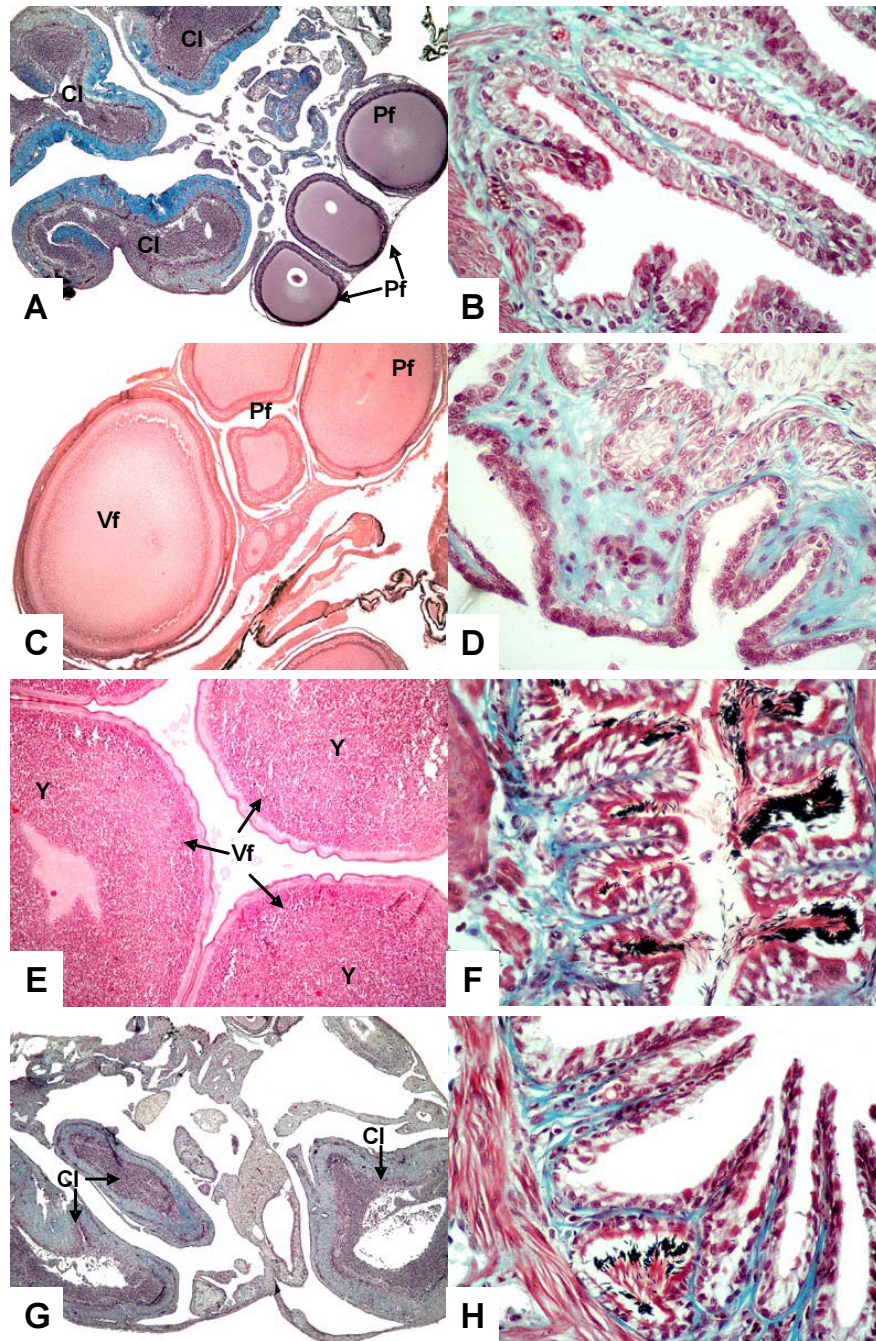


Fig. 4. Gonadal and oviductal changes throughout the reproductive cycle of *Sceloporus mucronatus*. A and B, quiescence (from February): A, previtellogenic follicles (Pf) and corpora lutea (Cl) were seen in this face, Masson's trichrome stain, 40X; B, oviduct without sperm, Masson trichrome stain, 400X. C and D, recrudescence (from August): C, previtellogenic (Pf) and vitellogenic (Vf) follicles in ovary, H-E stain, 40X; D, oviduct without sperm. E and F, maximal activity (from November): E, in the ovary, the increased size of vitellogenic follicles (Vf) was correlated with the yolk (Y) deposition within the cytoplasm, H-E stain, 40X; F, sperm retention in the folds of vagina, Masson's trichrome stain, 400X. G and H, regression (from December): G, in the ovary, immediately after ovulation, the postovulatory follicles initiate the corpora lutea (CL) formation, Masson trichrome stain, 40X; H, the vagina showing sperm retention zones, Masson trichrome stain, 400X.

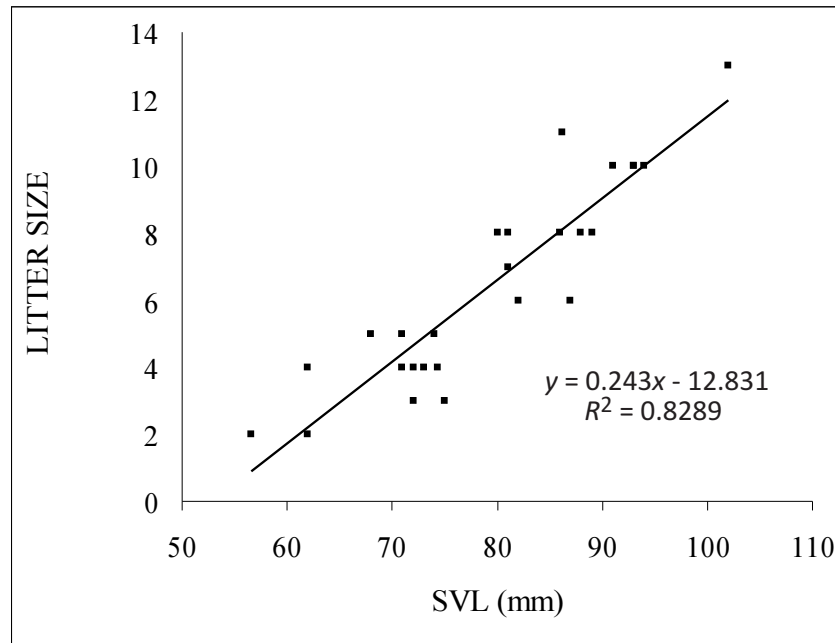


Fig. 5. Correlation between female snout-vent length (SVL) and the number of embryos in utero (litter size) in *Sceloporus mucronatus* from the Tecocomulco population.

Gestation began immediately after ovulation and continued for 5 months (Fig. 2). Births occurred in May, and SVL ($s_{\bar{x}}$) of neonates averaged 38.35 mm (1.35; $n = 16$). The smallest female with embryos in the oviduct was 56.5 mm SVL, in contrast to the observed 63 mm in the Ajusco population (Ortega-León et al. 2007). Relative litter mass was 0.37, considering only females with embryos in the last stages of development.

DISCUSSION

Tecocomulco vs. Ajusco Reproductive Phenology

The *S. mucronatus* population from Tecocomulco, Hidalgo, exhibits a typical reproductive cycle of lowland lizards (<2500 m), with maximum reproductive activity during the fall (Guillette and Méndez-de la Cruz 1993, Méndez-de la Cruz et al. 1998). This population's reproductive phenology differs in 2 main ways from that of the mountain population previously studied at Ajusco Mountain, near Mexico City.

First, at high elevation, maximal testicular development occurs during late spring and

early summer (Méndez-de la Cruz et al. 1988, Estrada-Flores et al. 1990), while at low elevation, activity is delayed until late summer and early fall. In both populations, vitellogenesis occurs in summer-fall. Macro- and microscopic data show that Tecocomulco males present testicular regression during October and November, even though abundant spermatozooids in the epididymis and deferent duct were observed. In the females, spermatozooids were found in the lumen of the vagina during October, suggesting that copulation also occurs during this month. It is important to note that sperm was not found in preceding months, which indicates that copulation is not concomitant with maximum testicular weight and that sperm is not stored from previous years. Copulation occurs during October and November; whereas ovulation occurs during November and December. Therefore, the reproductive cycle of *S. mucronatus* from Tecocomulco should be considered synchronous even though maximum development of testes and ovaries differs by 2 months (August vs. October).

Second, mean litter size was apparently higher in the Tecocomulco population (6.46, range 2–13) than in the Ajusco population (5.11, range 3–8). However, the estimation of

litter size based upon the number of recruited follicles was similar in both populations. The observed difference in litter size between populations might be determined by the atresia rate, which in turn may be regulated by endocrine factors influenced by environmental stimuli (Méndez-de la Cruz et al. 1993). Follicular atresia is defined as the death of ovarian follicles prior to ovulation (Byskov 1978) and may significantly decrease the number of eggs produced in some lizard species (Fox and Guillette 1987, Méndez-de la Cruz et al. 1993). Even though atresia is common in vitellogenic follicles, it may also occur in previtellogenic follicles (Byskov 1978). In fact, the previtellogenic follicles that do not mature within one given year necessarily became atretic.

Relative litter mass in *Sceloporus* species ranges from 0.15 to 0.47. According to this range, *S. mucronatus* from Tecocomulco exhibits high reproductive investment, with an RLM of 0.37. This RLM value is actually higher than the average of 0.32 for viviparous species within the genus (Rodríguez-Romero et al. 2004).

Mountain vs. Central Plateau Reproductive Phenology

Male *Sceloporus* lizards exhibit 2 distinct reproductive phenologies depending on geographic location. First, in mountain temperate areas with tropical influences of central México, maximum gonadal activity occurs during the spring-summer period, as observed in *S. grammicus*, *S. formosus*, and *S. mucronatus* (see Guillette and Méndez-de la Cruz 1993). Second, in desert areas of the Mexican Central Plateau, which extends from central México to the southwestern United States, maximum testicular activity (i.e., maximum testicular size and spermatogenesis) occurs in late summer and early fall, as observed in *S. cyanogenys*, *S. jarrovi*, *S. poinsetti*, *S. megalepidurus*, *S. grammicus disparilis* (see Guillette and Méndez-de la Cruz 1993, Gadsden et al. 2005), *S. torquatus* (Hernández 1991, Feria-Ortíz et al. 2001), and *S. mucronatus* (present study).

Evolution of Reproductive Phenology (Synchronous vs. Asynchronous Reproductive Cycles)

The synchronous fall reproduction between males and females occurs in several *Sceloporus* species that inhabit elevations lower than 2500 m, including *S. megalepidurus*, which is basal

in the viviparous clade (*S. megalepidurus*–*S. grammicus*–*S. torquatus*; see Méndez-de la Cruz et al. 1998). Thus, according to the phylogenetic relationships among sceloporine species, synchronous reproduction appears to be an ancestral trait, whereas asynchronous reproduction between sexes evolved once the viviparous species invaded mountain environments higher than 2500 m. One fact that supports this argument is that asynchronous reproductive cycles have only been found in mountain populations of *S. grammicus* and *S. mucronatus* at 3200–3400 m (Guillette and Casas-Anderu 1980, Méndez-de la Cruz et al. 1988). Therefore, the reproductive cycle of *S. mucronatus* from Tecocomulco (synchronous) could have been ancestral to the cycle observed in the Ajusco population (asynchronous).

One explanation for this scenario is that spring-summer reproductive activity in the males from mountain populations may have evolved because of a gain in fitness derived from early emergence. In other words, these males could have gained some advantage in reproductive success by starting behavioral interactions and the production of more mature spermatozoa before the onset of the mating season. This phenomenon is considered protandry (Olsson et al. 1999, Ortega-León et al. 2009).

A second and alternative scenario considers that fall reproductive activity in males, observed in the Mexican Central Plateau populations (i.e., *S. mucronatus* from Tecocomulco), evolved from the mountain populations (i.e., *S. mucronatus* from Ajusco) where spring reproductive activity is exhibited by males of viviparous populations (Méndez-de la Cruz et al. 1994, 1998). Supporting this hypothesis is the fact that the herpetofauna of the Mexican Plateau was derived from high-elevation mountain species during the Pleistocene (Martin 1958, Méndez-de la Cruz et al. 1994, Gadsden et al. 2005). Increasing aridity eliminated woodlands from the Central Plateau, requiring xeric adaptations by local populations. Synchronous reproduction, with gonadal activity of both sexes occurring simultaneously during the fall, is observed in populations of species from intermediate to low elevations (see Méndez-de la Cruz et al. 1998). Observations of 2 species (*S. grammicus* and *S. mucronatus*) with a wide elevation range in México suggest that the reptile invasion that occurred with the appearance of

the Mexican Central Plateau (Martin 1958) was associated with the shift from spring to fall reproductive activity. Populations of both species occurring above 3000 m have asynchronous reproduction, while those below 2500 m have synchronous reproduction. Because the change in timing of testicular maturation for these species may have occurred when climatic conditions became more arid and when the forests of the Central Plateau were replaced by xeric vegetation during the Pleistocene (Martin 1958), differences in reproductive activity between males from mountain populations and males from Central Plateau populations could be attributed to differences in the availability of resources. Drier conditions and lower food availability prevail at low elevations during spring and early summer, which could explain why reproductive activity is delayed until the fall, when resources are less scarce (Palacios-Orona and Gadsden-Esparza 1995).

In synchronous reproductive cycles (as seen in *S. mucronatus* from Tecocomulco), males reach maximum testicular size a few months before females exhibit full vitellogenesis. Also, copulation occurs during early regression (Méndez-de la Cruz et al. 1988, Villagrán-Santa Cruz et al. 1994, Méndez-Juárez 2003); thus, both sexes are reproductively active at the same time. In contrast, in asynchronous reproductive cycles (as seen in *S. mucronatus* from Ajusco), testes are in late regression or quiescence when females exhibit vitellogenesis; consequently, the sperm must be stored to fertilize the oocyte. Sperm storage should be considered the crucial mechanism to fertilize the oocyte in asynchronous cycles, as both sexes are reproductively active at different times. In the studied population of *S. mucronatus* from Tecocomulco, sperm was deposited in the vagina from October to December, when ovulation takes place (synchronous cycle). In the Ajusco population (asynchronous cycle), sperm was found in the oviduct as early as June—5 months prior to ovulation in October (Ortega-León et al. 2009); and in September, males showed testes in late regression and only remnants of spermatozoa in the epididymides (Estrada-Flores et al. 1990).

Asynchronous activity was reported for elevations lower than 2500 m in *S. jarrovi* (Ramírez-Bautista et al. 2002) and *S. grammicus* (Jiménez-Cruz et al. 2005). The reproductive cycles of these 2 species exhibit noticeable

differences between sexes in maximum gonadal activity and were therefore considered asynchronous cycles. According to figures in these papers, maximum testicular activity occurs in October (*S. jarrovi*) and September (*S. grammicus*), whereas maximum ovarian activity occurs in March (*S. jarrovi*) and April (*S. grammicus*). Nevertheless, these reported differences might be due to methodological problems, as both studies included egg mass along with ovarian mass to describe the ovarian cycle. In the article on *S. grammicus*, the methods are described as follows: “The largest eggs (embryo, oviductal, vitellogenic follicle, or nonvitellogenic follicle) on each side of the body also were weighed to 0.0001 g and multiplied by the number of eggs on that side. The total weight for both sides constituted female gonadal mass” (Jiménez-Cruz et al. 2005). Gametogenesis and embryogenesis are 2 different processes in the female reproductive cycle and must be separated to describe the reproductive cycle. Also, reproductive cycles vary among populations (Ibargüengoytía and Casalins 2007). Therefore, it is not appropriate to utilize samples from different areas to describe reproductive cycles. Samples used to describe the reproductive cycle of *S. jarrovi* (Ramírez-Bautista et al. 2002) came from different populations that were previously considered different species (Wiens et al. 1999). Thus, asynchronous reproductive activity may be present in elevations lower than 2500 m, but appropriate methodology should be utilized to determine presence.

What Promotes Asynchronous Cycles?

Depending on whether synchronous or asynchronous patterns are derived or ancestral, 2 scenarios may arise. First, if synchronous reproduction was the derived pattern, it may be a consequence of the drier conditions and relatively low food availability that prevail at low elevations during spring and early summer (Méndez-de la Cruz et al. 1994). Therefore, fall mating in the viviparous *Sceloporus* species evolved to coincide with the end of the rainy season, when males have plenty of energy to defend territories (Méndez-de la Cruz et al. 1994). Synchronous reproduction may have also been derived if selection favored males that exhibited slower spermatogenesis, which enabled them to copulate with a greater percentage (maybe as high as 100%) of receptive females (including 6- or 7-month-old females),

as in the Tecocomulco population (Villagrán-Santa Cruz et al. 1994). In comparison to the montane population of *S. mucronatus*, the Central Plateau population has smaller fertilized females (minimum SVL of reproductive females = 71 and 56.5 mm, respectively). Second, if asynchronous reproduction is the derived pattern, protandry could be acting as a selective force. Males that begin reproductive activity early in the season may have an advantage in behavioral interactions or may produce and mature more spermatozoa before the actual mating season (Olsson et al. 1999).

Sceloporus mucronatus is a testable model for understanding the mechanism that controls shifts in reproduction, because males exhibit both reproductive phenologies (spring–summer and summer–fall) and because the species is found close to the distribution limit of 2 important regions (temperate zones with tropical influence and zones with Nearctic influence). *Sceloporus mucronatus* also represents a good model for testing interesting hypotheses such as protandry (early emergence from periods of inactivity has been interpreted as protandry; Olsson et al. 1999).

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