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3-28-2008

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### Recommended Citation

Gadsden, Héctor and Estrada-Rodríguez, José L. (2008) "Demography of the Yarrow's spiny lizard, *Sceloporus jarrovii*, from the central Chihuahuan Desert," *Western North American Naturalist*. Vol. 68 : No. 1 , Article 7.

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## DEMOGRAPHY OF THE YARROW'S SPINY LIZARD, *SCELOPORUS JARROVII*, FROM THE CENTRAL CHIHUAHUAN DESERT

Héctor Gadsden<sup>1</sup> and José L. Estrada-Rodríguez<sup>2</sup>

**ABSTRACT.**—The demography of a population of Yarrow's spiny lizard, *Sceloporus jarrovi*, was examined from 2004 to 2006 in the canyon Las Piedras Encimadas, located in Gomez Palacio, Durango, México. Lizards were studied using a mark-recapture technique. Reproduction in females occurred between November and May, coinciding with dry conditions. Reproductive activity was highest (percent of females with vitellogenic follicles or embryos) in the middle of the dry season (November and December). Thirteen percent of females reached sexual maturity at an average age of 8.5 months. The population structure was similar in spring and fall, but not in summer. A notable feature of summer, coinciding with the wet season, was the greater number of hatchlings and juveniles. The overall sex ratio did not differ from 1:1. The density of adults varied from 12 to 62 animals · 0.5 ha<sup>-1</sup>. Temperate and arid-adapted populations of *S. jarrovi* exhibited broad similarity in timing of the reproductive season, whereas factors such as density, growth, age at sexual maturity, and survivorship differed.

**Key words:** *Sceloporus jarrovi*, Mexico, demography, Chihuahuan Desert, reproductive cycle, population structure, density, life history.

**RESUMEN.**—La demografía de una población de la lagartija espinosa de Yarrow, *Sceloporus jarrovi*, fue examinada de 2004 a 2006 en el Cañón "Las Piedras Encimadas," localizado en Gómez Palacio, Durango, México. Las lagartijas fueron estudiadas usando la técnica de captura-recaptura. La reproducción en las hembras ocurrió entre Noviembre y Mayo coincidiendo con las condiciones de sequía. La actividad reproductora fue mas alta (% de hembras con folículos vitelogénicos o embriones) a mediados de la estación seca (Noviembre y Diciembre). Trece por ciento de las hembras alcanzaron la madurez sexual en un promedio de 8.5 meses de edad. La estructura de la población fue similar en primavera y otoño pero no en verano. Una característica notable de verano es el número mayor de crías y jóvenes, coincidiendo con la estación húmeda. El radio sexual global no difirió de 1:1. La densidad de adultos varió de 12 a 62 animales · 0.5 ha<sup>-1</sup>. Las poblaciones adaptadas a clima templado y árido de *S. jarrovi* exhiben una similitud amplia en el período reproductor, mientras que los factores como la densidad, crecimiento, edad a la madurez sexual, y sobrevivencia difieren.

**Palabras clave:** *Sceloporus jarrovi*, México, demografía, Chihuahuan Desert, ciclo reproductor, estructura poblacional, densidad, historia de vida.

Many studies have been conducted on lizard life histories, population dynamics, and demography (Turner 1977, Dunham 1982, Ballinger 1983, Stearns 1994, Niewiarowski 1994, Clobert et al. 1998). Some studies have compared such parameters between species (e.g., Tinkle et al. 1970, Ballinger 1973, Dunham 1980, 1981, James 1991) or between populations of the same species (e.g., Pianka 1970, Tinkle and Ballinger 1972, Parker and Pianka 1975, Ballinger 1979, Dunham 1982, Van Devender 1982, Niewiarowski and Roosenburg 1993, Lemos-Espinal and Ballinger 1995).

Stearns (1984) suggested that the primary cause of similarities in general life history strategy among reptiles is their phylogenetic relationship, particularly at the group level.

His most important conclusion was that the patterns of covariation within squamates were fundamentally a result of dissimilarity in female body length. Differences between snakes and lizards vanished when the influence of body size was controlled. Nevertheless, Dunham and Miles (1985) proposed that lizards and snakes vary significantly in fecundity and age at maturity, even after the means were adjusted for differences in body length. Thus, contrary to Stearns (1984), life history differences between lizards and snakes are real, and are only partially a consequence of differences in body size. Dunham et al. (1994) suggested that the similarities between lizards and snakes are not the result of common ancestry, but are more likely due to physiological constraints imposed by

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reproductive mode and number of times these organisms breed per reproductive season. They concluded that local adaptation, phylogenetic constraints, foraging type, and allometric covariation may all exert significant influences on the evolution of life history traits.

Wiens et al. (1999) showed that *Sceloporus jarrovi* is actually a group of 5 evolutionary species (*Sceloporus jarrovi*, *Sceloporus sugillatus*, *Sceloporus cyanostictus*, *Sceloporus oberon*, and *Sceloporus minor*). Although our knowledge of several aspects of the ecology and life history of *S. jarrovi* is extensive for populations north of the Rio Grande (Tinkle 1967, 1969, Goldberg 1971, Ballinger 1973, 1979, 1980, Tinkle and Hadley 1973, Simon 1975, Ruby 1986, Smith and Ballinger 1994a, 1994b, Smith et al. 1994), little is known about demography and life history in populations from the temperate and desert zones of northern México (Goldberg 1997, Ramírez-Bautista et al. 2002). The subject of our study is a population of *Sceloporus jarrovi* (in the narrowest sense) that inhabits the central Chihuahuan desert in northern México. We report reproduction, growth, age, population structure, density, survivorship, and life history attributes for this population of *S. jarrovi*.

#### METHODS

Fieldwork was conducted in the canyon Las Piedras Encimadas (25°38'47"N, 103°38'40"W) 25 km northwest of Gomez Palacio, Durango, México (1425 m). The climate of this region is seasonal, with the highest temperatures and rainfall occurring in summer. Mean annual precipitation is 239 mm and mean annual temperature is 21°C. The vegetation is dominated by *Agave lechuguilla*, *Acacia greggii*, *Yuca filifera*, *Fouquieria splendens*, *Opuntia rufida*, *Opuntia leptocaulis*, and *Jatropha dioica*. According to Rzedowski (1978), this habitat is classified as xerophyllous shrubland. Throughout the study site, rocks and rock faces with crevices are numerous.

#### Reproduction

We collected specimens of *S. jarrovi* between April 2004 and March 2005 from other areas (within several kilometers of the marked population) for analysis of their reproductive condition. Specimens were brought into the laboratory and autopsied within 24 hours. Spec-

imens were killed with Nembutal, preserved in 10% formalin (Gadsden and Palacios-Orona 1997, Gadsden et al. 2001), and deposited in the collection of the Universidad Juárez del Estado de Durango (voucher specimens UJED-ESB-SJ-1-51). We used the smallest females that showed vitellogenic follicles or embryos in the uterus to estimate the minimum size (snout-vent length) at sexual maturity (Ramírez-Bautista et al. 2002). Litter size was determined by counting the embryos in the oviducts of adult females during the reproductive season.

#### Population Structure and Dynamics

Adult lizards of *S. jarrovi* were caught by noosing or by hand in the spring (19–23 April 2004, 16–21 April 2005, and 22–28 April 2006), summer (12–16 July 2004, 9–15 July 2005, and 25–30 July 2006), and fall (18–22 October 2004, 15–21 October 2005, and 7–12 October 2006).

We located lizards on rocks or in rock crevices along a 300-m section of rocky hill comprising approximately 0.5 ha. The site searches followed a particular path that was relatively constant throughout the study. Field work was done between 09:00 and 14:00 every day (Ballinger 1973, Smith and Ballinger 1994a). On each sampling date the lizards were caught by the same 3 people.

Each individual was permanently marked by toe-clipping, and a number was painted on its back for quick identification. For each capture, the following data were recorded: date, time of day, sex, and snout-vent length (SVL) measured to the nearest 1 mm with a ruler. In addition, the abdomens of females were carefully palpated to determine whether embryos were present. Lizards were released at the exact point of capture (Ballinger 1973, Dunham 1982, Van Devender 1982, James 1991).

Growth data were obtained through periodic recapture of animals of known age. The ages of lizards within a certain size class were estimated using growth rates and SVL at hatching. These data allowed construction of average growth trajectories for males and females (Tinkle and Dunham 1986).

Growth rate was estimated as follows:

$$GR = (SVL_2 - SVL_1) / \text{number of days},$$

where the growth rate ( $GR$ ,  $\text{mm} \cdot \text{day}^{-1}$ ) is the change in body length, which is the difference

between the 2nd ( $SVL_2$ ) and 1st ( $SVL_1$ ) lengths divided by the number of days between captures (Zúñiga-Vega et al. 2005).

To account for the fact that growth generally decreases with increasing SVL in reptiles (Andrews 1982), we divided lizards into 5 SVL size classes (class 1: hatchlings 24–35 mm; class 2: juveniles 36–47 mm; class 3: subadults 48–59 mm; class 4: adults 60–70 mm [ $<13$  months]; class 5: old adults 71–81 mm [ $>13$  months]) using 12-mm SVL intervals (Grant and Dunham 1990, Sexton et al. 1992). The significance of variation in growth rate among these different SVL size classes was assessed using ANOVA, followed by Duncan's new multiple range test (Bruning and Kintz 1977, Sokal and Rohlf 1981). Means are given with 1 standard error.

The SVL at initial capture of all individual lizards was used to determine the population structure (Griffiths 1999, Ramírez-Bautista et al. 2002). Sex ratio was based on these data.

The density of individual adult *S. jarrovi* was estimated using the small-sample Lincoln-Petersen and Schumacher-Eschmeyer methods (Krebs 1989). The Lincoln-Petersen method is based on a single episode of marking lizards and a 2nd single episode of recapturing individuals. The basic procedure is to mark a number of individuals over a short time, release them, and then recapture individuals to check for marks. For this method to be valid, the 2nd sample must be a random sample; that is, marked and unmarked individuals must have the same chance of being captured in the 2nd sample. The Schumacher-Eschmeyer method distinguishes only 2 types of individuals: marked (caught in 1 or more prior samples) and unmarked (never caught previously). Seber (1982) recommends the Schumacher-Eschmeyer estimator as the most robust and useful method for multiple censuses on closed populations. Ballinger (1973) and Ruby (1986) noted that individual *S. jarrovi* were regularly observed as being restricted to small areas, and the centers of activity were situated near specific crevices located in the dwelling habitat. Consequently, the possibility of migration or immigration of individuals in this population was reduced.

Survivorship ( $l_x$ ) was calculated as the proportion of individuals marked in 1 season that were recaptured the following year in the same season. Survivorship may be underestimated,

however, because some lizards may not have been recaptured, despite having survived (Smith and Ballinger 1994b).

A life table for the *S. jarrovi* population was constructed from data on age-specific fecundity ( $m_x$ ), age-specific survivorship ( $l_x$ ), and age at 1st breeding. Age classes were chosen to correspond to selected events in the life of the lizards. The 1st age class is composed of female eggs (a 1:1 sex ratio at fertilization was assumed), and subsequent age classes represent lizard ages at the approximate midpoint of successive reproductive seasons (Tinkle and Ballinger 1972, Stearns 1994).

Fecundity values ( $m_x$ ) for each age class were determined from clutch size and clutch frequency data and were adjusted to account for the proportion of females of each age that were actually reproductive.

Because of the small number of hatchlings marked, it was not possible to estimate numbers of eggs or survivorship for hatchlings. However, appropriate survivorship data can be obtained from the ratios of age class in this population, if we assume that the population has maintained a stationary age distribution. The analysis ignored year-to-year changes in age structure, and it utilized the average age composition over 3 years to obtain survivorship figures that permitted construction of a life table (Tinkle and Ballinger 1972, Stearns 1994).

## RESULTS

### Reproduction

Body size (SVL) of adult females averaged 68.3 mm ( $s_{\bar{x}} = 0.74$ , range 60–81 mm,  $n = 51$ ). The mean SVL of gravid females was 68.5 mm ( $s_{\bar{x}} = 1.3$ ,  $n = 16$ ). Gravid females represented 53% of all sexually mature females caught during the reproductive season ( $n = 30$ ). Reproductive activity in females (Fig. 1) began in November and declined in early May, with embryos present from January to May. Hatchlings were observed from May to July, a period when most of the annual precipitation occurred and food was abundant. All of the 14 females collected from February to April had embryos in utero. The embryonic developmental period was estimated from the date at which the 1st female was found with freshly ovulated eggs in utero (mid-January) to the date when the 1st neonate was found (late May). These data suggest a gestation period of about 133 days.

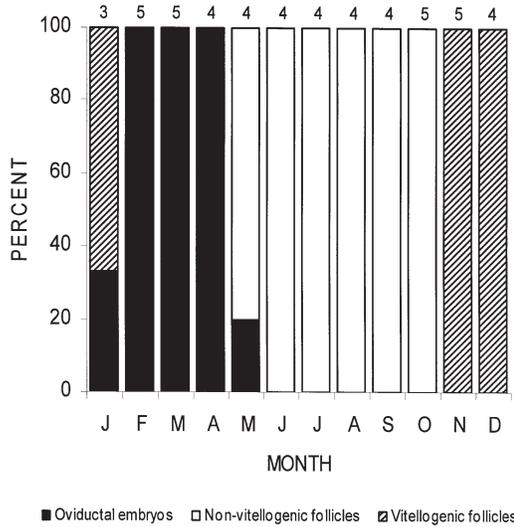


Fig. 1. Percentage of *Sceloporus jarrovi* in various reproductive stages in each month of the year. Sample sizes appear above the bars.

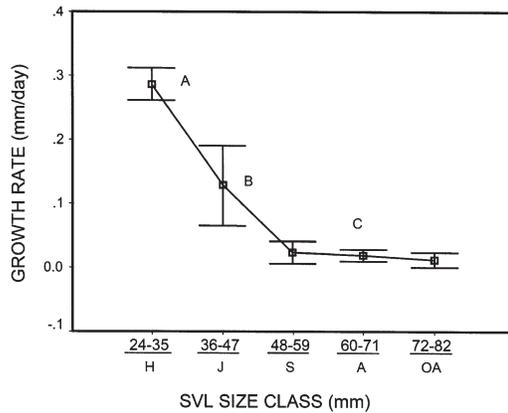


Fig. 2. Variation in growth rate within SVL size classes of the lizard *Sceloporus jarrovi*. Bars represent 1 standard error. Values having different capital letters are significantly different (Duncan's new multiple range test:  $P < 0.001$ ). H = hatchlings ( $n = 12$ ), J = juveniles ( $n = 5$ ), S = subadults ( $n = 3$ ), A = adults ( $n = 23$ ), and OA = old adults ( $n = 8$ ).

Population Structure and Dynamics

The relationship between SVL size classes and average growth rate for Yarrow's spiny lizard is illustrated in Figure 2. Growth rates were calculated over a mean of 197 days ( $s_{\bar{x}} = 19.6$ ,  $n = 38$  individuals). Growth was significantly faster (ANOVA:  $F_{4,46} = 181.2$ ,  $P =$

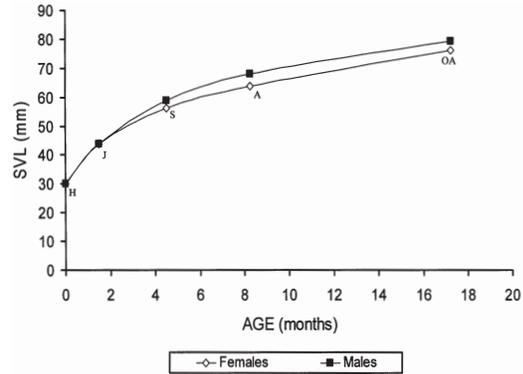


Fig. 3. Growth curves for the *Sceloporus jarrovi* population. Abscissa shows age since hatching; ordinate shows SVL. Closed squares and open rhombs represent means. H = hatchlings ( $n = 12$ ), J = juveniles ( $n = 5$ ), S = subadults ( $n = 3$ ), A = adults ( $n = 23$ ), and OA = old adults ( $n = 8$ ).

0.00001) in hatchlings (SVL < 36 mm;  $\bar{x} = 0.29$  mm · day<sup>-1</sup>,  $s_{\bar{x}} = 0.01$ ,  $n = 12$ ) than in juveniles ( $\bar{x} = 0.12$  mm · day<sup>-1</sup>,  $s_{\bar{x}} = 0.03$ ,  $n = 5$ ), subadults ( $\bar{x} = 0.02$  mm · day<sup>-1</sup>,  $s_{\bar{x}} = 0.008$ ,  $n = 3$ ), adults ( $\bar{x} = 0.01$  mm · day<sup>-1</sup>,  $s_{\bar{x}} = 0.004$ ,  $n = 23$ ), and old adults ( $\bar{x} = 0.01$  mm · day<sup>-1</sup>,  $s_{\bar{x}} = 0.005$ ,  $n = 8$ ). Males did not differ from females (ANCOVA: slopes,  $F_{1,29} = 0.261$ ,  $P = 0.772$ ; intercepts,  $F_{1,30} = 0.958$ ,  $P = 0.336$ ); their growth rate began to decrease at approximately 70 mm SVL.

By knowing the earliest date of hatchling emergence, the mean growth rate of individuals in different size classes, and the date of capture, it is possible to estimate the age of an individual. Based on the mean growth rate of hatchlings, juveniles, and subadults, individuals of both sexes reached the adult size class (60 mm SVL) at an average age of 8.5 months. The SVL of adults at the end of year 1 ranged between 63 mm and 70 mm, based on the mean growth rate of the young adult size class. Males and females showed an asymptote at 75 mm, at an age of approximately 1 year and 6 months (Fig. 3).

An adult male was captured in April 2004 (SVL = 69 mm) and recaptured in October 2005 (SVL = 80 mm). Given that it takes males 1 year to reach an SVL of 70 mm, the individual was approximately 2.5 years old. An adult female was captured in April 2004 (SVL = 75 mm) and recaptured in July 2006 (SVL = 77 mm). The approximate minimum age of this

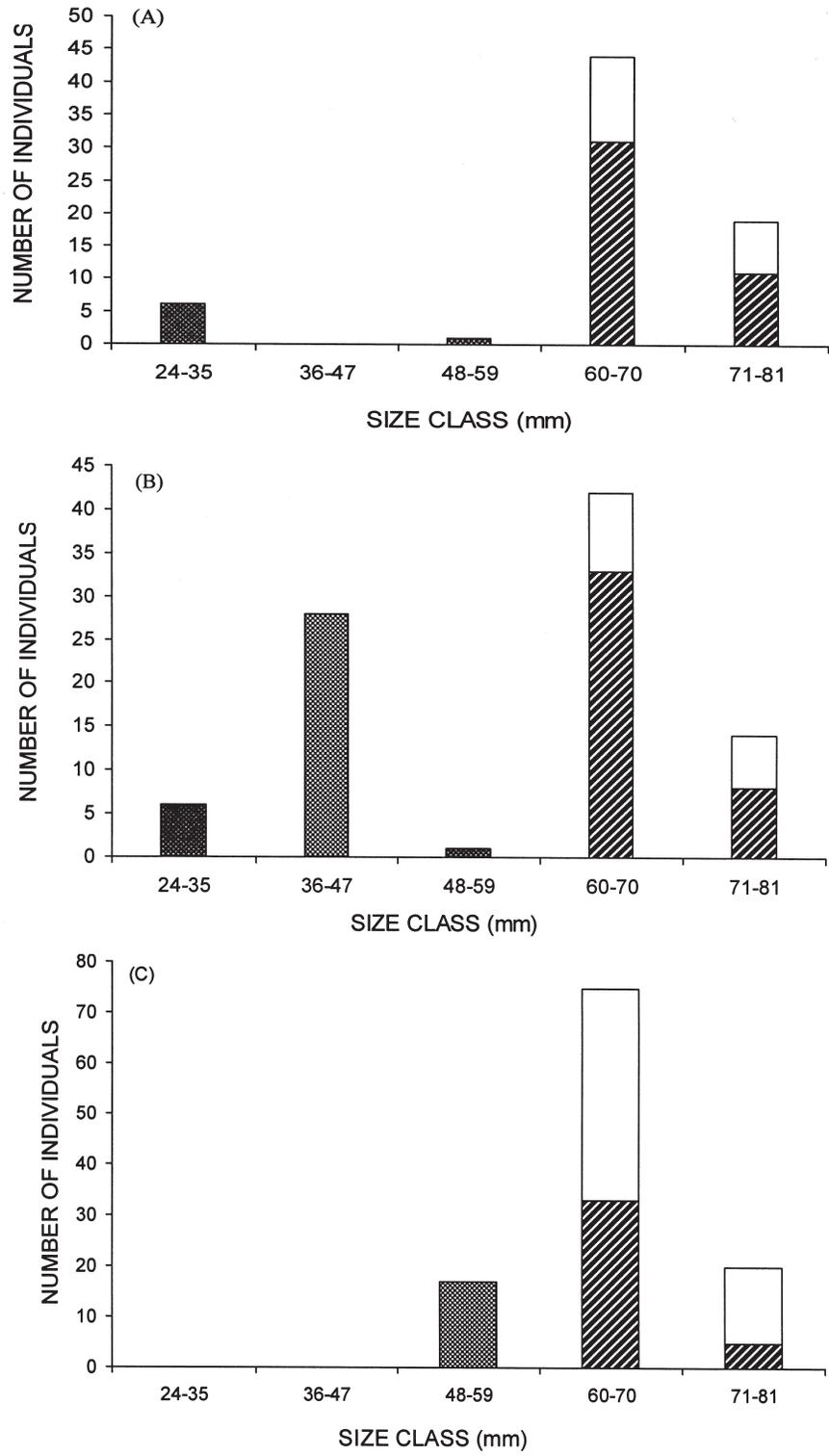


Fig. 4. Number of individuals in different size classes in spring (A), summer (B), and fall (C). Open bars represent males; lined bars represent females; and hatched bars represent hatchlings, juveniles, and subadults.

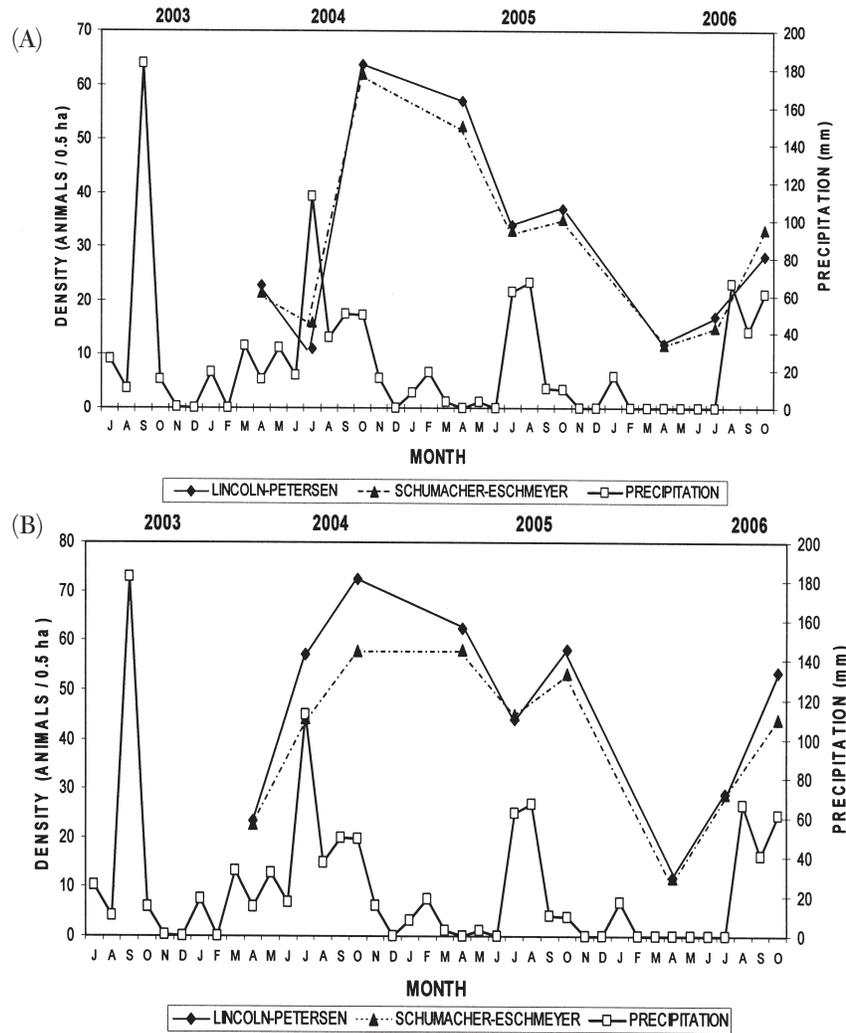


Fig. 5. Seasonal density (Lincoln-Petersen and Schumacher-Eschmeyer estimators) of *Sceloporus jarrovi* throughout a 3-year period and monthly precipitation for the study area (Las Piedras Encimadas, Durango, México): A, adults; B, all age classes.

female was 3.8 years, given that it takes females 1 year and 5 months to reach an SVL of 75 mm.

The population structure of *S. jarrovi* (Fig. 4) was similar in spring and fall but not in summer ( $\chi^2 = 89.5$ ,  $df = 8$ ,  $P < 0.005$ ). A notable feature of summer is the presence of hatchlings and juveniles. The relative number of adult females and males (SVL  $\geq 60$  mm) did not differ significantly among the 3 years ( $\chi^2 = 3.2$ ,  $df = 2$ ,  $P > 0.1$ ). Lizards in the 60–70 mm SVL size class were the most numerous in spring and fall.

The sex ratio (males:females) was heavily biased toward females in spring and summer

(0.5 and 0.37, respectively). During fall, the sex ratio of adult individuals became biased toward males (1.5). Nevertheless, the overall sex ratio (3 seasons pooled) was 0.77 (93 males: 121 females), which is not different from 1:1 ( $\chi^2 = 3.6$ ,  $P > 0.05$ ).

The densities (Schumacher-Eschmeyer) of adult *S. jarrovi* (Fig. 5a) in spring, summer, and fall (2004) were 21.6 animals  $\cdot$  0.5 ha $^{-1}$ , 15.9 animals  $\cdot$  0.5 ha $^{-1}$ , and 62.0 animals  $\cdot$  0.5 ha $^{-1}$ , respectively. Prior to the fall season in 2004, the amount of precipitation was irregular, although uninterrupted. The densities in spring, summer, and fall (2005) were 52.5 animals  $\cdot$  0.5 ha $^{-1}$ ,

TABLE 1. Survivorship ( $l_x$ ) of *Sceloporus jarrovi* from "Las Piedras Encimadas," Durango, México. Total survivorship values are weighted means. M = males, F = females,  $l_x$  = proportion of class surviving from 1 year to the following year,  $n$  = number of captured lizards in the age class.

Year	Season	All	Adults			Subadults			Juveniles			Hatchlings		
			M	F	Total	M	F	Total	M	F	Total	M	F	Total
2004/2005														
Spring														
	$l_x$	0.12	0.20	0.07	0.11	—	0	0	—	—	—	0	0.33	0.17
	$n$	26	5	14	19	—	1	1	—	—	—	3	3	6
Summer														
	$l_x$	0.15	0	0.25	0.17	—	0	0	0.21	0	0.15	—	—	—
	$n$	33	4	8	12	—	1	1	14	6	20	—	—	—
Fall														
	$l_x$	0.17	0.12	0.14	0.13	0	1	0.67	—	—	—	—	—	—
	$n$	42	25	14	39	1	2	3	—	—	—	—	—	—
2005/2006														
Spring														
	$l_x$	0.03	0	0.05	0.03	—	—	—	—	—	—	—	—	—
	$n$	34	13	21	34	—	—	—	—	—	—	—	—	—
Summer														
	$l_x$	0.09	0.00	0.14	0.11	—	—	—	—	—	—	0	0	0
	$n$	34	7	21	28	—	—	—	—	—	—	3	3	6
Fall														
	$l_x$	0.14	0.09	0.20	0.12	0	0.25	0.20	—	—	—	—	—	—
	$n$	43	23	10	33	2	8	10	—	—	—	—	—	—

TABLE 2. Number and proportions of each age class of *Sceloporus jarrovi* captured in "Las Piedras Encimadas," Durango, México, over a 3-year period.

Age class (months)	Sex	2004		2005		2006	
		$n$	Proportion	$n$	Proportion	$n$	Proportion
8.4	Male	9	0.26	20	0.47	4	0.25
	Female	16	0.44	30	0.58	14	0.42
13.4	Male	13	0.38	10	0.23	8	0.50
	Female	12	0.33	12	0.23	13	0.39
18.4	Male	5	0.15	7	0.16	2	0.13
	Female	5	0.14	10	0.19	5	0.15
23.4	Male	7	0.21	6	0.14	2	0.13
	Female	3	0.08	0	0	1	0.03
TOTAL			70		95		49

TABLE 3. Life table for the Durango population of *Sceloporus jarrovi* (see text for discussion of survivorship data);  $x$  = age class,  $m_x$  = number of female eggs produced by each adult female in each reproductive season,  $l_x$  = survivorship from 1st age class to midpoint of age class over which  $m_x$  is measured,  $R_0$  = replacement rate per generation<sup>a</sup>.

$x$	$l_x$	$m_x$	$l_x m_x$
0	1.00	0	0
8.4	0.17	2.0	0.34
13.4	0.15	3.0	0.45
18.4	0.06	3.2	0.19
23.4	0.04	3.4	0.14

<sup>a</sup> $R_0 = 1.12$

33.1 animals  $\cdot$  0.5 ha<sup>-1</sup>, and 35.1 animals  $\cdot$  0.5 ha<sup>-1</sup>, respectively. Prior to fall 2005, precipitation was rare during winter and spring and

increased in summer. The densities in spring, summer, and fall (2006) were 11.8 animals  $\cdot$  0.5 ha<sup>-1</sup>, 15.0 animals  $\cdot$  0.5 ha<sup>-1</sup>, and 33.3 animals  $\cdot$  0.5 ha<sup>-1</sup>, respectively. Prior to fall 2006, precipitation was almost 0 during winter, spring, and early summer, and increased in midsummer. Lincoln-Petersen estimates of *S. jarrovi* mimic those of the Schumacher-Eschmeyer method.

The density of individuals in all age classes (Fig. 5b) showed similar fluctuations, except in summer 2004, due to an abundance of juveniles in that season of the year. We observed predominantly adult recruitment in fall 2004, which increased the adult density significantly.

Estimates of survivorship ( $l_x$ ), population size, and age-class structure are given in Table

TABLE 4. Reproductive and demographic characteristics of different populations of *Sceloporus jarrovi* in its distribution range in the United States and México. SVL, MMS = snout-vent length minimum and maximum at sexual maturity. Means are presented with 1 standard error. TH = Tinkle and Hadley 1973; Ba = Ballinger 1973; SBa = Smith and Ballinger 1994a; SB = Smith and Ballinger 1994b, 1994c; R = Ruby 1978; R-B = Ramirez-Bautista et al. 2002; CO = Goldberg 1997.

Variables	Durango	Arizona	Chiricahua	Chiricahua	Chiricahua	Pinaleño	México	Chiricahua	Chiricahua	Morelos
	1425	1500-2500	1675	1675	1675	1825	2500	2500	2542-2670	3050
Elevation (m)										
Females										
SVL (mm)	68.3 ± 0.7 (51)	71.8 (52)	64.3 ± 1.02 (64)	—	—	—	70.7 ± 0.97 (62)	≥70 (7)	65.8 ± 0.5 (645)	65.3 ± 3.2 (4)
SVL MMS	60-81	55-94	60-90	—	—	1 year	60-86	70-90	—	62-68
Sexual maturity	6 months	—	5 months	—	—	—	—	1 year	—	—
Vitellogenesis	Nov-Jan	Oct-Nov	Oct-Feb	—	—	—	Aug-Nov	—	—	Aug-Nov
Ovulation	December	November	December	—	—	—	December	—	—	Nov-Dec
Gestation time	Jan-May	Feb-Apr	Mar-Jun	—	—	—	Jan-Apr	—	—	Dec- <sup>2</sup>
Males and Females										
Density (individuals · 0.5 ha <sup>-1</sup> )	20-40	—	—	16-36	—	37-48	—	—	74-115	—
Growth rates (mm · d <sup>-1</sup> )	0.09	—	—	0.12	—	—	—	—	0.16	—
Annual survivorship ( <i>l</i> <sub>x</sub> )	0.11 ± 0.02	—	0.36	—	—	—	—	0.45	0.15 ± 0.08	—
Sex ratio	0.77	—	0.76	—	—	0.62	—	0.87	—	—
Source	This study	TH	Ba	SBa	—	R	R-B	Ba	SB	CO <sup>a</sup>

<sup>a</sup>Actually *Sceloporus sugillatus* (see Wiens et al. 1989).

1. For the 2 annual periods (2004/2005 and 2005/2006), mean  $l_x$  for the entire population was 0.12 ( $s_{\bar{x}} = 0.02$ ) (adults only:  $\bar{x} = 0.11$ ,  $s_{\bar{x}} = 0.01$ ; subadults only:  $\bar{x} = 0.21$ ,  $s_{\bar{x}} = 0.15$ ; hatchlings only:  $\bar{x} = 0.08$ ,  $s_{\bar{x}} = 0.08$ ). For spring and summer (2004/2005), hatchlings and juveniles had the highest survivorship followed by adults and then subadults. In fall (2004/2005 and 2005/2006) subadults had the highest survivorship followed by adults. During 2005/2006, subadults had a higher survivorship than during 2004/2005.

The numbers and proportions of each age class (Table 2) captured over a 3-year period (2004–2006) permitted the generation of survivorship figures and the construction of a life table (Table 3). The calculated replacement rate ( $R_0 = 1.12$ ) for this population indicates that this population is able to maintain a stable population size given the survivorship and fecundity schedules that we have calculated. In this population, about 40% of the replacement rate is attributable to individuals around 1 year old, and 30% is attributable to individuals <1 year old.

## DISCUSSION

### Reproduction

The reproductive season for *S. jarrovi* in Las Piedras Encimadas, Durango, México, begins after the rains commence in July–September and continues during the driest months, until May. Fall reproduction permits females to give birth in midspring when food is abundant, as occurs in species of the *torquatus* group (Ballinger 1973, 1977, Fitch 1978, Ramírez-Bautista et al. 2002). A reproductive cycle that peaks in the fall is similar to that previously reported for this species (Ballinger 1973, Ramírez-Bautista et al. 2002; see Table 4). Nevertheless, the known differences in reproductive traits among populations of *S. jarrovi* reveal local adaptations (Ramírez-Bautista et al. 2002).

The smallest female *S. jarrovi* at our site probably reaches early sexual maturity at approximately 6 months of age. Likewise, data available for other female *S. jarrovi* from the low altitudes (1675 m) showed that females matured in the 1st mating season after birth at an age of approximately 5 months (Ballinger 1973). Ramírez-Bautista et al. (2002) and Ballinger (1973) estimated size at sexual maturity

of *S. jarrovi* females to be 60 mm. At high elevation (2500 m), sexual maturity is not attained in the 1st mating season after birth (Ballinger 1973). The body size of high-elevation females (SVL  $\geq 70$  mm) is considerably larger than that of females in this study.

### Population Structure and Dynamics

Growth in reptiles is influenced by both phylogenetic and environmental factors (Andrews 1982). *Sceloporus jarrovi* exhibits differences in growth rates among populations, related to rainfall and food availability (Smith and Ballinger 1994a), but still conforms to a generalized model of reptilian growth. Smith and Ballinger (1994a) studied 2 high-altitude *S. jarrovi* populations (2542 m and 2670 m, respectively), which had higher growth rates ( $0.16 \text{ mm} \cdot \text{d}^{-1}$  in both populations) than a low-altitude (1675 m) population ( $0.12 \text{ mm} \cdot \text{d}^{-1}$ ; see Smith and Ballinger 1994a). In Las Piedras Encimadas the mean growth rate for *S. jarrovi* was  $0.09 \text{ mm} \cdot \text{d}^{-1}$ . According to Ballinger (1979), transplant experiments showed some evidence for a genetic basis for these growth rate differences. However, evidence from a common garden experiment suggests that neonates from high-altitude parents grow at the same or slower rates than their low-altitude counterparts (Smith et al. 1994). Nevertheless, little information exists for direct comparisons of growth rates with other species within the *jarrovi* group.

Few population density data exist for *S. jarrovi*. Smith and Ballinger (1994a) found greater *S. jarrovi* densities in high-elevation populations ( $74\text{--}115$  lizards  $\cdot 0.5 \text{ ha}^{-1}$ ) than in a low-elevation population ( $16\text{--}36$  lizards  $\cdot 0.5 \text{ ha}^{-1}$ ). The density of adult *S. jarrovi* in Las Piedras Encimadas was similar to that in the low-elevation population, fluctuating between 20 and 40 lizards  $\cdot 0.5 \text{ ha}^{-1}$ , suggesting that, if any relationship between density and individual growth does exist, it is not inversely density dependent, as is usually assumed and observed (Scott 1990). In fact, lizard density is influenced by a complex variety of factors, including availability of food resources and thermal environment (Rose 1982, Christian and Tracy 1985, Sinervo 1990).

The density of adult *S. jarrovi* was higher in fall 2004 compared to the previous seasons and subsequent 2 years (Fig. 4). This large increase may be due to higher adult recruitment

in fall 2004 in response to previous supranormal precipitation. Whitford and Creusere (1977) suggested that the density of most lizard species varies directly with changes in productivity and relative abundance of arthropods. Likewise, the availability of insect prey changes according to the distribution and amount of rain throughout the year (Maury 1995).

Mean survivorship values ( $l_x$ ) obtained in this study (Table 1) for the entire population and for adults were lower than rates observed in high-elevation populations of *S. jarrovi* (Ballinger 1973, 1979, 1980, Smith and Ballinger 1994b). A drought during winter and spring 2005 (i.e., January–June; Fig. 4a) reduced the availability of insect prey. In Las Piedras Encimadas, lizards showed an abrupt prey shift in winter, eating many more ants and fewer other insects (Quezada-Rivera 2007). Reduction in food abundance affects food utilization in *S. jarrovi* (Ballinger and Ballinger 1979, Simon and Middendorf 1985) but apparently does not affect reproductive potential (Ballinger 1979). Thus, limited prey availability may not explain lower survivorship during 2005/2006. Consequently, in this study we do not know the specific proximate factors that produced this population reduction.

The life history characteristics of this population deviate from the expectation of Tinkle et al. (1970). These life history characteristics are similar to those of another low-elevation *S. jarrovi* population (Ballinger 1973). In our study, approximately 30% of the females mature in their 1st reproductive season. Without this early maturity, the replacement rate under the estimated survivorship schedules would not allow the stable pattern currently observed. Smith and Ballinger (1994b) report greater *S. jarrovi* survivorship at high elevations. Previously, Ballinger (1973) speculated (1) that survivorship in a high-elevation population of *S. jarrovi* must be greater because of delayed maturity of at high elevations and (2) that intraspecific variation exists in life history characteristics similar to that observed in other lizard species.

Further studies on other evolutionary species within the *jarrovi* group in Mexico (*S. jarrovi*, *S. sugillatus*, *S. cyanostictus*, *S. oberon*, and *S. minor*) are needed to further define the life-history relationships in this diverse group. Likewise, intraspecific comparisons of *S. jarrovi* from dissimilar geographic and climatic loca-

tions (temperate and arid) would increase the understanding of differing environmental conditions and their influence on the life history of Yarrow's spiny lizard. These studies will need to report sound data on temperature, moisture, predator pressure, and food availability, all of which potentially affect life history parameters in lizards.

#### ACKNOWLEDGMENTS

This study was supported by SEP-CONACYT grant 43142-Q. We thank S.V. Leyva-Pacheco and J.R. Estrada-Arellano for field assistance. O. Hinojosa de la Garza gave H. Gadsden support and encouragement throughout data analysis and manuscript preparation. Permit SEMARNAP-SGPA/DGVS/06193.

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Received 18 December 2006  
Accepted 14 September 2007