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ECOLOGY OF THE MEXICAN ALPINE BLOTCHED GARTER SNAKE (*THAMNOPHIS SCALARIS*)

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ABSTRACT—We report the first information on seasonal abundance, sex ratio, body size, reproduction, and diet for a population of *Thamnophis scalaris* from the State of Mexico. Data were collected during 1992 and from 1998 to 2000 at Toluca. *Thamnophis scalaris* showed a bimodal peak of activity in spring-early summer and in autumn. The sex ratio of adults was significantly different from 1:1, but can be misleading because of the unknown natural history of *T. scalaris*. Sexual size dimorphism was only apparent in relative tail length of adults. Four litters were born from July 1 to 17. Mean litter size was 7.0 ± 1.4 snakes per litter. Male and female neonates were of similar snout-vent length (SVL) and mass at birth. The sex ratio of neonates was 1:1. Of the stomachs examined, 81% contained earthworms and 19% contained vertebrates. Vertebrates (lizards and viperine snakes) were ingested only by *T. scalaris* >40.0 cm SVL. This suggests an ontogenetic shift in the diet of *T. scalaris*. The mean vertebrate prey mass was $21.4 \pm 10.0\%$ of snake mass. No differences were found in prey type between the sexes.

RESUMEN—Se reporta la primera información sobre la abundancia temporal, proporción sexual, tamaño corporal, reproducción y dieta de una población de *Thamnophis scalaris* del Estado de México. Los datos fueron colectados en 1992 y de 1998 al 2000 en la ciudad de Toluca. *Thamnophis scalaris* tuvo un patrón de actividad bimodal en primavera-principio de verano y en otoño. La proporción sexual de los adultos fue significativamente diferente de 1:1, pero puede ser malinterpretada debido al desconocimiento de la historia natural de *T. scalaris*. El dimorfismo sexual fue evidente sólo para la longitud relativa de la cola de los adultos. Nacieron 4 camadas entre el 1 y 17 de julio. El tamaño medio de la camada fue de 7.0 ± 1.4 culebras por camada. El tamaño (longitud del hocico a la cloaca, LHC) y el peso de las crías al nacer fueron similares entre machos y hembras con una proporción sexual de 1:1. El 81% de las culebras tuvieron lombrices en los estómagos, y el 19% tuvieron vertebrados. Los vertebrados (lagartijas y serpientes viperinas) fueron ingeridos sólo por *T. scalaris* >40.0 cm de LHC. Esto sugiere un posible cambio ontogénico de la dieta de *T. scalaris*. El peso medio de los vertebrados ingeridos fue el $21.4 \pm 10.0\%$ del peso de las culebras. No se encontraron diferencias en el tipo de presa ingerida entre los sexos.

New World garter snakes (*Thamnophis*) are well studied in relation to ecology, morphology, and behavior (e.g., Arnold, 1993; Ford and Burghardt, 1993; Rossman, 1996), but we lack information on the ecology of Mexican *Thamnophis*. *Thamnophis scalaris* occurs across the Transverse Volcanic axis of Central Mexico, from Jalisco to Veracruz, at elevations ranging from 2,103 to 4,273 m. This species is rare at localities where *T. melanogaster* and *T. eques* occur. *Thamnophis scalaris* has been confused with its sister species *T. scalaris* because both are sympatric and morphologically similar (Rossman, 1996). Little

is known about the life history and ecology of *T. scalaris*. Isolated observations tell us that earthworms, frogs (*Hyla plicata*), salamanders (*Pseudoeurycea belli* and *P. leprosa*), lizards (*Barisia imbricata* and *Sceloporus aeneus*), and deermice (*Peromyscus maniculatus*) are prey of *T. scalaris* (Fouquette and Rossman, 1963; Sanchez-Herrera, 1980; Lemos-Espinal and Ballinger, 1992; Uribe-Peña et al., 1999; Venegas-Barrera and Manjarrez, 2001a). The litter size is 8 to 15 neonates (Ramirez-Bautista et al., 1995; Rossman et al., 1996; Contreras et al., 2001), and *T. scalaris* is preyed upon by *T. eques* (Venegas-Barrera and

Manjarrez, 2001*b*). Here we report on a single population of *T. scalaris* from the State of Mexico, describing seasonal abundance, sex ratio, body size, reproduction, and diet.

METHODS—The population is located at the “El Cerrillo” campus of the Universidad Autónoma del Estado de México, 17 km NW of Toluca City (99°41'W, 19°24'N) at an elevation of 2,550 m. The habitat is grassland surrounded by cultivated fields, with an adjoining 1-ha seasonal pond. Rainfall averages 500 to 600 mm, with 85% falling in summer; mean annual environmental temperature is 15°C. Two collectors caught snakes in monthly visits of 1 to 4 d, primarily in 1992 and also between 1998 and 2000. Most collecting occurred from 1100 to 1500 h from January to December, when snakes are more active (Manjarrez, 1998), but visits were less frequent during winters (December to February). Because sampling intensity varied among months, we determined monthly frequency of snakes by dividing the number of snakes captured monthly by the number of days sampled each month. Snakes were collected by hand, searching under rocks and all available shelters. All snakes found alive were taken to the laboratory and measured for snout-vent length (SVL), tail length (TL; when complete), and head length (HL; from posterior end of interparietal suture to the tip of the rostrum) by using digital calipers. Also, they were forced to regurgitate and then weighed to the nearest 0.01 g with an electronic balance. Sex was determined by inspecting the thickness of the tail near the vent or by manually everting the hemipenis in small snakes. Adult females were palpated gently on the abdomen to detect whether or not they contained embryos. Gravid females were housed in individual cages with a paper shelter and water bowl, and maintained under natural (Toluca) photoperiod of 12 h light and laboratory temperatures ranging between 20 to 25°C until neonates were born. Neonates were measured (SVL, TL, and HL), weighed, and sexed within 24 h of birth. We report means and standard deviations.

RESULTS—*Seasonal Abundance*—Over the 2 y (1998 and 1999) when *Thamnophis scalaris* was sampled throughout the entire year, the earliest and latest dates that snakes were seen and collected were 28 January and 15 December, respectively. The mean overall activity period (defined as the range of capture dates) was 187 ± 71.4 d ($n = 2$ y, range = 137 to 238 d). *Thamnophis scalaris* showed a bimodal peak of abundance; 38% of all snakes were collected in spring and early summer (April to July, $n = 37$ snakes), and 51% in late summer and autumn (August to November, $n = 49$), while 11% ($n = 11$) were collected in winter (December to March) (Fig. 1). The monthly frequency of snakes captured by day sampled was not correlated with monthly rainfall (Spearman $r_s = 0.11$,

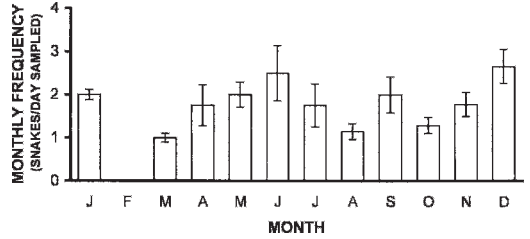


FIG. 1—Monthly frequency of *Thamnophis scalaris* captured by day sampled (± 1 SE) in Toluca, Mexico, during 1992 and 1998 through 2000.

$P = 0.69$, $n = 12$) or temperature (Spearman $r_s = 0.17$, $P = 0.61$, $n = 12$).

Body Size—Because no data are available of adult body size in *T. scalaris*, we considered adults to be the snakes >34.5 cm SVL, which was the size of the smallest gravid female collected of 100 individuals collected (see reproduction text). The adults comprised 15 males and 34 females (Fig. 2). The sex ratio of adults was significantly different from 1:1 ($\chi^2 = 7.36$, $df = 1$, $P = 0.004$). Of the juveniles (range = 20.0 to 34.0 cm SVL), 20 were males and 24 females. The sex ratio of juveniles did not differ significantly from 1:1 ($\chi^2 = 0.36$, $df = 1$, $P = 0.32$). Only 4 neonates were collected; 1 was male and 3 were females. Sexual size dimorphism was only apparent in relative tail length (TL/SVL) of adult *T. scalaris*, which was significantly longer in males (0.31 ± 0.09 cm; range = 0.10 to 0.41 cm) than in females (0.24 ± 0.11 cm; range = 0.16 to 0.54 cm; Student $t_{36} = 2.3$, $P = 0.02$). Adult males and females were similar in relative head length (HL/SVL; males: 0.38 ± 0.04 cm; range = 0.33 to 0.50 cm; females: 0.38 ± 0.08 cm;

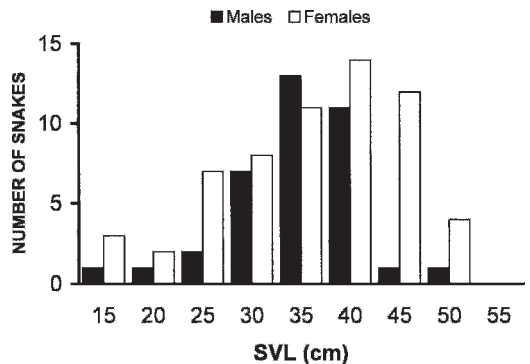


FIG. 2—Frequency distribution of snout-vent length (SVL) in male and female *Thamnophis scalaris* from Toluca, Mexico.

TABLE 1—Maternal identity of 4 female *Thamnophis scalaris* captured in Toluca, Mexico, and data on their neonates born in the laboratory. Mean \pm 1 SD for snout-vent length (SVL, cm) and neonate mass (g).

Female		Neonates				
Date of capture	SVL	Birth date	<i>n</i>	SVL (range)	Mass (range)	Sex ratio M:F
16 May 1998	36.5	13 June 1998	7	11.67 \pm 0.81 (10.2–12.5)	1.25 \pm 0.17 (0.95–1.47)	2:5
16 May 1998	37.0	1 June 1998	8	12.91 \pm 0.69 (11.6–13.5)	1.18 \pm 0.07 (1.08–1.27)	5:3
2 June 1999	37.0	12 June 1999	8	12.95 \pm 0.61 (12.0–13.9)	1.24 \pm 0.07 (1.12–1.35)	0:8
1 June 2000	38.5	17 June 2000	5	10.68 \pm 0.32 (10.4–11.2)	1.71 \pm 0.14 (1.52–1.85)	2:3

range = 0.32 to 0.50 cm; Student $t_{46} = 0.17$, $P = 0.86$), mean body size (males: 38.9 \pm 3.4 cm SVL; range = 34.5 to 48.0 cm; females: 40.1 \pm 4.0 cm SVL; range = 34.5 to 50.0 cm; Student $t_{47} = 1.07$, $P = 0.29$), and mean body mass (males: 40.1 \pm 7.1 g; range = 34.0 to 59.4 g; females: 44.0 \pm 13.4 g; range = 24.8 to 84.0 g; Student $t_{36} = 1.15$, $P = 0.25$). The overall adult female to male size ratio (Fitch, 1981) was 1.0 for both SVL and mass.

Reproduction—Four (11.7%) of 34 adult females were gravid. The mean SVL of gravid females was 37.2 \pm 0.8 cm (range = 36.5 to 38.5 cm; $n = 4$; Table 1). Four litters were born in the laboratory from 1 to 17 June. Litter size was 7.0 \pm 1.4 snakes (range = 5 to 8; Table 1). Small sample size prevented testing for a correlation between litter size and maternal SVL. Neonate size and mass were 12.1 \pm 1.1 cm (range = 10.2 to 13.9 cm, $n = 4$ litters) and 1.25 \pm 0.17 g (range = 0.95 to 1.85 g, $n = 4$ litters), respectively. Male and female neonates were of similar SVL (Mann-Whitney $W_5 = 11.0$, $P = 0.85$) and mass (Mann-Whitney $W_6 = 7.0$, $P = 0.41$) at birth. The slopes of the mass and SVL relationship also were similar between males (slope = 0.029) and females (slope = 0.024; ANCOVA $F_{1,22} = 0.16$, $P = 0.69$), with SVL the covariate. Neonatal SVL varied among litters (one-way ANOVA $F_{3,20} = 14.6$, $P = 0.001$), but there was no relationship between mean litter SVL and maternal SVL (Spearman $r_s = 0.8$, $P = 0.20$, $n = 4$). The sex ratio of neonates from the 4 litters born in captivity was 9 males:19 females (Table 1), statistically similar to 1:2 ($\chi^2 = 0.017$, $df = 1$, $P = 0.91$).

Diet—Of 95 snakes that were forced to regurgitate, 16 (16.8%) had identifiable prey in

their stomachs. The ingested prey was mostly earthworms (81% of stomachs), with 19% containing vertebrates. The vertebrate prey were 1 deer mouse *Peromyscus maniculatus* (10 g), 1 adult lizard *Barisia imbricata* (12.32 g, 8.5 cm SVL), and 1 rattlesnake *Crotalus triseriatus* (4.41 g, 18.0 cm SVL, 4.2 cm TL). Earthworms were ingested by both small (<40.0 cm SVL; $n = 11$ snakes) and large (>40.0 cm SVL; $n = 2$ snakes) *T. scalaris*, while vertebrates were ingested only by large snakes ($n = 3$ snakes; G test = 8.7, $df = 1$, $P = 0.004$). The mean vertebrate prey mass was 21.41 \pm 10.0% (range = 10.3 to 30.1%) of snake mass. No difference was found in prey type between the sexes (G test = 0.78, $df = 1$, $P = 0.60$).

DISCUSSION—Snakes were collected in all months, except February, with abundance peaking in spring, early summer, and autumn. This abundance pattern is similar to that of the sympatric garter snakes *T. melanogaster* and *T. eques* (Drummond and Macias-Garcia, 1989; Manjarrez, 1998) and is common in natricines from temperate areas (Gibbons and Semlitsch, 1987; Parker and Plummer, 1987). Seasonal snake abundance is affected by demography, availability of prey, vulnerability to predators, and abiotic variables (Parker and Plummer, 1987; Greene, 1997). Monthly temperature and rainfall had no apparent relationship with monthly abundance fluctuations in *T. scalaris* at Toluca. A complementary explanation for monthly snake abundance is that snakes are inactive and inconspicuous for prolonged periods of day or weeks (Gibbons and Semlitsch, 1987), and only inactive snakes coiled under rocks were collected in this study. It could

represent biased sampling resulting from limited snake availability.

Rossman et al. (1996) reported a maximum SVL of 60.1 cm, larger than the maximum size (50.0 cm SVL) obtained in our study. In all natricines and 65% of snake species for which data are available (Fitch, 1981; Shine, 1993), adult females are larger than adult males, and neonate males and females are similar in size at birth (Shine, 1993). Sexual size dimorphism was only apparent in relative tail length of adult *T. scalaris* at Toluca. This might be an artifact of a limited data set in our study population. Large sample sizes are necessary to adequately determine patterns of sexual size dimorphism in neonate and adults size of *T. scalaris*.

The size of the smallest gravid female was 34.5 cm SVL, which is 2.8 times the mean SVL of a neonate. Parker and Plummer (1987) found that minimum mature size in snakes is 2.5 to 2.9 times neonate size, and the same pattern occurred in female *T. scalaris* from Toluca. According to available data, *Thamnophis* species reach sexual maturity at 2 to 4 y of age (Seigel, 1996). Mean litter size was 7 neonates, a value smaller than the fewest (8) previously reported for 3 other litters of this species (Rossman, 1996; Contreras et al., 2001).

The overall sex ratio of neonates was biased in favor of females (1:2). In 2 of 16 natricine species that have been studied, sex ratios of neonate snakes differ from 1:1 (Seigel and Ford, 1987). In adult *T. scalaris*, sex ratio was biased in favor of females (1:2). Adult size was based on an estimate of the smallest gravid female that was the minimum size considered as an adult. Generally, males are reproductively active at a smaller size than females (Shine, 1993). In 13 *Thamnophis* species, Shine (1991) reported that females are on average 13% larger than conspecific males; therefore, our data for *T. scalaris* suggest that we might be underestimating the actual adult sex ratio. Other species of *Thamnophis* show sex ratios biased in favor of females (Parker and Plummer, 1987). The basic question is whether the deviation is real, reflecting actual population structure, or is apparent, reflecting different behavioral traits of adult males and females (Parker and Plummer, 1987). Observed sex ratio in adult *T. scalaris* might be misleading because their natural history is poorly understood, and the small sample sizes from different years were pooled in this study. We do not have

reports that suggest sexual differences in activity, preferences of microhabitat, foraging, or thermoregulatory behavior in *T. scalaris*, which could also explain some of differences observed in the sex ratio.

We detected a possible ontogenetic shift in the diet of *T. scalaris*. Small snakes (<40.0 cm SVL) ingested invertebrates, and large snakes (>40.0 cm SVL) ingested vertebrates and invertebrates. Earthworms are a common prey in some neonatal or juvenile garter snakes, but lizards and snakes are an uncommon prey in adult *Thamnophis* species. Juvenile *T. radix*, *T. sirtalis*, *T. eques*, and *T. melanogaster* eat earthworms almost exclusively, whereas adults consume other vertebrates, such as fishes, tadpoles, and frogs (Macías-García and Drummond, 1988; Seigel, 1996; Manjarrez, 2003). However, large sample sizes are necessary to adequately determine if an actual ontogenetic shift in diet occurs in *T. scalaris* from Toluca. Reptiles comprise only a minor component of the diet of *Thamnophis* and have been only reported in *T. elegans*, *T. proximus*, and *T. scalaris* (Seigel, 1996). The ingestion of a viperine species by a colubrid species is rare in snakes. Rattlesnakes (*C. triseriatus*) have not been reported as part of the diet of *T. scalaris*. Ophiophagy has been reported in approximately 100 snake species (Mitchell, 1986), and only few species routinely prey on venomous snakes (Greene, 1997). This prey spectrum indicates that *T. scalaris* is not aquatic, as are its sympatric conspecifics, *T. eques* and *T. melanogaster*. It forages on terrestrial prey in mesic forest and among marginal vegetation.

In summary, our analysis of a population of *T. scalaris* at Toluca supports and extends previous anecdotal reports on the ecology and reproduction of this endemic Mexican snake. Given their abundance and limited distribution, this species would be well suited for more intensive ecological and behavioral studies.

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