Reproductive Activity of Three Sympatric Viviparous Lizards at Omiltemi, Guerrero, Sierra Madre del Sur, Mexico

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Abstract.—We studied the reproductive characteristics of sympatric populations of *Sceloporus formosus scitulus*, *Sceloporus omiltemanus* (Phrynosomatidae), and *Mesaspis gadovii* (Anguidae) at the Omiltemi forest reserve (Guerrero, Mexico). Males are larger and reach larger body sizes at reproductive maturity and are more colorful than females in both *Sceloporus*, whereas males are smaller than females and reach sexual maturity at similar body sizes in *M. gadovii*. These species are single brooded and follow a common pattern of annual reproductive activity. The reproductive activity of females and males of the three species is seasonal; vitellogenesis is initiated in late summer and continues in autumn/rainy season, gestation occurs throughout the winter/dry season, and parturition occurs in early spring. All three species have intersexual synchrony in reproductive activity. In spite of similar reproductive schedules, some subtle features related to the length of each of the reproductive stages could be observed. *Sceloporus formosus scitulus* has a more extended reproductive season, and large females start vitellogenesis earlier than do small ones. Males have a prolonged reproductive activity and a short nonreproductive season. In contrast, the reproductive cycle of the other two species is defined by shorter reproductive season and less intrasexual asynchrony for both sexes than found in *S. f. scitulus*. The seasonal pattern of reproduction shared by these three species is characteristic of other viviparous lizards at high elevations in tropical and subtropical latitudes of Central and South America, being convergent for different lizard families. This convergence in reproductive patterns suggests a common evolutionary response to environmental factors associated with montane habitats, whereas specific differences observed within species are attributed to the particular evolutionary history of each taxon.

North and Central American viviparous lizards commonly have seasonal reproduction. At boreal latitudes, viviparous species, such as *Phrynosoma douglasi* (Phrynosomatidae, Goldberg, 1971; Powell and Russel, 1991) and *Elgaria coerulea* (Anguidae, Vitt, 1973), exhibit spermiogenesis, vitellogenesis, and gestation during spring and summer, the same as oviparous species. At tropical and subtropical latitudes, most viviparous females begin vitellogenesis during the summer months, ovulate in the fall, and are gravid during the winter; births occur during the spring and summer of the following year (i.e., Phrynosomatidae, Méndez de la Cruz et al., 1998; Zamudio and Parra-Olea, 2000; Anguidae, Guillette and Casas-Andreu, 1987; Scincidae, Guillette, 1983; Ramírez-Bautista et al., 1996, 1998; and Xenosauridae, Ballinger et

al., 2000; Smith et al., 2000). In contrast, Xantusid females from the lowlands (i.e., *Lepidophyma pajapanensis*, Méndez de la Cruz et al., 1999; *Lepidophyma tuxtlae*, Greene, 1970; Castillo-Cerón and López-González, 1990) show a common reproductive pattern among diverse habitats, starting vitellogenesis in December after a six-month period of ovarian quiescence, ovulate by March, and give birth by June.

In males, the annual reproductive activity can be seasonal or continuous. Among seasonal species sperm production, courtship, and copulation can occur during the spring and summer before ovulation, defining asynchronous reproduction between males and females, or occur during fall months being synchronous with ovulation. Asynchronous reproduction has been reported in high altitude species of the genus *Sceloporus* (Guillette and Casas-Andreu, 1980; Guillette and Sullivan, 1985; Estrada-Flores et al., 1990; Méndez de la Cruz et al., 1998), in *Eumeces copei* at 2,600–3,100 m (Ramírez-Bautista et al., 1996), and also in Xantusids of low altitudes (*L. pajapanensis* at 300–

400 m, Méndez de la Cruz et al., 1999; *Lepidophyma tuxtlae*, Castillo-Cerón and López-González, 1990). Synchronous reproductive activity, occurring during the fall, is known for species of *Sceloporus* at moderate elevations (Ortega and Barbault, 1984; Guillette and Méndez de la Cruz, 1993; Méndez de la Cruz et al., 1998).

Continuous reproductive activity is not common in viviparous lizards of Central and North America. It has been reported in males of *E. copei* (Ramírez-Bautista et al., 1996), *Barisia imbricata* (Guillette and Casas-Andreu, 1987), and in both sexes of *Sceloporus bicanthalis* (Manríquez-Morán, 1995; Hernández-Gallegos et al., 2002). In *Mesaspis monticola* at high elevations in Costa Rica, Vial and Stewart (1985) found continuous spermiogenesis, and females with asynchronous reproductive activity; this lizard was considered biannual because of an extended reproductive period.

Méndez de la Cruz et al. (1998) suggested that the reproductive pattern of *S. bicanthalis* is an intermediate pattern between the reproductive cycles of oviparous (spring and summer breeders) and viviparous species (fall breeders). According to Hernández-Gallegos et al. (2002), that pattern does not appear to be associated with climate or environmental features because sympatric and syntopic species of *S. bicanthalis* exhibit seasonal reproduction, suggesting that the reproductive phenology in this lizard could have a strong historical component. Thus, reproductive patterns of lizards have been associated with environmental factors, reproductive mode, and phylogeny.

Sceloporus omiltemanus (*torquatus* species group), *S. formosus scitulus* (*formosus* species group; Phrynosomatidae; Bell et al., 2003), and *Mesaspis gadovii* (Anguidae) are sympatric viviparous species found at high elevations in the region of Omiltemi in the state of Guerrero, Mexico. The reproductive biology of these three species is unknown. The aim of this study is to compare the annual reproductive activity and other reproductive features of these sympatric phylogenetically distant species to establish whether there is a common reproductive response to similar environmental clues such as altitude, temperature, and rainfall.

MATERIALS AND METHODS

Study Area and Climate.—The studied populations are located in the ''Parque Ecológico Estatal Omiltemi, Guerrero'' of the Sierra Madre del Sur of Guerrero, Mexico, 15 km west of Chipalcingo city. The collecting site is near the Ranchería de Omiltemi (17°32′N 99°41′W, altitude 2,200–2,500 m). The area contains montane forests that have been said to be some of
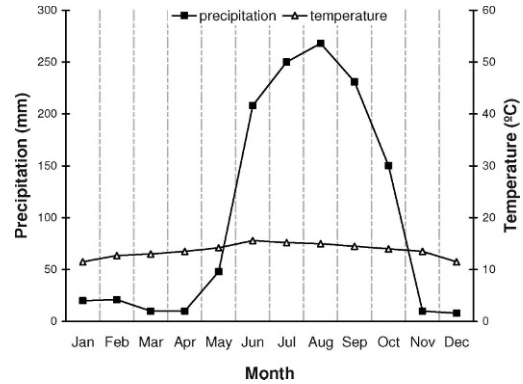

FIG. 1. Annual variation of rains and temperature from the study area. Data correspond to multiannual means of monthly precipitation and temperature averages (from Luis-Martínez, 1993).

Mexico's most diverse and complex subtropical mixed oak-pine forests (Flores-Villela, 1993). Mean annual rainfall is 1,246.5 mm, and mean annual temperature is 13.7°C. The rainy season usually occurs from May to October, peaking in August, whereas November to April are the months with the least precipitation (<10 mm each month; Luis-Martínez, 1993; Fig. 1).

Field and Laboratory Methods.—Specimens of the three species were collected monthly from February 1985 to December 1985. For each individual, total body mass (± 0.01 g) and snout–vent length (SVL; ± 0.01 mm) were recorded. Specimens were fixed in 10% formalin and preserved in 70% ethanol and deposited in the herpetological collection of the Museo de Zoología ''Alfonso Luis Herrera'' Facultad de Ciencias, Universidad Nacional Autónoma de Mexico (MZFC). A midventral incision permitted us to record the following morphometric data (Vernier caliper; ± 0.01 mm) and observations in situ: for males, longest and shortest diameters of the testes (to calculate testicular volume, see Guillette and Sullivan, 1985) and epididymides convolution; for females, ovarian diameter, diameter of the largest ovarian follicle, number of large follicles, presence of corpora lutea, number of oviductal embryos, and diameter of two incubatory chambers per female. Reproductive tracts of males were dissected from the abdominal cavity, dried with a paper towel, weighed (± 0.0001 g), and stored in 70% ethanol. Subsequently, the tracts were dehydrated, embedded in paraplast, sectioned at 6 μm, and stained with hematoxylin-eosin. Histological slides were used to determine the reproductive stage according to the classification of Ballinger and Nietfeldt (1989).

Reproductive Analysis.—The presence of sperm in the seminiferous tubules and ducts was used to determine sexual maturity in males. The reproductive condition of females was categorized in reproductive stages: previtellogenic (without vitellogenic follicles); vitellogenic (with vitellogenic follicles, diameter >2 mm and yellowish); pregnant (with oviductal embryos), and postreproductive (with distended and flaccid oviducts). The SVL of the smallest female with vitellogenic follicles or oviductal eggs was considered to determine sexual maturity of each species. One oviductal egg or embryo of each pregnant female was examined to determine the embryonic stage of development according to Dufaure and Hubert's (1961) staging table. Mean litter size was calculated using the number of embryos present in all pregnant females. Pearson correlations were used to evaluate the relationship between litter size and female SVL for each species. Reproductive stage data for each animal were used to establish the percentage of males and females in each reproductive stage each month and throughout the year. We used parametric serial run tests (Zar, 1999) to detect intra- and intersex variation in reproductive stages by month (synchrony) and over time (seasonality).

Ovarian and follicular diameters and testicular mass and volume were analyzed by means of regression on female and male SVL, respectively. When regressions were significant, the residuals of these regressions were compared, eliminating the effect of overall body size (Ramírez-Bautista and Vitt, 1997). To test for significant differences among collection months, we used ANOVA or Kruskal-Wallis tests (as appropriate) followed by a posteriori tests (Tukey or Nemenyi, respectively) to determine which months differed. Annual reproductive activity and climatic data were examined to determine whether some type of relationship existed among them by means of multiple regressions.

<div align="center">RESULTS</div>

Sceloporus formosus scitulus.—Adult females and males are slightly different in body size (mean ± SD = 65.43 ± 8.94 mm SVL, $N = 68$, and 68.9 ± 8.07 mm, $N = 53$, respectively, $Z = -2.2$, $P = 0.027$). Also, a marked sexual dichromatism occurs in this species. Males have a metallic green color on the dorsum with blue spots on the head; tail and throat are of metallic blue color, and the ventral region exhibits two lateral blue patches bordered by a black line. In contrast, females have an olive green dorsal coloration, with dark irregular patches, and the ventral region is cream (Flores-Villela and
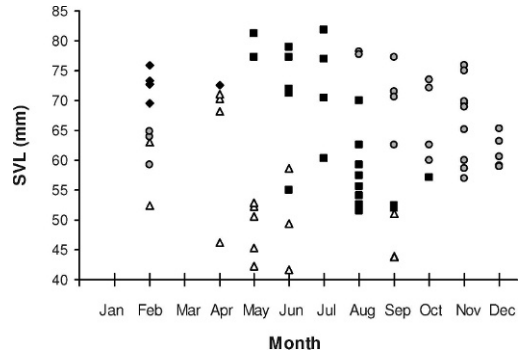

FIG. 2. Size distribution (SVL) of females in different reproductive stages considered for population of *Sceloporus formosus scitulus*. △, Previtellogenic females; ○, Pregnant females; ■, Vitellogenic females; ◆, Postpartum females.

Muñoz-Alonso, 1993). Females reach sexual maturity at a slightly smaller SVL than males. The smallest female with vitellogenic follicles was 51.5 mm in SVL, and the smallest female with oviductal embryos was 58.58 mm. The smallest male with reproductive testes (stage 6 of Ballinger and Nietfeldt, 1989) had a SVL of 54.25 mm; all males over 55 mm SVL were reproductive (stage 6). Individuals from 28.6–50 mm SVL were juveniles.

There were no differences in the occurrence of females in each reproductive stage among sequential months in previtellogenic (nonparametric serial run test $U_{(2)\ 5,5} = 4$, $P = 0.167$) and vitellogenic females ($U_{(2)\ 5,5} = 4$, $P = 0.167$). However, pregnant and postpartum females occurred only in particular months ($U_{(2)\ 4,0} = 1$, $P = 0.0001$ and $U_{(2)\ 1,0} = 1$, $P = 0.0001$, respectively). Thus, although asynchrony in the reproductive condition among females was observed, there was a well-defined period of pregnancy and parturition. There was a significant difference in the SVL in vitellogenic females of the first trimester of the vitellogenic period and the SVL of vitellogenic females in the second trimester (Yates corrected chi-square $X_{0.05,1} = 9.80$, $P = 0.0017$, $N = 23$). These results suggest that older females begin vitellogenic growth and pregnancy earlier than primiparous females (see Fig. 2). There was no significant relationship between ovarian and follicular diameter and SVL ($N = 63$, $r^2 = 0.042$, $P > 0.10$, and $N = 63$, $r^2 = 0.0002$, $P = 0.91$, respectively). There was significant variation among months for each variable (Fig. 3A, $H_{9,62} = 35.3$, $P = 0.0001$, and $H_{9,61} = 37.64$, $P = 0.0002$, respectively). Ovarian diameter is related with precipitation and temperature ($N = 63$, $r^2 = 2.36$, $P < 0.0001$; precipitation $\beta = 0.3$; temperature $\beta = 0.27$). Follicular diameter was
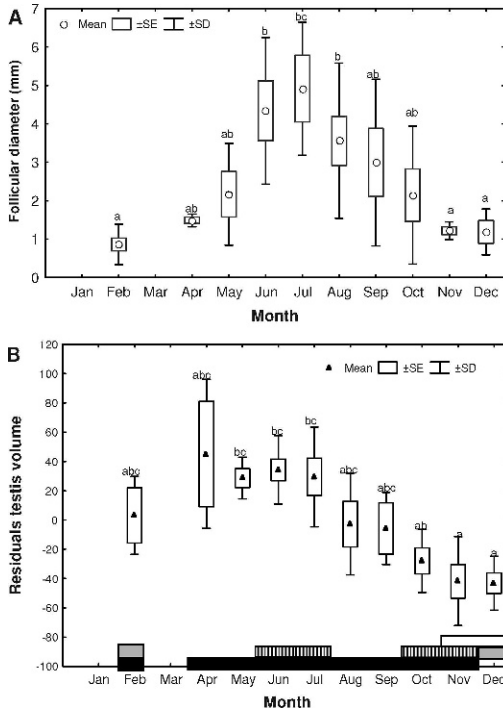
FIG. 3. (A) Monthly follicular diameter of *Scelo-porus formosus scitulus*. Different superscripts indicate significant differences among months. (B) Monthly changes in adjusted testis volume in population of *S. f. scitulus*. Different superscripts indicate significant differences among months. At the bottom of the graph, the reproductive stages of the males can be observed: white bar, reproductive stage 2 (early spermatogenesis, primary spermatocytes, no lumen); light grey bar, reproductive stage 4 (spermiogenesis, undifferentiated spermatids at luminal margin); dark grey bar, reproductive stage 5 (mature testis, meta-morphosing spermatids at luminal margin); black bar, reproductive stage 6 (mature testis, mature sperm in seminiferous tubules and epididymides); vertical striped bar, reproductive stage 7 (postreproductive testis, early regression, mature sperm at luminal margin and cellular debris in the lumen, epididymi-des with abundant sperm); cross-hatched bar, repro-ductive stage 8 (complete regression, there is not cellular division neither lumen).
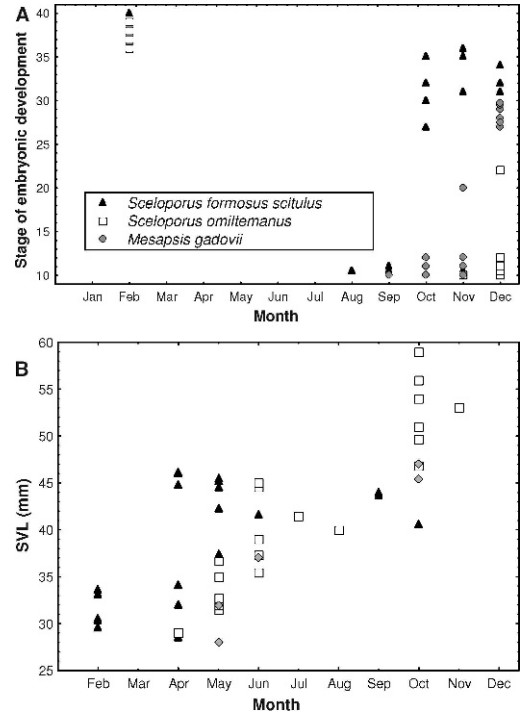
FIG. 4. (A) Stage of embryonic development by month in the three species studied. Notice that pregnancy occurs during the months of minimal precipitation and temperature. Lasts stages of embry-onic development are observed during the dry season. (B) Neonates and juveniles by month of capture in the three species. Births occur during the driest months. In *Sceloporus formosus scitulus*, the first neonates were observed in February, but they also were found until April. In *Sceloporus omiltemanus*, the first neonates appear in April, and in *Mesaspis gadovii*, they appear in May when the first rains occur.

also related with precipitation and temperature ($N = 63$, $r^2 = 0.39$, $P < 0.0001$; precipitation $\beta = 0.28$, temperature $\beta = 0.39$).

Litter size, as estimated from the number of oviductal embryos, varied between 2 and 12 with a mean of 6.04 ± 2.76 SD ($N = 27$). A positive correlation between SVL of the female and the number of oviductal embryos was found ($N = 27$, $r = 0.9$, $P < 0.0001$). The first stages of embryo development were observed during the peak of the rainy season (August and September), and development continues during

the dry season. Although pregnancy seems to be synchronous among females, births seem to extend from February until April reflecting the asynchrony in the reproductive activity ob-served in females. These observations suggest that gestation period lasts approximately six months (Fig. 4).

Adult males were reproductive between February to November; during November and December, new spermatogesis has initiated. The occurrence of reproductive males in stage 6 was not significantly different among months (non-parametric serial runs test $U_{(2)\ 5,5} = 5$, $P = 0.357$), whereas the reproductive stages 2, 4, and 7 occur only in some months ($U_{(2)\ 2,0} = 1$, $P = 0.0001$, $U_{(2)\ 2,1} = 1$, $P = 0.0001$, and $U_{(2)\ 4,0} = 1$, $P = 0.0001$, respectively). Thus, males have an extended reproductive season of at least nine months (Fig. 3B). However, the presence of abundant sperm in the epididymis of males that have testes in complete regression or in the

first stages of spermatogenesis during the driest months could indicate that the reproductive season of males could be extended almost throughout the year.

We found a significant relationship between testis mass and testis volume with SVL ($N = 48$, $r^2 = 0.368$, $P < 0.0001$, and $N = 48$, $r^2 = 0.35$, $P < 0.0001$, respectively). Thus, we used the residuals of these regressions to examine variation of testis volume and mass by month. There was significant variation in adjusted testis mass ($F_{9,38} = 9.95$, $P < 0.0001$) and in testis volume ($F_{9,43} = 8.54$, $P < 0.0001$, Fig 3A) among months. Adjusted testis mass and volume were related to precipitation and temperature ($N = 48$, $r^2 = 0.35$, $P < 0.0001$, precipitation $\beta = -0.47$, temperature $\beta = 0.93$; and $N = 48$, $r^2 = 0.34$, $P < 0.0001$, precipitation $\beta = -0.21$, temperature $\beta = 0.76$, respectively).

Sceloporus omiltemanus.—Adult females and males are different in SVL (mean $\pm$ SD = 83.08 $\pm$ 9.79 mm SVL, $N = 39$, and 98.11 $\pm$ 9.78 mm, $N = 25$, respectively, $t_{63} = -5.99$, $P < 0.0001$). Males have a grey or brown-grey dorsum and venter with two black-bordered blue patches; neck and gular region are of the same color. Venter of females is immaculate cream (Flores-Villela and Muñoz-Alonso, 1993). The smallest female with vitellogenic follicles was 61 mm in SVL, and the smallest female with oviductal embryos was 75 mm. For males, the smallest individual with reproductive testes (stage 6 of Ballinger and Nietfeldt, 1989) had a SVL of 82 mm. Individuals from 28.6 and 60 mm SVL were juveniles; males between 60 and 79 mm SVL were considered subadults.

Although asynchrony in reproductive condition among females was observed, it was not as evident as in *S. f. scitulus*, perhaps because of the smaller sample size of *S. omiltemanus*. There was a well-defined period of vitellogenesis (June to November) and pregnancy (winter months) (Fig. 5A). There was no significant relationship between ovarian and follicular diameter and SVL ($N = 32$, $r^2 = 0.018$, $P > 0.45$, and $N = 42$, $r^2 = 0.0008$, $P = 0.95$, respectively). There was no significant variation among months in ovarian diameter ($H_{9,32} = 11.2$, $P = 0.26$) and follicular diameter ($F_{9,32} = 2.044$, $P = 0.66$, Fig. 4A). There was no significant relationship of ovarian diameter and follicular diameter with precipitation and temperature ($N = 32$, $r^2 = 0.6$, $P = 0.89$; $N = 42$, $r^2 = 0.09$, $P = 0.59$, respectively).

Estimated litter size varied between six and eight with a mean of 6.23 $\pm$ 1.36 SD ($N = 13$). A positive correlation between female SVL and number of oviductal embryos was found ($N = 13$, $r = 0.66$, $P < 0.05$). Ovulation, fertilization, and the first stages of embryonic development
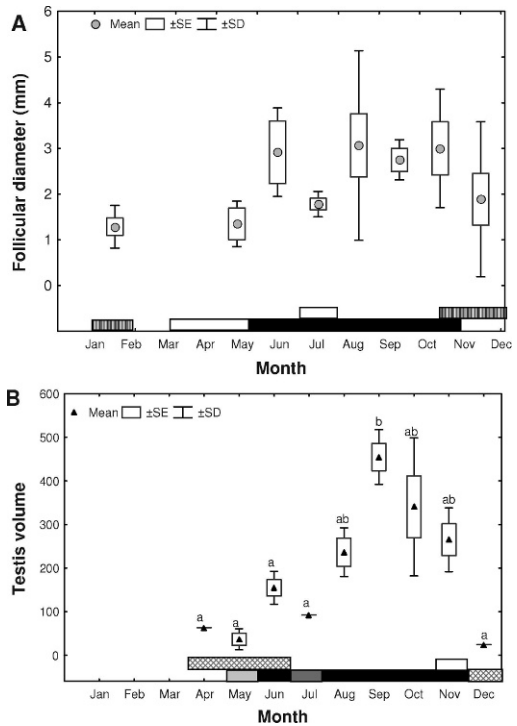

FIG. 5. Monthly changes in follicular diameter and testis volume in the population of *Sceloporus omiltemanus*. Different superscripts indicate significant differences among months. In the bottom of the graph, reproductive stages can be observed. (A) Follicular diameter; black bar, vitellogenic females; vertical striped bars, gravid females; white bars, previtellogenic females. (B) Testis volume and reproductive stages of the males. Conventions of the bottom bars are the same as in Figure 3B.

were observed during November and December. Although pregnant females were collected only during three months, gestation would last approximately five months. Embryonic development occurs during the winter, and in February the embryos reach developmental stages 36–39 (Fig. 4A). However, neonates are only observed in the field in April (Fig. 4B); parturition could occur in early spring, being apparently synchronous among females.

Some adult males began to have reproductive testes in June; however, all males were reproductive between August and November. Males with inactive testes (stage 8) were observed in December, and between April and June, we observed males in which new spermatogenesis was initiated (stages 4 and 5). These males did not have spermatozoa in their ducts during the nonreproductive season. Males have a well-defined reproductive season, being reproductive for 5–6 months (Fig. 5B). We did not find a significant relationship between testis volume
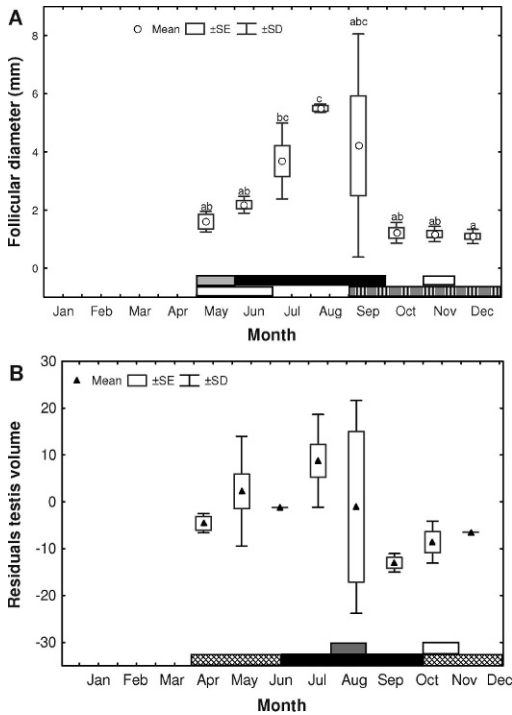
FIG. 6. Monthly changes in follicular diameter and testis volume in the population of *Mesaspis gadovii*. Different superscripts indicate significant differences among months. In the bottom of the graphs, the reproductive stages can be observed. (A) Follicular diameter and reproductive stages of the females. Conventions of the bottom bars are the same as in Figure 5A. (B) Testis volume and reproductive stages of the males. Conventions of the bottom bars are the same as in Figure 3B.

and SVL ($N = 25$, $r^2 = 0.042$, $P < 0.31$). Testis volume varied among months ($H_{8,26} = 20.81$, $P = 0.008$, Fig. 5B). Multiple regression of testis volume with precipitation and temperature data was significant ($N = 26$, $r^2 = 0.24$, $P = 0.04$; precipitation $\beta = 0.75$, temperature $\beta = -0.53$).

Mesaspis gadovii.—Adult females and males are different in SVL (mean $\pm$ SD = 83.86 $\pm$ 7.91 mm SVL, $N = 34$, and 89.40 $\pm$ 9.39 mm, $N = 31$, respectively, $t_{64} = -2.57$, $P = 0.012$). There is a slight dichromatism in males and females; the dorsum of the males is dark brownish, whereas in females it is reddish-brown (Flores-Villela and Muñoz-Alonso, 1993). Females reach sexual maturity at a similar SVL to males. The smallest female with vitellogenic follicles was 76 mm in SVL, and the smallest female with oviductal embryos was 71 mm; females attain sexual maturity around 70 mm SVL. The smallest male with reproductive testes had a SVL of 71 mm, and all males were at stage

6 over this size. Neonates were 28.65–32 mm and juveniles between 35 and 67 mm in SVL.

Vitellogenic females occurred between June and September, and pregnant females were observed from September to December (Fig. 6A). However, specimens from January to May were not collected. Pregnant females from December had embryos at developmental stages from 27–29, indicating that embryo development is at midgestation. Neonates were observed during May, suggesting that parturition occurs in early spring, and gestation lasts six to seven months. There was a significant relationship between ovarian diameter and SVL ($N = 31$, $r^2 = 0.14$, $P < 0.034$), but there was no significant relationship between follicular diameter and SVL ($N = 33$, $r^2 = 0.00017$, $P = 0.81$). Using the regression residuals of ovarian diameter data and the original follicular diameter, we found that there was significant variation among months for both variables ($H_{7,32} = 18.47$, $P = 0.01$; and $H_{7,34} = 23.98$, $P = 0.0012$; Fig. 6A). Adjusted ovarian diameter was not related to precipitation and temperature ($N = 32$, $r^2 = 0.26$, $P = 0.051$; precipitation $\beta = 0.73$, temperature $\beta = -0.24$). Follicular diameter was related to precipitation and temperature ($N = 34$, $r^2 = 0.34$, $P < 0.0002$; precipitation $\beta = 0.77$, temperature $\beta = -0.20$).

Litter size varied between four and 12 with a mean of 7.25 $\pm$ 1.94 SD ($N = 16$). A positive correlation between SVLs of females and the number of oviductal embryos was found ($N = 16$, $r = 0.88$, $P < 0.05$,). The first stages of embryo development were observed during fall (October to November, Fig. 4); development continued during winter and spring, parturition occurred in early spring when postreproductive females and neonates were observed.

All adult males were potentially reproductive from May to August. Males collected between September and December had testes in regression, and in some males new spermatogenesis had begun. Therefore, males have a defined reproductive season, being reproductive at least four months (Fig. 6B). However, males with quiescent testis from September to October had little sperm in the epididymis, whereas males with testes in the first stages of spermatogenesis had empty ducts. We found a significant relationship between testis volume and SVL ($N = 30$, $r^2 = 0.34$, $P < 0.0001$). Thus, we used the residual of this regression to test variation of testis volume by month. There was no significant variation in adjusted testis volume among months ($F_{7,23} = 2.03$, $P = 0.093$). This result contrasts with the histological observation of a well-defined reproductive season. The difference between analyses may be a consequence of small sample size and the

fact that, in several months, there was no collection of individuals (winter and early spring months). Adjusted testicular volume was related with precipitation and temperature ($N = 31$, $r^2 = 0.25$, $P = 0.018$; precipitation $\beta = -0.64$, temperature $\beta = 0.88$).

<h2 style="text-align:center">DISCUSSION</h2>

Sexual dimorphism in body size and color pattern commonly occurs in the genus *Sceloporus* (Fitch, 1978; Wiens et al., 1999; Smith et al., 2003). Males of the two species studied had larger SVL than females and exhibit marked differences in dorsal and ventral coloration compared with females. Sexual dimorphism may evolve by sexual selection through mate choice, intrasexual competition, or both (Andersson, 1994). Svensson et al. (2001) have proposed male competition as the main force influencing the evolution of sexual dimorphism in some phrynosomatid lizards. Sexual dimorphism also occurs in some anguid species. It may involve differences in overall body size (*Ophioides fragilis*, Pizzatto, 2005), head dimensions, with males having larger heads than have females (*M. monticola*, Vial and Stewart, 1989; *Mesaspis juarezi*, Karges and Wright, 1987; *M. gadovii*, Flores-Villela and Muñoz-Alonso, 1993), and dorsal and ventral color pattern (*M. juarezi*, Karges and Wright, 1987; *M. gadovii*, Flores-Villela and Muñoz-Alonso, 1993). Females of *M. gadovii* were larger than males. However, it seems that sexual dimorphism in body size and color pattern is not as obvious as in *Sceloporus* species. Thus, the three studied species follow the tendency observed for sexual dimorphism in other congeneric species.

The three studied species are reproductively active (late vitellogenesis, ovulation, spermiation, courtship, and mating) during the rainy and warmer season of Omiltemi that corresponds to the end of spring, summer, and autumn of more temperate species. Ovulation and early gestation takes place at the end of the rainy season, and pregnancy occurs during the driest and coolest months of the year with births at the end of this season. These tropical high-elevation species follow a known pattern for other viviparous Mexican species described by Méndez de la Cruz et al. (1999); males and females exhibit courtship, mating, and ovulation during autumn, pregnancy in the winter and parturition in spring. However, these authors found that male and female cycles can be dissociated or not according to elevation. In fact, at high altitudes of tropical latitudes, some species of *Sceloporus* show asynchronous reproduction between sexes; sperm maturation and mating occur during early summer, whereas

ovulation occurs in the fall, requiring female storage of sperm (Guillette and Casas-Andreu, 1980; Guillette and Sullivan, 1985; Estrada-Flores et al., 1990; Méndez de la Cruz et al., 1998). However, in synchronous reproduction, mating and ovulation occur simultaneously in autumn (Ortega and Barbault, 1984; Guillette and Méndez de la Cruz, 1993; Méndez de la Cruz et al., 1998); this pattern occurs in several species from the southwestern United States to central Mexico at altitudes below 2,500 m (Méndez de la Cruz et al., 1999). We do not have field data on mating for any of the species studied; however, histological analyses of testes and sexual ducts showed that males have mature testes with sperm in sexual ducts at the same time as females are vitellogenic and ovulate, suggesting synchronous reproductive cycles for these three species and following the pattern observed by Méndez de la Cruz et al. (1999).

Guillette and Sullivan (1985) demonstrated that, in some species of *Sceloporus*, the onset of testicular activity is correlated with increasing ambient temperatures. In contrast, ovarian activity is not correlated with temperature but appears to be greatest during the rainy season. However, rainfall pattern and elevation also can be related to spermatogenic activity. In fact, for *Sceloporus mucronatus*, reproductive cycles have been described for several populations at different altitudes with different climatic patterns (Estrada-Flores et al., 1990; Méndez de la Cruz et al., 1994, 1998). In all studied populations, females conserve the typical fall/rainy reproductive activity of viviparous species. In contrast, the synchronicity of reproduction for males and females varies among populations related to altitudinal distribution. In high elevation populations (3,200–3,400 m) the pattern is asynchronous (Estrada-Flores et al., 1990; Méndez de la Cruz et al., 1998), whereas at 2,500 m altitude, it is synchronous (Méndez de la Cruz et al., 1994). Méndez de la Cruz et al. (1994) concluded that the variation in the onset of male reproduction of this species is caused by differences in rainfall patterns. Thus, as environmental temperature and precipitation are not correlated in some localities, asynchrony of male and female gonadal activity occurs. In Omiltemi, both climatic variables are clearly correlated; therefore, reproductive cycles of these viviparous species are synchronous. These lizards have reproductive cycles synchronized with environment in such a way that reproductive activity (final gametogenesis, mating, and ovulation) occurs when environmental conditions provide maximum energy for reproductive effort.

However, gestation takes place during the coolest and driest months with births at the end of this season when rains start. For other viviparous species, Goldberg (1971) suggested that this is a strategy for producing young at the onset of the spring growing season; this would allow maximum growth prior to the onset of the next winter and may increase juvenile survivorship. Also, Guillette and Bearce (1986) stated that this early birth and growth period might provide an additional breeding season to the population if the new born reach sexual maturity and have a chance to reproduce the first fall after birth. Early sexual maturity occurs in other viviparous species of *Sceloporus* (in *Sceloporus jarrovi*, 60% of females reach sexual maturity within 6–7 months from birth [Ballinger, 1973] and in *Sceloporus torquatus* [Guillette and Méndez de la Cruz, 1993]). Méndez de la Cruz et al. (1995) concluded that viviparity in this region has evolved as an adaptation to living at high elevation in a tropical climate in which pregnant females can bask and feed throughout the winters and develop embryos ready for birth at the beginning of the growing season.

In spite of having similar reproductive patterns, the reproductive activity of the species studied here has some important differences related to the length of male and female reproductive activity. The reproductive pattern of *S. f. scitulus* may exhibit some geographical variation, as observed by Davies and Dixon (1961) in Chilpancingo, Guerrero, (a few hundred meters of elevation below Omiltemi) where a female with oviductal eggs was found in the middle of June, two months earlier than in Omiltemi. Unfortunately, the Davies and Dixon paper and the present study constitute the only information about reproduction in this species. Additionally, studies about the reproductive cycle of other species of the *formosus* group, a highly diversified species group (Smith, 2001), includes only *Sceloporus formosus formosus* (Guillette and Sullivan, 1985) and *Sceloporus malachiticus* (Marion and Sexton, 1971).

The prolonged period of vitellogenesis in *S. f. scitulus* is related to a high reproductive asynchrony among females. Females of the population studied here initiated their reproductive activity differentially according to their age/size, with older (larger) females beginning first. Larger females probably make a lower investment of energy in growth but a major energetic contribution to reproduction, as indicated by their larger clutches than those of smaller females. Females of *S. f. formosus* also exhibit this asynchronous pattern, with an extended vitellogenesis from May to December

(Guillette and Sullivan, 1985). However, asynchrony among females of other populations of *Sceloporus formosus* is not related to monthly differences in SVL (Guillette and Sullivan, 1985), even when a positive relationship between SVL and clutch size also occurs. Furthermore, although specimens included in the Guillette and Sullivan (1985) study came from different localities, the authors claimed that female asynchrony was not caused by sampling effects. This pattern of asynchronous reproduction among females of the same population appears common in tropical species with extended breeding periods but rare in temperate species (Fitch, 1970, 1982). The period of vitellogenesis of *S. f. scitulus* appears shorter than in the Costa Rican *S. malachiticus* (Marion and Sexton, 1971). It goes over the end of summer months and early fall. Birth period is also short, including January and February. These observations suggest that female asynchrony in *S. malachiticus* is significantly lower than in *S. f. scitulus* and *S. f. formosus*, even when samples from a wide altitudinal range (800–3,200 m) were included in the *S. malachiticus* study.

Male and female reproduction seems to be synchronized in *S. f. scitulus*, because both sexes with active gonads were found in the same period. Such a broad reproductive period in males may be considered necessary to guarantee fertilization of asynchronous females. Similarly, male and female activity appears synchronized in *S. malachiticus* (Marion and Sexton, 1971). However, males of *S. f. scitulus* were not sampled in all months, which limit conclusions about their reproductive phenology. In contrast, males are active earlier than females in *S. f. formosus*, defining an intersexual asynchronous cycle (Guillette and Sullivan, 1985), which appears typical of species from high elevations at tropical latitudes (Méndez de la Cruz et al., 1998). However, the male reproductive cycle of this species was described based only on testicular volume that may not necessarily reflect the reproductive condition of testes, as we observed in *S. f. scitulus*. Reproduction in taxa of the *formosus* group of *Sceloporus* follows a common pattern independent of the fact that they occur at different tropical latitudes: summer-fall/rainy season of reproductive activity with gestation during coolest/dry months and parturition during the dry season and starting spring; however, there are clear differences in the time of beginning and length of female and male reproductive activity among these taxa.

Reproductive activity of *S. omiltemanus* is clearly defined and less extended for males and females than in *S. f. scitulus*. Reproductive activity of *S. omiltemanus* is very similar to that

described for *S. mucronatus*, a closely related species (Martínez-Méndez and Méndez de la Cruz, 2007), particularly to the population from Acocomulco, Hidalgo (Méndez de la Cruz et al., 1994), which is also located at 2,500 m elevation. *Sceloporus omiltemanus*, exhibits a well-defined late summer–early fall pattern of reproduction, with active males and females during the same months. This pattern is common to other populations of *S. mucronatus* from the Mexican plateau. These observations and those derived from previous studies on the reproductive cycle of other species of the *torquatus* group (*Sceloporus cyanogenys*, *S. jarrovii*, *S. mucronatus*, *S. torquatus*, and *Sceloporus poinsetti*, see Gadsden et al., 2005; Guillette and Méndez de la Cruz, 1993; Feria-Ortíz et al., 2001) suggest that a common reproductive pattern characterizes this species group. This has been interpreted as evidence of a single evolutionary event of the reproductive pattern in this species group (Ramírez-Bautista et al., 2002). This pattern is also found from the base of the clade (*megalepidurus*, *grammicus*, *torquatus*). In fact, it is observed in *Sceloporus megalepidurus* and in *Sceloporus grammicus* (Guillette and Méndez de la Cruz, 1993; Méndez de la Cruz et al., 1998).

There are only a few studies on reproduction of Anguid lizards from the Americas (alligator lizards, *E. coerulea*, Vitt, 1973; *Gerrhonotus* spp., Goldberg, 1972, 1975), some observations on *M. juarezi* (Karges and Wright, 1987), a species of *Ophisaurus* (*Ophisaurus attenuatus* Fitch, 1989) in the northern temperate zone, and *Ophiodes fragilis* in the southern hemisphere (Pizzatto, 2005). For Mexican viviparous anguid lizards of the genus *Barisia*, Guillette and Casas-Andreu (1987) found that *B. imbricata* and *Barisia ciliaris* have a reproductive cycle in which vitellogenesis occurs during summer and early fall; the embryonic development occurs between fall and winter and parturition in spring. Karges and Wright (1987) mentioned that the reproductive cycle of *M. juarezi* apparently involves overwinter gestation with parturition in late spring. *Mesaspis gadovii* has a similar cycle and, as in *S. omiltemanus,* well-defined and synchronous reproductive activity for males and females. Thus, the pattern of reproductive activity in late summer–early fall/rainy months, gestation during fall and winter/driest months, with parturition at the end of the winter and spring/start of rainy months, is also conserved in viviparous species of Anguidae.

This pattern is common in evolutionary distant lizard families not only from North-Central American viviparous lizards living in mountain environments; it also has been found for viviparous lizards in subtropical-temperate South American Andes (Liolaemidae, Leyton et al., 1982; Ramírez-Pinilla, 1991). In contrast, temperate Northern hemisphere viviparous lizards and most Australian viviparous lizards show less interspecific variation; all species breed in late spring and summer (Shine, 1985; Craig and Shine, 1985; Murphy et al., 2006; Duvall et al., 1982). However, in extreme cold climate, viviparous lizards in South America, South Africa, and Australia start vitellogenesis and have reproductive activity in autumn; completion of vitellogenesis and ovulation occurs in early spring with births from early to midautumn (e.g., Ibargüengoytía and Cussac 1996; Jones and Swain 1996; Van Wyk and Mouton, 1998; Flemming and Mouton, 2002). Some of these species of extreme cold environments have extended periods of vitellogenesis and gestation lasting more than one year to reproduce and then skipping reproduction one or more years (biennial to multiannual reproductive cycles, Van Wyk, 1991; Ibargüengoytía, 2004; Cree and Guillette, 1995; Edwards et al., 2002).

Convergence in reproductive phenology in viviparous lizards and specifically in the summer-fall reproductive pattern of these and other viviparous taxa distributed at high tropical elevations suggest a common evolutionary response to environmental factors associated with montane habitats. Protection of the embryos from cold and dry conditions of winter season, growth acceleration of neonates, and consequently, early sexual maturation, are some of the main factors suggested to explain the evolution of this pattern. Specific differences observed within this broad reproductive pattern (i.e., length of the reproductive activity, litter size, and sexual dimorphism) are attributed to the particular evolutionary history of each taxon.

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