Demography of a Semelparous, High-Elevation Population of *Sceloporus bicanthalis* (Lacertilia: Phrynosomatidae) from the Nevado de Toluca Volcano, Mexico

DEMOGRAPHY OF A SEMELPAROUS, HIGH-ELEVATION POPULATION OF *SCELOPORUS BICANTHALIS* (LACERTILIA: PHRYNOSOMATIDAE) FROM THE NEVADO DE TOLUCA VOLCANO, MEXICO

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ABSTRACT—We studied demography of a population of viviparous lizard, *Sceloporus bicanthalis,* from Nevado de Toluca Volcano, Mexico, using mark-recapture methods. Age structure of this population varied seasonally due to an increase in number of juveniles over summer, although neonates were observed in every month. Estimated average density was 304 individuals/ha. Snout-vent length at sexual maturity in viviparous *S. bicanthalis* was 31 mm in males and 32 mm in females. Males survived longer than females, with an expected lifespan of 15 months, compared to 8 months for females. Net reproductive rate of this population was 1, suggesting it was at equilibrium, while generation time was 7 months. This high-elevation population has a semelparous life cycle.

RESUMEN—Estudiamos la demografía de una población de lagartijas vivíparas, *Sceloporus bicanthalis,* ubicada en el volcán Nevado de Toluca, México, usando la técnica de captura-marcaje-recaptura. La estructura poblacional varió estacionalmente debido al aumento de juveniles durante el verano, aunque las crías fueron observadas en todos los meses. La estimación de la densidad promedio fue de 304 lagartijas/ha. La longitud hocico-cloaca a la madurez sexual de la lagartija vivípara *S. bicanthalis* fue de 31 mm en machos y 32 mm en hembras. Los machos sobrevivieron más meses que las hembras, con una esperanza de vida de 15 meses comparados con 8 meses para las hembras. La tasa reproductora neta para esta población fue de 1, sugiriendo que la población se encontró en equilibrio, y el tiempo generacional fue de 7 meses. Esta población de gran altura tiene un ciclo de vida de tipo semélparo.

There have been several studies of demography of species and populations of *Sceloporus* in the United States; however, few populations in Mexico and Central America have been the subject of mark-recapture studies (e.g., Gadsden-Esparza et al., 1993; Ramírez-Bautista, 1995; Lemos-Espinal et al., 1998, 2003; Maury-Hernández, 1998; Ortega-Rubio et al., 2000; Gadsden-Esparza et al., 2001; Castañeda-Gaytán et al., 2003). Studies of more species and populations of *Sceloporus* in Mexico and Central America have the potential to provide useful information because there is a high diversity of *Sceloporus* in Mexico and Central America (Köhler and Heimes, 2002) and because *Sceloporus* occurs in a wide range of habitats and elevations. Further study of this diversity within a genus (*Sceloporus*) can provide greater insight into factors influencing evolution and ecology of demography of lizards.

The viviparous lizard *Sceloporus bicanthalis* is a small, diurnal, ground-dwelling phrynosomatid lizard, restricted to the Neovolcanic Axis in the center of Mexico at 2,100–4,200 m elevation (Smith et al., 1993; Benabib et al., 1997). Its geographic distribution is disjunct and many populations are isolated. Although these lizards have been the subject of past studies (e.g.,

Guillette, 1981, 1982; Andrews et al., 1999; Hernández-Gallegos et al., 2002; Rodríguez-Romero et al., 2002, 2004), these studies have provided no detailed information about population dynamics and life-history traits. Our goal was to provide demographic data for a high-elevation population (4,200 m) of *S. bicanthalis* that will expand the existing database on life-history strategies of *Sceloporus* and contribute to future comparative studies of lizards.

MATERIALS AND METHODS—We studied a population of *S. bicanthalis* on Nevado de Toluca Volcano, 25 km SW Toluca in the state of Mexico (18°21 N, 98°36′W) at 4,200 m elevation. Mean annual temperature is 6.5°C, annual precipitation is 1,000–1,400 mm, the dry season is June–August, and the wet season is December–February (Enciclopedia de los Municipios de México, 1988). Vegetation in the study area consisted primarily of three alpine grasses (*Festuca tolucencis*, *Calamagrostis tolucencis*, *Eryngium protiflorum*; Rzedowski, 1981). Individuals of *S. bicanthalis* are associated with grasses and, occasionally, open areas (Rodríguez-Romero, 1999).

Lizards in the study plot (50 by 100 m = 0.5 ha) were marked and released monthly during December 1998–October 2000. We chose October 2000 to complete the field work because we observed a total replacement of all marked individuals in our population. Moreover, we followed this high-elevation population for other purposes to 1995 (Hernandez-Gallegos, 1995; Manríquez-Morán, 1995; Rodríguez-Romero, 1996). Sampling was conducted in the field for 3 days each month and consisted of two or three people searching the plot 4–7 h/day and collecting lizards by hand or noose. Each lizard was individually marked by toe clipping (Tinkle, 1967; Medica et al., 1971; Ferner, 1979) and, after processing, lizards were released at the site of initial observation. Snout-vent length was measured with a ruler (to nearest mm) and mass was recorded with a Pesola spring balance (Pesola AG, Baar, Switzerland; to nearest 0.1 g). Sex of male neonates, juveniles, and adults was determined by presence of two enlarged postanal scales, and animals were considered reproductively active (i.e., sexually mature) when they exhibited darker or bluish coloration on the chest and throat, and secretions from femoral pores (Galán, 1999; Rodríguez-Romero, 1999; Hernandez-Gallegos et al., 2002). Females were determined to be pregnant (i.e., sexually mature) by palpation or by presence of a distended abdomen; vitellogenic females were assessed by presence of bite marks on the neck or abdominal areas (indicative of recent courtship and mating) and palpation (Hardy, 1962; Fitch, 1973; Cuellar, 1993; Galán, 1999; Paulissen, 1999, 2000; Olsson et al., 2002; Hernandez-Gallegos et al., 2002).

We defined structure of the population using sex and age-size groups. We differentiated three age-size groups: neonates (20–29 mm snout-vent length with umbilical scar), juveniles (30–35 mm snout-vent length without evidence of coloration or femoral secretions), and adults as previously mentioned (≥36 mm snout-vent length), based on size and characteristics of sexual

maturity reported for this species by Hernández-Gallegos et al. (2002).

We estimated size of population in each sex-age group for each month of the study. These data were pooled and analyzed with the Jolly-Seber model using the program JOLLY (Pollock et al., 1990), which is used to compute estimates for rate of survival, size of population, and rate of immigration from capture-recapture data. The program computes these statistics using the model suggested by Jolly (1965), which allows both death and immigration. A goodness-of-fit test was performed to determine if this model was appropriate. The procedure of Pollock et al. (1990) is recommended when there are sessions of ≥3 samples conducted at equal intervals (e.g., every month, as in our study) during the period of interest.

We used the method of Tinkle and Dunham (1986) to calculate productivity. This method calculates the approximate number of neonates that each female produces during the reproductive season. We used previously published data (Rodríguez-Romero et al., 2002, 2004) in which females approaching parturition (April–September) were captured and kept in the laboratory until parturition occurred. In this population, all females have only one litter per reproductive season and the mean size of litter in these females was 7.32 (Rodríguez-Romero et al., 2002). To calculate productivity, we multiplied number of females marked in a reproductive season by this average size of litter. After this, we divided the number of marked newborns by the estimated productivity to provide an estimate of survival of neonates (Tinkle and Dunham, 1986). From this estimate of fecundity and survivorship of the three age-size classes, we constructed a life table.

All statistical analyses were performed with the software Statgraphics Plus for Windows (Manugistics, Inc., Warrenton, Virginia) and Statistica for Windows to construct the graphics (StatSoft, Inc., Tulsa, Oklahoma). Calculations of survivorship, goodness-of-fit tests, and some demographic parameters were performed with Jolly software (Pollock et al., 1990). Unless otherwise stated, means are given ± 1 *SE*.

RESULTS AND DISCUSSION—*Size at Sexual Maturity*—Minimum snout-vent length of male *S. bicanthalis* with darker or bluish chest, throat, or both, and secretions of femoral pore was 31 mm, and vitellogenic females (with bite marks) were 32 mm. *Sceloporus bicanthalis* reached sexual maturity at a smaller snout-vent length than another population of the same species in the mountains of central Mexico (e.g., in Zoquiapan, state of Mexico at 3,500 m elevation; minimum snout-vent length at sexual maturity was 35 mm in males and 40 mm in females; Manríquez-Morán, 1995; Hernández-Gallegos et al., 2002). In our population, minimum size at maturity also is smaller than other species of *Sceloporus* from other mountain ranges in Mexico (e.g., *S. palaciosi*, 38 mm—Méndez de la Cruz and Villagrán-Santa Cruz,

TABLE 1—Demographic structure of a population of *Sceloporus bicanthalis* on Nevado de Toluca Volcano, 25 km SW Toluca, Mexico, Mexico. Numbers of individuals on the 0.5-ha study site are reported.

Months	Neonates		Juveniles		Adults		Total
	Males	Females	Males	Females	Males	Females	
December	0	1	1	2	19	14	37
January	0	1	10	18	40	59	128
February	2	1	17	3	41	63	127
March	0	1	0	0	43	52	96
April	0	0	0	0	37	48	85
May	2	5	0	0	28	36	71
June	14	10	2	0	29	36	91
July	9	5	2	0	15	20	51
August	2	4	11	3	12	17	49
September	1	2	8	0	8	16	35
October	19	13	20	18	17	13	100
November	3	9	12	17	14	13	68
December	1	2	11	11	12	13	50
Totals	53	54	94	72	315	400	988

1998; *S. grammicus*, 39–42 mm—Lemos-Espinal et al., 1998). It is also among the smallest at maturity for all *Sceloporus* studied to date (e.g., *S. poinsetti*, 90 mm—Ballinger, 1973; *S. jarrovi*, 60 mm—Ballinger, 1973; *S. scalaris*, 47 mm—Newlin, 1976; Ballinger and Congdon, 1981; *S. clarki*, 90 mm—Tinkle and Dunham, 1986; *S. undulatus*, 42–66 mm—Tinkle, 1972; Tinkle and Ballinger, 1972; Vinegar, 1975*b*; Tinkle and Dunham, 1986; Jones and Ballinger, 1987; *S. virgatus*, 47 mm—Vinegar, 1975*a*; *S. magister*, 80 mm—Tinkle, 1976). The different size at sexual maturity in other species is attributed to time of parturition or appearance of hatchlings during the year, and no species mentioned before reaches sexual maturity in the first year (Ballinger, 1973). In fact, neonates in our population, regardless of date of birth during the continuous reproductive cycle (Hernandez-Gallegos et al., 2002), grow fast and reach sexual maturity before even 1 year of age, at least in populations in central Mexico.

Age Structure—We observed peaks in abundance of neonates during June and October. Juveniles were conspicuous in June and numbers of juveniles increased quickly during the final one-third of the year, reaching their maximum in October. Juveniles grew fast and only adults were observed during the first one-third of the next year (reaching their highest levels during January–June; Table 1). *Sceloporus bicanthalis* exhibited seasonal fluctuations in age structure, which may be related to seasonality of recruit-

ment, as well as that most lizards in this population likely survive only a year at most (Rodríguez-Romero et al., 2004). In addition, as shown in other species of *Sceloporus*, activity of different portions of the population may vary throughout the year (Rose, 1981). *Sceloporus scalaris* from Durango, Mexico (the ancestral, oviparous sister species), shows a seasonal pattern in age structure, with recruitment of juveniles primarily occurring October–December (Ortega-Rubio et al., 2000). This similar structure and recruitment suggests an ancestral and, perhaps, a strong phylogenetic effect on population dynamics.

Density—Mean density in our population was 304.2 ± 32.2 individuals/ha, with a peak of 695.2 individuals/ha in November–December 1999, during which time the maximum number of neonates and juveniles were observed (Fig. 1). Lowest densities were during the transition between winter and spring in 1999 (March–April) with 122.8 individuals/ha (Fig. 1). These data are among the highest densities observed in *Sceloporus* (e.g., *S. undulatus*, 2–72/ha—Tinkle, 1972, 1982; Tinkle and Ballinger, 1972; Vinegar, 1975*b*; Ferguson et al., 1980; Tinkle and Dunham, 1986; Jones and Ballinger, 1987; Gadsden-Esparza and Aguirre-León, 1993; Parker, 1994; *S. clarki*, 6–46.6/ha—Tinkle, 1982; Tinkle and Dunham, 1986; *S. grammicus*, 42–135/ha—Lemos-Espinal et al., 1998; Ortega-Rubio et al., 1999; *S. scalaris*, 50–140/ha—Ballinger and Congdon, 1981; Ortega-Rubio et al., 2000; *S.*
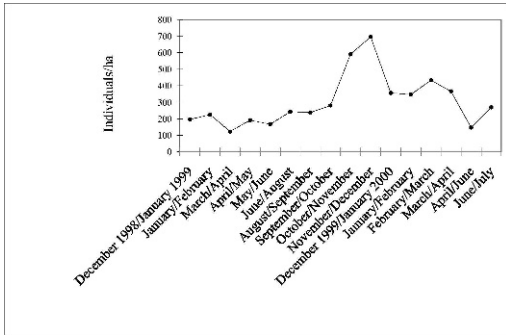
FIG. 1—Mean density (number of individuals/ha) for a population of *Sceloporus bicanthalis* on the Nevado de Toluca Volcano, 25 km SW Toluca, Mexico, Mexico.
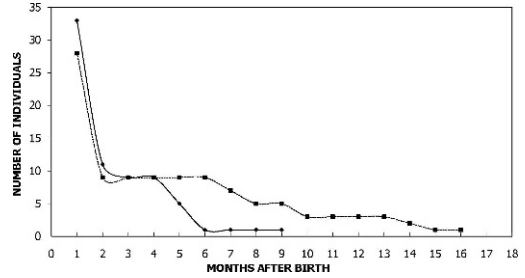

FIG. 2—Average survivorship of neonatal *Sceloporus bicanthalis* during 18 consecutive months on the Nevado de Toluca Volcano, 25 km SW Toluca, Mexico, Mexico (■ = males; ♦ = females).

merriami, 41–228/ha—Ruby and Dunham, 1987; *S. jarrovi*, 103.3/ha—Ruby and Dunham, 1984; *S. graciosus*, 208/ha—Tinkle, 1973; *S. magister*, 14.8/ha—Tinkle, 1976).

Neonatal Survivorship—We marked and released 93 pregnant females, and using a mean litter size of 7.32 (Rodríguez-Romero, 1999), we estimated that the number of neonates produced on the study area was 681. We later captured 98 neonates, suggesting that survivorship of neonates is ≥14.4% in *S. bicanthalis*. This is similar to estimates of survivorship for most species of *Sceloporus* (e.g., *S. undulatus*, 1–44%—Tinkle and Ballinger, 1972; Vinegar, 1975*b*; Ferguson et al., 1980; Tinkle and Dunham, 1986; Jones and Ballinger, 1987; *S. clarki*, 11%—Tinkle and Dunham, 1986; *S. virgatus*, 15–30%—Vinegar, 1975*a*; *S. scalaris*, 24–31%—Ballinger and Congdon, 1981; Ortega-Rubio et al., 2000; *S. jarrovi*, 33–46%—Ruby and Dunham, 1984; *S. magister*, 17%—Tinkle, 1976).

The cumulative survivorship of newborn male and female *S. bicanthalis* declined rapidly throughout the study (Fig. 2). Survivorship of females dropped rapidly from 33.3% in the first month to 3% after the fourth month, suggesting that average survival of females is ca. 8 months. For neonatal males, cumulative survivorship was higher and dropped more slowly than for females. Data suggest a lifespan of 15 months (Fig. 2). Other *Sceloporus* also show higher survivorship by males than females (e.g., *S. undulatus*, Tinkle and Dunham, 1986; *S. virgatus*, Vinegar, 1975*a*; *S. jarrovi*, Ruby and Dunham, 1984; *S. scalaris*, Ballinger and Congdon, 1981), although the reverse is true in other populations and species of *Sceloporus* (e.g., *S. clarki*, Tinkle

and Dunham, 1986; *S. undulatus*, Tinkle, 1972). In some cases, male and female lizards have similar survivorship (e.g., *S. undulatus*, Vinegar, 1975*b*; Ferguson et al., 1980; Jones and Ballinger, 1987).

Life Table—We used capture-recapture data to generate a life table (Table 2). The net reproductive rate (R_0) of our population was 1; our population of *S. bicanthalis* apparently is stable. Many populations of *Sceloporus* have R_0-values near 1 (e.g., *S. clarki*—Tinkle and Dunham, 1986; *S. scalaris*—Ortega-Rubio et al., 2000; *S. jarrovi*—Ballinger, 1973; Ruby and Dunham, 1984; *S. poinsettia*—Ballinger, 1973; *S. graciosus*—Tinkle, 1973; *S. undulatus*—Tinkle and Ballinger, 1972). Few populations have R_0-values >1 (e.g., >1.1; *S. scalaris* in southeastern Arizona—Ballinger and Congdon, 1981; *S. undulatus* from South Carolina and Colorado—Tinkle and Ballinger, 1972). More populations have low R_0-values (e.g., <0.9; *S. undulatus*—Tinkle, 1972; Tinkle and Ballinger, 1972; Vinegar, 1975*b*; Ferguson et al., 1980; Tinkle and Dunham, 1986; Jones and Ballinger, 1987; *S. jarrovi*—Ballinger, 1979). However, in some cases, there is substantial temporal variation in R_0 (e.g., range for *S. virgatus* was 0.495–1.769 depending on year—Vinegar, 1975*a*; range for *S. undulatus* from northern Mississippi was 0.596–1.496 depending on year—Parker, 1994).

Average generation time of *S. bicanthalis* in our population was 7.0 months. This is among the shortest generation times reported for *Sceloporus*, and may be the lowest observed in a high-elevation lizard. For example, *S. clarki* from central Arizona has a generation time of 3 years (Tinkle and Dunham, 1986), *S. virgatus* from southeastern Arizona has a generation time of 2–

TABLE 2—Life table for a population of *Sceloporus bicanthalis* at the Nevado de Toluca Volcano, 25 km SW Toluca, Mexico, Mexico: x = age in months; n_x = number of survivors at the start of age x; l_x = proportion of original population alive at the start of age interval (n_x/n_0); d_x = proportion of original population dying in the age interval; q_x = age-specific mortality (d_x/l_x); m_x = age-specific fecundity; $l_x m_x$ = age-specific contribution to the net reproductive rate (R_0); $x l_x m_x$ = data to calculate average generation time; L_x = average number of individuals alive during the interval; e_x = life expectance of those attaining age X (net reproductive rate R_0 = 1.0; average generation time = 7.0 months).

Age group	x (months)	n_x	l_x	d_x	q_x	m_x	$l_x m_x$	$x l_x m_x$	L_x	e_x
Neonates	0	92.5	1.000	0.708	0.7	0.0	0	0.0	0.645	1.644
Juvenile	5	27.0	0.292	0.022	0.1	0.0	0	0.0	0.281	1.480
Adults	7	25.0	0.270	0.270	1.0	3.7	1	7.0	0.135	1.000

3.02 years (Vinegar, 1975a), and *S. scalaris* from Durango has a generation time of 1.19 years (Ortega-Rubio et al., 2000). In Arizona, generation time for a low-elevation population of *S. jarrovi* was 1.86 years, 2.60 years for a high-elevation population in the Chiricahua Mountains (Ballinger, 1979), and 2.18 years for a population in the Pinaleño Mountains (Ruby and Dunham, 1984). Generation time of *S. graciosus* in southern Utah was 2.98 years (Tinkle, 1973), in *S. magister* from southern Utah, it was ca. 2.75 years (Tinkle, 1976), and *S. undulatus* from throughout its range varies from 1.15 to 2.4 years (Tinkle, 1972; Tinkle and Dunham, 1986; Jones and Ballinger, 1987; Parker, 1994).

Life History—Our population of *S. bicanthalis* tended to be among the smallest at maturity, highest in density, and with the shortest generation time of any *Sceloporus* that has been studied. Indeed, of those *Sceloporus* studied so far, our population is among the closest to an annual cycle, with only a few lizards (only one male) surviving >1 year. This life-history strategy is similar to the oviparous population of *S. aeneus* at 2,800 m in the state of Mexico (Rodríguez-Romero et al., 2004). To date, both phylogenetic sister species of *Sceloporus* show a semelparous life-history strategy, similar to other semelparous tetrapods as reported by Smith and Charnov (2001) for the desert woodrat, *Neotoma lepida,* in southwestern North America and by Karsten et al. (2008) for the chameleon, *Furcifer labordi,* in Madagascar. Both of these tetrapods inhabit environments that are hot, dry, or both. However, one difference between the studies of *Neotoma* and *Furcifer* and our own is that our population inhabits cooler mountains in the temperate zone. We suggest that not only tropical hyperarid and hot, or isolated, environments can mold semelparous life histories, but that semelparity also can occur at high-elevation zones in central Mexico (2,800–4,200 m; Rodríguez-Romero et al., 1999, 2002, 2004), at least in two temperate species of lizards.

These and previous data provide the groundwork for more studies that may reveal patterns regarding semelparous life-history strategies in vertebrates that inhabit environmentally extreme areas of the world, and provide insight into the role of semelparity in evolution of tetrapods. We suggest that the next step in evolutionary and comparative studies of reptilian life-history strategies is a mega-analysis using published studies of related species, incorporating new and recent phylogenies. This approach can uncover the adaptiveness of life-history strategies in extreme environments.

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