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Diet and Reproductive Biology of the Viviparous Lizard *Sceloporus torquatus torquatus* (Squamata: Phrynosomatidae)

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ABSTRACT.—The reproductive cycle and diet of a population of the viviparous lizard *Sceloporus torquatus torquatus* from the Pedregal de San Angel, Distrito Federal, México, were studied. Ovarian activity began in June, and by October, one to five preovulatory follicles per ovary were present. Ovulation took place in November and December, and parturition occurred in late April or early May. Relative litter and egg masses were higher at the end of development than at the beginning. Testes increased in size from June through September, when they reached their maximum volume and weight. Testicular regression began at this point and was particularly accentuated in October and November. The diet of both sexes was composed primarily of insects; however, plant material (small flowers and fruits), spiders, isopods, and occasionally earthworms were also consumed. Both sexes consumed plant material throughout the year. In the dry season, males ingested twice as much food as females.

RESUMEN.—Se estudiaron el ciclo reproductor y la dieta de una población de la lagartija vivípara *Sceloporus torquatus torquatus* que habita en el Pedregal de San Angel, Distrito Federal, México. La actividad ovárica comenzó en junio, y para octubre se encontraron de uno a cinco folículos preovulatorios por ovario. La ovulación ocurrió entre noviembre y diciembre, y el parto a fines de abril o principios de mayo. La masas relativas de la camada y de los huevos fueron mayores a finales del desarrollo embrionario que al principio. Los testículos aumentaron de tamaño desde junio hasta septiembre, cuando alcanzaron su volumen y peso máximos. Posteriormente comenzó la regresión testicular, la cual fue particularmente acentuada en octubre y noviembre. La dieta de ambos sexos consistió principalmente de insectos; sin embargo, también se consumieron, además de materia vegetal (flores y frutos pequeños), arañas, isópodos y ocasionalmente lombrices de tierra. Ambos sexos consumieron materia vegetal durante todo el año. En la época seca, las hembras consumieron alrededor de la mitad del alimento consumido por los machos.

Fitch (1970) stated that the reproductive season in temperate lizards usually occurs during the spring and summer. However, reproductive patterns in which gametogenesis, courting, copulation, and fertilization occur in the fall have been reported since the early 1970s (Goldberg, 1971; Ballinger, 1973). Guillette and Casas-Andreu (1980) pointed out that fall reproductive activity is common in viviparous lizards inhabiting high elevations in temperate zones. More recent papers have reported this reproductive modality in additional species and have attempted to explain its advantages (Guillette and Bearce, 1986; Guillette and Casas-Andreu, 1987; Ramírez, 1991; Guillette and Méndez de la Cruz, 1993; Ramírez-Bautista et al., 1996, 1998).

Intra- and interspecific variation in reproduction and life-history traits of lizards is partially explained by the physical environment (Benabib, 1994). However, it has been shown that factors such as phylogenetic inertia (Ballinger, 1983), foraging behavior (Vitt and Price, 1982),

predator escape behavior (Vitt and Condgon, 1978), and individual morphology (Vitt, 1981) can be important in molding the reproductive biology of lizards. It has been suggested that differences in life history within a species may be the result of physiological or developmental responses to environmental conditions, rather than phylogenetic effects or genetic sources (e.g., Stearns, 1980). Thus, a better understanding of the influence of environmental conditions in molding life-history traits requires knowledge of their variation among populations of the same species.

Sceloporus torquatus torquatus is a viviparous lizard occurring in central México (Smith, 1936). It is usually confined to rocky habitats, although it is entirely arboreal in some areas (Smith, 1936; Duellman, 1961). Werler (1951), Fitch (1970), and Feria-Ortiz (1989) provided some data on its reproductive biology. Uribe-Alcocer et al. (1995) described the histological changes exhibited by the ovaries in the female reproductive cycle.

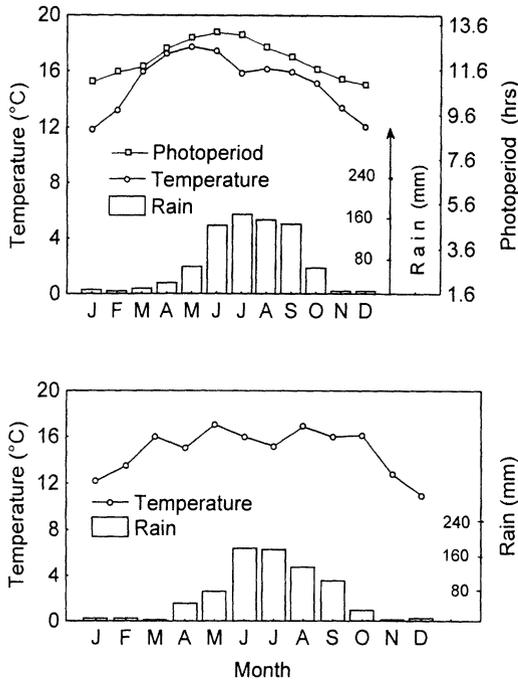


FIG. 1. Temperature, precipitation, and photoperiod; mean monthly values for the lower part of the Pedregal de San Angel, Distrito Federal. Top: Means for 30 years of records. Bottom: Means for the surveyed year. Data obtained from a meteorological station in the study area.

Guillette and Méndez-de la Cruz (1993) reported on the reproductive cycle of a population from Cerro Gordo, near San Juan Teotihuacán, in the state of México. We describe the reproductive cycle of a population of *S. t. torquatus* from the Pedregal de San Angel, Distrito Federal, México. In addition, nutritional dependence of the embryos is analyzed, and diets for the dry and wet seasons are provided.

MATERIALS AND METHODS

Study Area.—The study was carried out in the lower part of the Pedregal de San Angel, Distrito Federal, México (99°13'–99°08'W longitude, 19°14'–19°18'N latitude), at an elevation of 2250–2300 m. The area is covered with solidified lava flows from the Xitle volcano; the crevices in these volcanic rocks serve as shelters for the lizards. Vegetation consists of microphilous scrub, dominated by *Senecio praecox* and *Schinus molle* (Rzedowski, 1954). The climate is temperate subhumid with rainfall occurring mainly from May to October (wet season) and a dry winter (Fig. 1). Precipitation and temperature data for the surveyed year were similar to the average values of 30 years of climatic records, suggesting that climatic conditions during the survey were typical for the study area (Fig. 1).

Fourteen to 17 adults were sampled each month from November 1984 to November 1985. Lizards were killed with ether and the following data taken: sex, snout–vent length (SVL; ± 0.1 mm), and body mass (BM; ± 0.1 g). Specimens were dissected and their stomach, gonads, and (in the case of gravid females) oviductal eggs (developing embryos and yolk) extracted. Testes were weighed with an analytical balance (± 0.01 mg). The length and width of each testis (± 0.01 mm) were used to obtain the testicular volume (V), calculated using the volume of an ellipsoid: $V = (4/3)\pi(L/2)(W/2)^2$.

Ovaries were weighed (± 0.01 mg) and number of follicles and diameter of the largest follicle recorded. In the case of gravid females, both the number of corpora lutea and the diameter of the largest corpus (± 0.01 mm) were also recorded. In addition, the entire complement of oviductal eggs was extracted. The embryos were weighed (± 0.01 mg) and their diameter measured (± 0.01 mm). The developmental stage of the embryos was determined by comparison with the table of embryonic development for the viviparous lizard, *Lacerta vivipara* (Defaure and Hubert, 1961). Embryos and yolk were then dried to constant mass at 60°C. Relative clutch (litter) mass (RCM) was calculated by dividing the total litter mass by the body mass without the litter. Relative oviductal egg mass (REM) was calculated by dividing the average oviductal egg mass by the body mass without the litter.

For each specimen, stomach volume was measured with and without its food contents by volumetric displacement, and the difference between these two volumes was used to estimate the volume of stomach contents. Stomach contents were identified to the order level whenever possible. The number of items of each prey taxon was recorded. A Petri dish containing the stomach contents was placed over a paper sheet with a millimetric scale on it, and the area covered by each prey taxon on the paper, as well as those areas covered by unidentified material (parasites, inorganic, plant, and organic but very digested matter) was estimated. Finally, the volume of each item (SVO, for item i) was calculated by the equation: $SVO_i = (AO_i/ASC) SCV$, where AO_i is the area covered by the item i , ASC is the total area covered by the stomach contents, and SCV the stomach contents volume. The volume, incidence (number of stomachs in which a given prey item was found) and number of organisms (density) of each prey taxon were recorded for both the dry and wet seasons. Relative volume, density, and incidence values were obtained by dividing the value for a given taxon by the corresponding total sum for all the taxa. An importance value for each taxon was

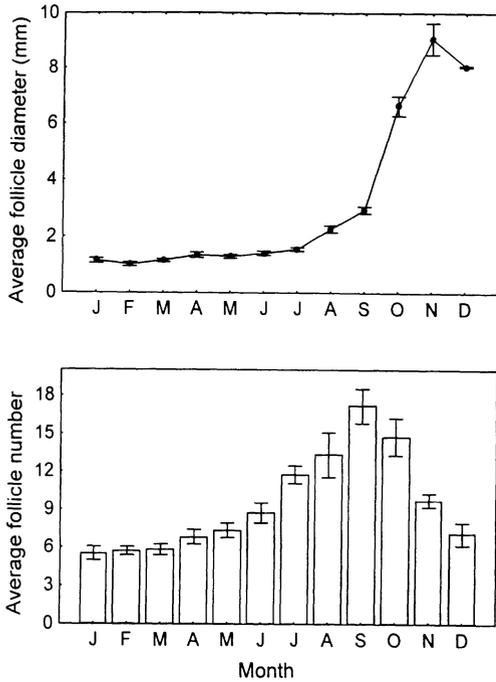


FIG. 2. Monthly changes in (top) the mean diameter of the largest follicle and (bottom) the mean number of follicles per ovary. Values presented represent the mean \pm 1 standard error.

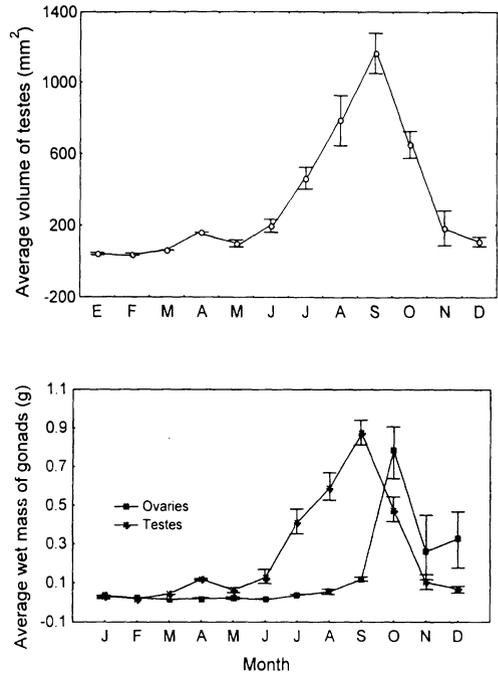


FIG. 3. Monthly changes in (top) the mean testicular volume and (bottom) the mean ovarian and testicular wet masses. Values presented represent the mean \pm 1 standard error.

calculated by adding the relative volume, density, and incidence.

Unless otherwise indicated, results are expressed as mean \pm 1 SE. To detect the existence of significant changes in the adjusted, mean monthly values for the gonad (ovaries or testes) mass, ANCOVA analyses were performed using SVL as a covariate and gonad mass as the response variable. The adjusted monthly mean values were then compared with a Bonferroni test. In general, standard, parametric statistical tests were performed when the data (whether they required transformation or not) fulfilled assumptions. Otherwise, nonparametric tests (Mann-Whitney or Kruskal-Wallis) were performed. All the statistical analyses were performed with the SPSS statistical package (SPSS Inc., 1997).

RESULTS

Size and Approximate Growth

Mean SVL of adult males and females were 92.2 ± 1.1 mm and 90.6 ± 6.5 mm, respectively. These means were not significantly different ($t_{166} = 0.59$, $P > 0.05$). Mean BM of adult males and females were 30.74 ± 1.13 g and 29.09 ± 0.62 g, respectively. The difference between these means was not significant ($t_{166} = 1.38$, $P > 0.05$).

The SVL of the smallest female containing oviductal eggs was 73 mm. The SVL of the next three smallest females with enlarged vitellogenic follicles were 76 mm, 77 mm, and 78 mm. Thus, females attain sexual maturity at a minimum SVL of about 73 mm. The SVL of the three smallest males with enlarged testes were 70.5 mm, 77.0 mm, and 79.0 mm. This indicates that males reach sexual maturity at approximately the same size as females.

Mean SVL of oviductal embryos close to parturition (development stage 40) from four females collected in April was 27.4 ± 0.9 mm, whereas in a sample of 11 juvenile lizards collected in November, mean SVL was 65.2 ± 0.1 mm. The mean SVL of four immature specimens collected in March and April was 74 mm (73–76 mm).

Ovarian Cycle

From January to June, ovaries remained small, and there were no significant changes in their mass. Mean diameter of the largest follicles was 1.25 ± 0.03 mm (0.6–2.0 mm; $N = 66$). Also, during these months the average number of follicles per ovary was relatively low (Fig. 2). From June to October, ovary mass increased significantly ($F_{11,109} = 27.17$; $P < 0.01$; Fig. 3). Also, from May to September, the number and di-

iameter of follicles increased significantly (Kruskall-Wallis $H_{11} = 123.7$ and 104.4 , $N = 187$ and 111 , respectively; $P < 0.001$; Fig. 2). In August, some of the follicles were dull yellow and slightly larger than the rest; the difference in size was larger in September. In this month, each ovary had from three to seven follicles distinctly larger than the rest (mean diameter of largest follicles = 4.94 ± 0.31 mm). In the following months, vitellogenic follicles continued to increase in size. However, the number of follicles decreased markedly (Fig. 2), which suggests high follicular atresia.

Ovulation took place from late November to early December. Mean diameter of freshly ovulated follicles was 10.22 ± 0.16 mm. Corpora lutea resulting from the ovulation were relatively large at the beginning of pregnancy (November and December) but decreased rapidly in size (median diameter = 4.15 mm, $N = 7$, vs. 1.92 mm, $N = 8$, in January; Mann-Whitney $Z = -3.24$; $P < 0.01$). From January to April (i.e., during gestation), the corpora lutea decreased slightly in size. However, there were no significant changes in their diameter (Kruskall-Wallis $H_3 = 7.69$, $N = 40$, $P > 0.05$). After parturition, the size reduction was faster, and by June corpora lutea were almost indistinguishable, even with the aid of a microscope.

Gestation and Parturition

Pregnancy lasted approximately five months, from late November/early December to late April/early May. Embryonic development was relatively slow during the first gestational months (December to February, when ambient temperature is at its lowest). In February, the mean diameter of embryos from 10 females (one embryo per female) was only 7.7 ± 0.54 mm. In this month, the embryos reached the embryonic stage number 31, 32, 33, or 35 (in one, two, six, and one females, respectively). From February to March, embryos continued to develop slowly, whereas from March to April their mean diameter nearly doubled (Fig. 4), and April embryos close to parturition (embryonic stage 40) weighed four times as much as the March embryos (embryonic stage 36). Parturition occurred between late April and early May.

During gestation, a significant increase in the average wet mass of oviductal eggs was evident ($F_{4,45} = 36.7$, $P < 0.0001$; Fig. 4). In contrast, the average dry mass of the eggs decreased considerably during the gestation. At the onset of development, mean dry egg mass was 0.26 ± 0.01 g, whereas at the end of development mean dry egg mass was only 0.18 ± 0.01 g. This difference was highly significant ($t_{12} = 5.64$; $P < 0.001$).

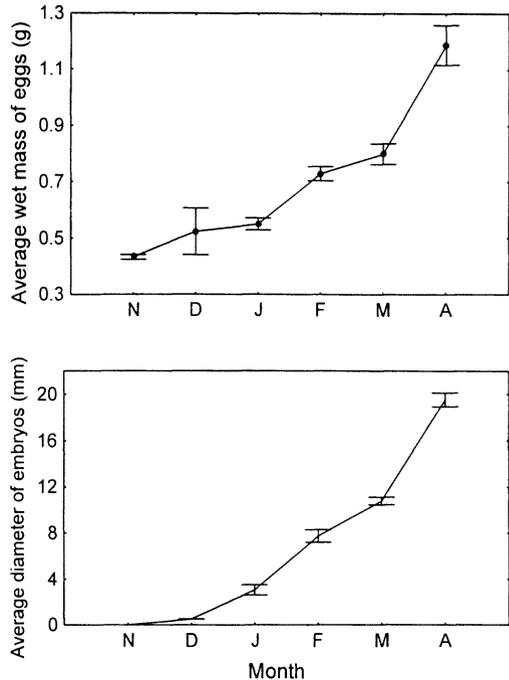


FIG. 4. Monthly variation in (top) the average egg wet mass and (bottom) the average diameter of embryos. Values presented represent the average \pm 1 standard error.

Litter Size

The number of oviductal eggs per female varied from three to 10 (6.48 ± 0.25 ; $N = 50$). Mean RCM and REM were 0.2 ± 0.011 and 0.033 ± 0.003 , respectively. Nevertheless, RCM and REM values increased significantly over gestation [$\log(\text{RCM}) = -2.46 + 0.43$ (month), $r^2 = 0.60$, $N = 50$, $P < 0.0001$; and $(\text{REM})^{1/2} = 0.09 + 0.04$ (month), $r^2 = 0.73$, $N = 50$, $P < 0.0001$, respectively, Table 1]. Litter size (LS) was positively correlated with body mass ($\text{LS} = 0.171 + 1.42 \text{ BM}$, $r^2 = 0.42$, $N = 50$, $P < 0.01$) and size of pregnant females ($\text{LS} = -7.83 + 1.60\text{SVL}$, $r^2 = 0.40$; $N = 50$, $P < 0.01$). Likewise, litter mass (LM) increased with female size ($\text{LM} = 0.16 + 8.14 \text{ SVL}$, $r^2 = 0.26$, $N = 50$, $P < 0.01$) and female body mass ($\text{LM} = 1.65 + 21.11\text{BM}$, $r^2 = 0.30$, $N = 50$, $P < 0.01$). The average mass of oviductal eggs was not correlated with LS, SVL, or BM ($P > 0.05$). Relative litter mass was not correlated with any of these variables either ($P > 0.05$). However, REM was negatively correlated with LS ($\text{RCM} = -0.004\text{LS} + 0.058$, $r^2 = 0.21$, $P < 0.05$) and SVL ($\text{RCM} = 0.007\text{SVL} + 0.096$, $r^2 = 0.11$, $P < 0.05$).

Testicular Cycle

Testicular mass changed significantly during the year ($F_{11,58} = 36.5$, $P < 0.001$; Fig. 3). From

TABLE 1. Relative litter mass (RCM) and relative egg mass (REM) values for different time intervals in embryonic development (and throughout gestation) of *Sceloporus torquatus torquatus*.

Month	N	LS $\bar{x} \pm SE$	RCM $\bar{x} \pm SE$ (range)	REM $\bar{x} \pm SE$ (range)
November–January	18	7.0 \pm 0.6	0.13 \pm 0.007 (0.09–0.19)	0.019 \pm 0.001 (0.012–0.037)
February–March	22	6.7 \pm 0.3	0.21 \pm 0.009 (0.12–0.27)	0.034 \pm 0.001 (0.028–0.043)
April–May	9	6.0 \pm 0.4	0.33 \pm 0.025 (0.24–0.48)	0.052 \pm 0.003 (0.037–0.073)
November–May	50	6.5 \pm 0.25	0.20 \pm 0.011 (0.09–0.48)	0.033 \pm 0.003 (0.012–0.073)

December to May, testes remained small, showing their minimum size and mass in February. Testicular growth was most evident from June to September, being faster in July and August. In these months, testicular mass increased significantly. Testicular regression began in October, after the testes had reached their maximum size in September. In October and November, reductions in testicular mass were significant, and it was actually in these months that essentially all of the decrease in testicular mass took place, even though from December to February, the testes suffered a slight, further decrease in mass. In the latter month, the testes size was only about 3.33% of their size in September.

Food Consumption

There were no noticeable differences in the type of prey consumed by male and female *S. torquatus* (Table 2). In both sexes, the stomach contained mainly insects and to a lesser extent spiders, isopods, centipedes, and plant material (mainly small flowers and fruits). However, in October the remains of a *S. torquatus* were found in the stomach of a male. During the wet season, the most important prey items were coleopterans, hymenopterans, homoptera, lepidopterans (larvae), and hemipterans, in that order. During the dry season, the types of prey consumed were essentially the same, although the most important prey items were hymenopterans, hemipterans, orthopterans, homoptera, and coleopterans, in that order. Thus, lepidopteran larvae were less important in the dry season, whereas the importance value for the orthopterans increased. Also, if the immature stages are taken into account, the consumed prey diversity was larger in the wet than in the dry season.

The average volume of food ingested per individual was significantly larger in the wet than in the dry season both in male and females ($t_{65} = 3.89$, $P < 0.001$, and $t_{110} = 9.55$, $P < 0.001$, respectively). However, the volume of plant ma-

terial ingested showed no significant differences between months in either sex (Kruskal-Wallis $H_{1,1} = 12.8$ and 14.5 for males and females, respectively; $P > 0.05$; Fig. 5). During the wet season, the average volume of the stomach contents for males and females was 1.22 ± 0.13 ml and 1.08 ± 0.08 ml, respectively. These averages were not significantly different ($t_{32} = -0.99$; $P > 0.05$). Similarly, in this period the amount of plant material consumed by males and females were not significantly different (median = 10.8 and 9.7, respectively; Mann-Whitney $Z = -0.90$, $P > 0.05$). With regard to incidence, 18 of 42 males (42.8%) and 30 of 58 females (55.1%) consumed plant material. In the dry season, male stomach content volume was greater than female stomach content volume (0.59 ± 0.07 ml vs. 0.27 ± 0.03 ml; $t_{44} = -4.9$; $P < 0.001$). The amount of plant material consumed was significantly greater in males than in females (median = 11.6 and 10.7, respectively; Mann-Whitney $Z = -2.3$, $P > 0.05$). Fourteen of 21 males (66%) and 34 of 61 females (55.7%) consumed plant material.

DISCUSSION

Ovarian Cycle

The reproductive pattern of the females of *S. t. torquatus* from the Pedregal de San Angel is similar to that exhibited by the population of *S. torquatus* in Teotihuacán, state of México (Guillette and Méndez-de la Cruz, 1993), in other species of the *torquatus* group (Crisp, 1964; Goldberg, 1971; Ballinger, 1973; Méndez-de la Cruz et al., 1988), and all viviparous species of *Sceloporus* surveyed to date, except for *S. bicanthalis* (Guillette and Casas-Andreu, 1980; Guillette and Sullivan, 1985; Guillette and Bearce, 1986; Guillette and Méndez-de la Cruz, 1993). Furthermore, fall breeding followed by gestation in winter and parturition in spring is exhibited by other, more distantly related, viviparous lizards, such as *Barisia imbricata* (Guillette and Casas-Andreu, 1987), *Liolaemus huacahuasicus* (Ra-

TABLE 2. Volume, incidence, density, and importance values for the prey taxa found in the stomach contents of *Sceloporus torquatus torquatus* during the wet and dry seasons.

Prey taxon	Volume (ml)	Incidence	Number of individuals	Importance value
<i>Wet season (N = 98)</i>				
Coleoptera adults	16.217	82	373	0.721
Larvae	2.205	13	80	0.123
Pupae	0.031	1	1	0.004
Hymenoptera adults	16.175	52	590	0.760
Larvae	0.633	3	3	0.020
Homoptera adults	9.232	56	357	0.528
Nymphs	0.297	3	9	0.018
Lepidoptera (larvae)	15.276	35	69	0.375
Hemiptera adults	1.96	22	62	0.135
Nymphs	0.312	2	18	0.022
Diptera adults	0.706	9	16	0.048
Larvae	0.277	6	2	0.024
Pupae	0.117	6	5	0.022
Orthoptera	1.915	5	10	0.050
Dermaptera	0.233	6	6	0.026
Neuroptera	0.212	3	4	0.015
Aranae	0.587	10	15	0.049
Oligochaeta	0.759	4	10	0.030
Isopoda	0.381	6	7	0.027
TOTAL	67.525	324	1637	
<i>Dry season (N = 61)</i>				
Hymenoptera	4.432	66	113	0.805
Hemiptera	3.816	27	58	0.439
Orthoptera	7.928	12	17	0.411
Homoptera	4.124	26	45	0.411
Coleoptera adults	1.6	26	31	0.274
Larvae	0.465	5	7	0.062
Diptera adults	1.108	13	43	0.225
Larvae	0.072	1	1	0.010
Lepidoptera (larvae)	0.906	11	12	0.121
Neuroptera	0.034	1	1	0.009
Aranae	0.361	10	14	0.101
Isopoda	0.753	8	10	0.096
Chilopoda	0.298	3	2	0.031
TOTAL	25.897	209	354	

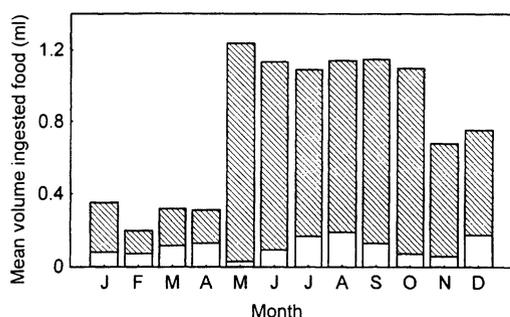


FIG. 5. Mean monthly volumes for the stomach contents of *Sceloporus torquatus torquatus* at the Pedregal de San Angel, Distrito Federal. Hatched and stippled areas represent animal and plant material, respectively.

mírez, 1991), and *Eumeces copei* and *E. lynxe* (Ramírez-Bautista et al., 1996, 1998). However, other viviparous lizards showing fall ovarian activity ovulate in late winter to early spring, and give birth in summer (e.g., *Cordylus p. polyzonus*, *C. giganteus*, and *Pseudocordylus m. melanotus*; Flemming and Van Wyk, 1992; Flemming, 1993; Van Wyk, 1994) or early spring to midsummer, after approximately 14 months of gestation (e.g., *Hoplodactylus maculatus*; Cree and Guillette, 1995).

Gestation and Parturition

Oviductal eggs lost about 30% of their dry mass during embryonic development, whereas their wet mass increased by more than 100%. This pattern of change in the egg dry and wet masses is typical of oviparous species, in which the mother provides no organic material to the developing embryos (Blackburn, 1994). In viviparous species, egg wet mass increases markedly during embryonic development, because the

mother usually provides water to the embryos (Blackburn, 1994). However, the direction and extent of change in egg dry mass varies among species. In *Mabuya bistriata* and *M. heathi*, essentially all neonate dry mass is acquired during embryonic development (Vitt and Blackburn, 1983, 1991), whereas in *Barisia imbricata* (Guillette and Casas-Andreu, 1987) and *Lacerta vivipara* (Avery, 1975), the dry mass of the freshly ovulated egg is similar to that of the neonate. In most surveyed species, including *S. t. torquatus*, egg dry mass decreases to some extent, indicating that part of the yolk is used in catabolic reactions to sustain development and growth of the embryos (Thompson, 1981; Stewart and Castillo, 1984). For instance, in *Sphenomorphus quoyii*, eggs lose 10% of their dry mass during embryonic development, and there is no need to suppose that the embryos receive any organic material from the mother (Thompson, 1981, 1982). It is possible that, in *S. t. torquatus*, the mother provides water and inorganic ions to the embryos, and lipids and proteins in the yolk represent the main source of energy to sustain and nourish embryonic development. However, it is still necessary to analyze the chemical composition of the freshly ovulated eggs and neonates to determine the degree of lecithotrophy in this species (Blackburn, 1994).

Litter Size

Mean litter size of *S. t. torquatus* in the Pedregal de San Angel was smaller than that reported by Guillette and Méndez-de la Cruz (1993) for the population of *S. torquatus* at Teotihuacán, México. In a prior paper, Méndez-de la Cruz et al. (1992b) compared the litter sizes of these populations and suggested that the smaller litter size in the population at the Pedregal de San Angel was because of the relatively low primary productivity in this area, a result of poor soil accumulation.

Olsson and Shine (1997) demonstrated that, in *Lacerta agilis*, clutch and hatchling sizes are inversely correlated. In *S. t. torquatus*, litter size and average oviductal egg mass were not correlated. In addition, REM decreased with snout-vent length and litter size, whereas RCM and SVL were not correlated. In *S. t. torquatus*, like many other species surveyed, litter size increases with female size; however, in this species, unlike other species of lizards (Stewart, 1979; Olsson and Shine, 1997), egg mass is similar in females of different sizes. This suggests that a particular neonate size could be favored by natural selection. A similar situation was found in the oviparous lizards *Uta stansburiana* (Ferguson et al., 1990) and *Sceloporus virgatus* (Smith et al., 1995).

Testicular Cycle

The testicular cycle in the population of *S. t. torquatus* from the Pedregal de San Angel is similar to that exhibited by the population of the same species near Teotihuacán, in the state of México (Guillette and Méndez-de la Cruz, 1993). It is also similar to those in other species of the *S. torquatus* group (Goldberg, 1971; Ballinger, 1973; Garrick, 1974; Méndez-de la Cruz et al., 1994). As in the case of the ovarian cycle, the similarity between the testicular cycles in the species of the *S. torquatus* group could be a result of their phylogenetic relationship. However, a population of *S. mucronatus* from Ajusco Mountain exhibits a testicular cycle that differs from that found in *S. torquatus* in that testicular mass is largest in spring-summer, long before ovulation takes place (Méndez-de la Cruz et al., 1988). The testicular cycle exhibited by *S. mucronatus* also occurs in viviparous groups of *Sceloporus* (e.g., Guillette and Casas-Andreu, 1980; Guillette and Sullivan, 1985). However, a fall testicular cycle also is exhibited by other, more distantly related viviparous lizards such as the tropidurid *Liolaemus huacahuasicus* (Ramírez, 1991), the cordylid *Cordylus giganteus* (Van Wyk, 1995), and the scincid *Eumeces lynxe* (Ramírez-Bautista et al., 1998). This suggests that environmental conditions may affect male and female reproductive activity in different ways.

In *S. mucronatus* and *S. jarrovi*, testes have sperm from August through early December, which suggests a reproductive activity period of about four and a half months (Goldberg, 1971; Villagrán-Santa Cruz et al., 1994). Given the resemblance between the testicular cycles of these species and that of *S. torquatus*, it is possible that in this species mating takes place during the fall months. Indeed, a mating attempt was observed in October.

Diet

Diet of male and female *S. t. torquatus* were similar, consisting mainly of terrestrial invertebrates (mostly insects) and, to a lesser extent, plant material (small flowers and fruits). These results are similar to those reported by Búrquez et al. (1986) for this population. An omnivorous diet also has been reported in several species with small body size (Banta, 1961; Smith and Milstead, 1971; Méndez-de la Cruz et al., 1992a). However, the advantage represented by the ingestion of plant food is still unclear. As expected, food consumption was lower in the dry than in the wet season. However, the fact that in the dry season food consumption in females was about half of that in males indicates there are other factors that influence food consumption in females. In the dry months of the year, females

are pregnant, and the volume occupied by the embryos in their bodies may limit food ingestion (Méndez-de la Cruz et al., 1992a). Also, reduced food ingestion could be caused by a diminished appetite in pregnant females brought about by progesterone (Crews and Garrick, 1980).

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LITERATURE CITED

- AVERY, R. A. 1975. Clutch size and reproductive effort in the lizard *Lacerta vivipara* (Jacquin). *Oecologia* 19:165–170.
- BALLINGER, R. E. 1973. Comparative demography of two viviparous iguanid lizard (*Sceloporus jarrovi* and *Sceloporus poinsetti*). *Ecology* 54:269–283.
- . 1983. Life-history variations. In R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.), *Lizard Ecology: Studies of Model Organism*, pp. 241–259. Harvard Univ. Press, Cambridge, Massachusetts.
- BANTA, B. H. 1961. Herbivorous feeding of *Phrynosoma platyrhinos* in southern Nevada. *Herpetologica* 17:136–137.
- BENABIB, M. 1994. Reproduction and lipid utilization of tropical populations of *Sceloporus variabilis*. *Herpetol. Monogr.* 8:160–180.
- BLACKBURN, D. G. 1994. Standardized criteria for the recognition of embryonic nutritional patterns in squamate reptiles. *Copeia* 1994:925–935.
- BÚRQUEZ, A., O. FLORES-VILLELA, AND A. HERNÁNDEZ. 1986. Herbivory in a small Iguanid lizard, *Sceloporus torquatus torquatus*. *J. Herpetol.* 20:262–264.
- CREE, A., AND L. J. GUILLETTE JR. 1995. Biennial reproduction with a fourteen-month pregnancy in the gecko *Hoplodactylus maculatus* from Southern New Zealand. *J. Herpetol.* 29:163–173.
- CREWS, D., AND L. D. GARRICK. 1980. Methods of inducing reproduction in captive reptiles. In J. B. Murphy and J. T. Collins (eds.), *Reproductive Biology and Diseases of Captive Reptiles*, pp. 49–70. Society for the Study of Amphibians and Reptiles. Lawrence, Kansas.
- CRISP, T. 1964. Studies of reproduction in the female ovoviviparous iguanid lizard *Sceloporus cyanogenys* (Cope). *Tex. J. Sci.* 16:481.
- DEFAURE, J. P., AND J. HUBERT. 1961. Table de développement du lézard vivipare: *Lacerta (Zootaca) vivipara* Jackin. *Arch. Anat. Microscop. Morphol. Exp.* 50:309–328.
- DUCELLMAN, W. E. 1961. The amphibians and reptiles of Michoacán, México. *Univ. Kans. Publ. Mus. Nat. Hist.* 15:1–148.
- FERGUSON, G. W., H. L. SNELL, AND A. J. LANDWER. 1990. Proximate control of variation of clutch, egg, and body size in a West-Texas population of *Uta stansburiana stejnegeri* (Sauria: Iguanidae). *Herpetologica* 46:227–238.
- FERIA-ORTIZ, M. 1989. Contribución al conocimiento del ciclo de vida de *Sceloporus torquatus torquatus* (Lacertilia: Iguanidae) al sur del Valle de México. *Bol. Soc. Herpetol. Mex.* 1:31–33.
- FITCH, H. S. 1970. Reproductive cycles of lizard and snakes. *Univ. Kans. Publ. Mus. Nat. Hist., Misc. Publ.* 52:1–124.
- FLEMMING, A. F. 1993. The female reproductive cycle of the lizard *Pseudocordylus m. melanotus* (Sauria: Cordylidae). *J. Herpetol.* 27:103–107.
- FLEMMING, A. F., AND H. J. VAN WYK. 1992. The female reproductive cycle of the lizard *Cordylus p. polysonus* (Sauria: Cordylidae) in the southwestern Cape Province, South Africa. *J. Herpetol.* 26:121–127.
- GARRICK, D. L. 1974. Reproductive influences on behavioral thermoregulation in the lizard, *Sceloporus cyanogenys*. *Physiol. Behav.* 12:85–91.
- GOLDBERG, S. R. 1971. Reproductive cycle of the ovoviviparous iguanid lizard *Sceloporus jarrovi* Cope. *Copeia* 1972:227–232.
- GUILLETTE JR., L. J., AND D. A. BEARCE. 1986. The reproductive and fat body cycles of the lizard, *Sceloporus grammicus disparilis*. *Trans. Kansas Acad. Sci.* 89:31–39.
- GUILLETTE JR., L. J., AND G. CASAS-ANDREU. 1980. Fall reproductive activity in the high altitude Mexican lizard, *Sceloporus grammicus microlepidotus*. *J. Herpetol.* 14:143–147.
- . 1987. The reproductive biology of the high elevation Mexican lizard, *Barisia imbricata imbricata*, with notes on the other *imbricata* subspecies. *Herpetologica* 43:29–38.
- GUILLETTE JR., L. J., AND F. R. MÉNDEZ-DE LA CRUZ. 1993. The reproductive cycle of the viviparous Mexican lizard *Sceloporus torquatus*. *J. Herpetol.* 27:168–174.
- GUILLETTE JR., L. J., AND W. P. SULLIVAN. 1985. The reproductive and fat body cycles of the lizard, *Sceloporus formosus*. *J. Herpetol.* 19:474–480.
- MÉNDEZ-DE LA CRUZ, F. R., L. J. GUILLETTE JR., M. VILLAGRÁN-SANTA CRUZ, AND G. CASAS-ANDREU. 1988. Reproductive and fat body cycles of the viviparous lizard, *Sceloporus mucronatus* (Sauria: Iguanidae). *J. Herpetol.* 22:1–12.
- MÉNDEZ-DE LA CRUZ, F. R., G. CASAS-ANDREU, AND M. VILLAGRÁN-SANTA CRUZ. 1992a. Variación anual en la alimentación y condición física de *Sceloporus mucronatus* (Sauria: Iguanidae) en la Sierra del Ajusco, Distrito Federal, México. *Southwest. Nat.* 37:349–355.
- MÉNDEZ-DE LA CRUZ, F. R., M. FERIA-ORTIZ, AND O. CUELLAR. 1992b. Geographic variation of reproductive traits in a Mexican viviparous lizard, *Sceloporus torquatus*. *C. R. Soc. Biogéogr.* 68:149–156.
- MÉNDEZ-DE LA CRUZ, F. R., M. VILLAGRÁN-SANTA CRUZ, AND O. CUELLAR. 1994. Geographic variation of spermatogenesis in the Mexican viviparous lizard *Sceloporus mucronatus*. *Biogeographica* 79:59–67.
- OLSSON, M., AND R. SHINE. 1997. The limits of repro-

- ductive output: offspring size versus number in the sand lizard (*Lacerta agilis*). *Am. Nat.* 149:179–188.
- RAMÍREZ, P. P. M. 1991. Reproductive and fat body cycles of the viviparous lizard *Lialoemus huacahuasicus*. *J. Herpetol.* 25:205–208.
- RAMÍREZ-BAUTISTA, A., L. J. GUILLETTE JR., G. GUTIÉRREZ-MAYÉN, AND Z. URIBE-PEÑA. 1996. Reproductive biology of the lizard *Eumeces copei* (Lacertilia: Scincidae) from the Eje Neovolcánico, México. *Southwest. Nat.* 41:103–110.
- RAMÍREZ-BAUTISTA, A., J. BARBA-TORRES, AND L. J. VITT. 1998. Reproductive cycle and brood size of *Eumeces lynxe* from Pinal de Amoles, Querétaro, México. *J. Herpetol.* 32:18–24.
- RZEDOWSKI, J. 1954. Vegetación del Pedregal de San Angel, Distrito Federal, México. *An. Esc. Nac. Cienc. Biol. México* 8:59–129.
- SMITH, D. D., AND W. W. MILSTEAD. 1971. Stomach analysis of the crevice spiny lizard (*Sceloporus poinsettii*). *Herpetologica* 27:147–149.
- SMITH, G. R., R. E. BALLINGER, AND B. R. ROSE. 1995. Reproduction in *Sceloporus virgatus* from the Chiricahua Mountains of southeastern Arizona with emphasis on annual variation. *Herpetologica* 51:342–349.
- SMITH, H. M. 1936. The lizards of the *torquatus* group of the genus *Sceloporus* Wiegmann, 1928. *Univ. Kans. Sci. Bull.* 24:539–691.
- SPSS, INC. 1997. *SPSS-X User's Guide*. SPSS, Inc., Chicago, Illinois.
- STEARNS, S. C. 1980. A new view of life history evolution. *Oikos* 35:266–281.
- STEWART, J. R. 1979. The balance between number and size of young in the live bearing lizard *Gerrhonotus coeruleus*. *Herpetologica* 35:342–350.
- STEWART, J. R., AND R. E. CASTILLO. 1984. Nutritional provision of yolk of two species of viviparous reptiles. *Physiol. Zool.* 57:377–383.
- THOMPSON, J. 1981. A study of the sources of nutrients for embryonic development in a viviparous lizard, *Sphenomorphus quoyii*. *Comp. Biochem. Physiol.* 70A:509–518.
- . 1982. Uptake of inorganic ions from the maternal circulation during development of the embryo of a viviparous lizard, *Sphenomorphus quoyii*. *Comp. Biochem. Physiol.* 71A:107–112.
- URIBE-ALCOCER, M., M. E. MÉNDEZ, J. E. GONZÁLEZ, AND L. J. GUILLETTE JR. 1995. Seasonal variation in ovarian histology of the viviparous lizard *Sceloporus torquatus torquatus*. *J. Morphol.* 226:103–119.
- VAN WYK, J. H. 1994. Physiological changes during the female reproductive cycle of the viviparous lizard *Cordylus giganteus* (Sauria: Cordylidae). *Herpetologica* 50:480–493.
- . 1995. The male reproductive cycle of the lizard, *Cordylus giganteus* (Sauria: Cordylidae). *J. Herpetol.* 29:522–535.
- VILLAGRÁN-SANTA CRUZ, M., F. R. MÉNDEZ-DE LA CRUZ, AND L. PARRA. 1994. Ciclo espermatogénico del lacertilio *Sceloporus mucronatus* (Reptilia: Phrynosomatidae). *Rev. Biol. Trop.* 42:289–296.
- VITT, L. J. 1981. Lizard reproduction: habitat specificity and constraints on relative clutch mass. *Am. Nat.* 117:506–514.
- VITT, L. J., AND D. G. BLACKBURN. 1983. Reproduction in the lizard *Mabuya heathi* (Scincidae): a commentary on viviparity in New World *Mabuya*. *Can. J. Zool.* 61:2798–2806.
- . 1991. Ecology and life history of the viviparous lizard *Mabuya bistriata* (Scincidae) in the Brazilian Amazon. *Copeia* 1991:916–927.
- VITT, L. J., AND J. D. CONGDON. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *Am. Nat.* 112:596–608.
- VITT, L. J., AND H. J. PRICE. 1982. Ecological and evolutionary determinants of relative clutch mass in lizard. *Herpetologica* 38:237–255.
- WERLER, J. E. 1951. Miscellaneous notes on the eggs and young of the Texan and Mexican reptiles. *Zoologica* 36:37–48.

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