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BUNCH GRASS LIZARD, *SCELOPORUS SCALARIS*, POPULATION DYNAMICS AT LA MICHILIA BIOSPHERE RESERVE, MEXICO

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We studied the population dynamics of *Sceloporus scalaris* from 1979 to 1982 using mark-recapture methods. The estimated population density was 50 adults per hectare. The sex ratio was approximately 1:1, with females slightly predominating at older ages. Based on morphological data, four well-differentiated age classes were established - juveniles, sub-adults, adults <1yr and adults >1 yr. The mean clutch size was 8.8 eggs per female, but varied widely (5 to 12) in relation to female body size. The estimated number of hatchlings in 10 hectares was 2245 and embryo mortality was 13.89%. After hatching, the average mortality was higher than 76% for all ages and both sexes. The population life table indicates a Slobodkin Type IV survivorship curve, with a net reproductive rate of 1.059. The average generation time for this population was 1.2 years.

Key words: lizard, Mexico, population dynamics, *Sceloporus scalaris*

INTRODUCTION

The bunch grass lizard, *Sceloporus scalaris* Wiegmann, is a very common and abundant Mexican lizard distributed in 22 states in Mexico and the south-western United States of America (USA) (Smith, 1939). Despite its broad distribution in Mexico, most of the studies of this species have been done in the USA (Ballinger & Congdon, 1980, 1981; Bock, Smith & Bock, 1990; Smith, Ballinger & Congdon, 1993; Mathies & Andrews, 1995). Also, most of the previous studies have concerned only taxonomic (Smith & Poglayen, 1958; Stebbins, 1966; Anderson, 1972; Smith & Hall, 1974; Thomas & Dixon, 1976; Van Devender & Lowe 1977; Mink & Sites 1996) and reproductive (Stebbins, 1954; Anderson, 1962; Greene, 1970; Smith & Hall, 1974; Newlin, 1976) aspects of this species. There has been only one previous study dealing with the population dynamics of this species, and it was done in the United States (Ballinger & Congdon, 1981). The lack of recent literature pertaining to *S. scalaris* does not allow us to discuss our results in the light of more up-to-date findings.

The accurate establishment of population attributes, such as age at maturity, age specific fecundity, mortality and survivorship, is a basic requirement for understanding the evolutionary adaptations of any population (Barbault, 1975; Vinegar, 1975; Andrews & Wright, 1994; Smith, 1996). Research has attempted to establish the evolutionary patterns that outline the demographic attributes of populations (Tinkle, 1969; Tinkle, Wilbur & Tilley, 1970; Ballinger, 1973; Parker & Pianka, 1975; Barbault, 1975, 1981). However, to achieve an accurate evaluation of evolutionary theories in population demography and dynamics, it is necessary to develop much more detailed studies comparing as many populations as possible. The purpose of this work was to study the main attributes and dynamics of one population of this species in north-west Mexico.

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MATERIALS AND METHODS

The study site, La Michilía Biosphere Reserve, is in the state of Durango, México, between 104° 20' and 104° 07' W, and 23° 20' and 23° 30' N. The climate is temperate with a mean annual temperature ranging between 17.4 °C and 20.7 °C, and a mean annual precipitation of 567 mm, with most rain occurring during the summer. Vegetation of the zone is typically highly diversified oak-pine forest, with 207 plant species of which 18 are *Quercus* species and 10 are *Pinus* species (Martínez & Saldivar, 1978).

A study plot measuring 500 x 1000 m was marked with stakes every 10 m and censused over 4 years during the following months: October 1979, May 1980, April and September 1982, and every month in 1981. Each of the visits lasted 15 days. Three people walking slowly in parallel looked at the soil and vegetation in the zone, in the search for lizards, for 4 to 7 hr per day. Censuses were made during 50 minute random searches of the plot. Each census started from a different randomized location within the transect, to avoid bias caused by the alteration of lizard activity over the course of the day. For each lizard observed, we recorded its location in relation to distance and bearing from the nearest stake. We then captured the individual by hand. Captured individuals were marked both by toe clipping and by paint code, and the following data were recorded: sex, snout-vent length, tail length and body mass. Body lengths were measured to the nearest 0.1 mm with metal calipers (Scala 222) and body mass was measured to the nearest 0.1 g using a Pesola spring balance.

Density

Using only the last three days of capture-recapture data, density was calculated using the Petersen index (Bailey, 1952; Caughley, 1977). Monthly adult density results thus obtained were analysed by month with the Analysis of Variance test (ANOVA; Sokal & Rohlf, 1969) followed by the Tukey-Kramer procedure (Sokal & Rohlf, 1969).

Population Structure

Lizards were classified by sex and age group from morphological data. Because most of the *S. scalaris* individuals are born over a period of only 15 days, for both clutches, classification by age group can be easily accomplished using the SVL short cohort period data. Differences in secondary sexual morphology between males and females, such as ventral and belly colour patches in males, were evident from a very early age, so the sex ratio was easily determined.

Natality

Natality was determined using the average fecundity estimates for resident females and the estimates of female numbers by age class. To estimate the average fecundity of resident females, we autopsied 120 gravid females from outside the study plot (Ortega & Barbault, 1986). The relationship of clutch size to female body size for these females was used to estimate clutch size for females in the study plot.

TABLE 1. Average density (number of individuals per hectare) of *Sceloporus scalaris* calculated for each visit to the study site. The average corresponds to the density calculated during the last three days of each sampling period ± SD.

Month	Year	No. adults	No. subadults
October	1979	10±2	-
May	1980	34±8	-
January	1981	29±5	123±18
February	1981	47±6	107±21
March	1981	76±12	15±3
April	1981	91±24	-
May	1981	85±19	-
June	1981	58±9	-
July	1981	38±18	-
August	1981	42±9	1±0.4
September	1981	19±3	4±1
October	1981	40±4	222±26
November	1981	30±5	195±21
December	1981	42±3	180±14
April	1982	128±17	-
September	1982	-	-

Tail Autotomy

To calculate the proportion, by age class, of individuals with tail losses, every collected lizard was carefully examined in the search for any indication of tail breakage and regeneration. We did not count individuals whose tail loss was caused by our manipulation.

Mortality and Survivorship

Mortality rate was estimated by analysing the recapture data for marked individuals of each age class. After a specific period, we estimated the number of missing individuals. This estimate, determined for each age class, was equated to mortality. Prenatal or embryonic mortality was determined by counting the number of atrophic eggs found in the oviducts of autopsied females, and by contrasting the number of corpora lutea in the ovaries with the total number of eggs found in the oviducts. By integrating the specific fecundity for each sex and age group with age-specific mortality and survival, we generated the *S. scalaris* population life table.

RESULTS

Density

Table 1 shows the average density (per hectare) calculated for each working field visit. The estimated densities for 1981 vary widely from one season to another, and even from month to month. ANOVA results indicate that there are highly significant differences between the months ($F_{11,24}$=8.727; P<0.001). The Tukey-Kramer procedure shows there are two well-differentiated groups of months, according to their density values: March, April and May were the months with the highest density (P<0.01), and September, November and January were those with the lowest densities (P<0.01).

Population Structure

In accordance with our classification of age class and sex, and using the morphological characteristics of the individuals, we differentiated four age-groups for *Sceloporus scalaris* at La Michilía Biosphere Reserve (Fig. 1). For the first clutch there were: (1) juveniles, younger than 3 months, with SVL<38 mm for males and <31 mm for females; (2) subadults, 3 to 7 months, with SVL 38.1 to 51 mm for males and 31.1 to 46 mm for females; (3) adults I, 7 to 12 months old and reaching sexual maturity, with SVL size 51.1 to 55 mm for males and 46.1 to 54.5 mm for females. The second clutch contained: (1) juveniles, younger than 3 months, with SVL <38 mm for males and <34 mm for females; (2) subadults, 3 to 5.5 months, with SVL 38.1 to 47 mm for males and 34.1 to 45 mm for females; (3) adults I, 5.5 to 12 months old and reaching sexual maturity, with SVL size 47.1 to 51 mm for males and 45.1 to 50.5

mm for females. For both clutches, (4) the adults II were older than one year, reaching a maximum size of 62 mm SVL for both males and females. It was not possible to determine from size alone whether the individual was 2, 3 or 4 years old.

Table 2 shows numbers estimated (derived from the density estimates) for each age and sex group for 10 hectares throughout the year. The juveniles appear during late August and their numbers increase rapidly, reaching a maximum in October. The juvenile phase ended in January and was replaced in February by the subadult, which declined during March, being replaced by the adult I group. The adult I group showed a slow decline from March to September. Males and females older than one year reached their maximum density during February and their minimum during September.

Table 2 also makes possible the determination of the sex ratio within each of the different age groups throughout the year. At the younger ages, the ratio is almost 1:1. However, for the older ages there is a tendency for females to be more abundant during the summer months, but this tendency is not statistically significant (χ^2= 15.226; df =11; P<0.05). Overall, females make up 55.16% of the population.

NATALITY

From the autopsied females (Ortega & Barbault, 1986), it was established that the average clutch size for *S. scalaris* females and for both clutches was 8.79 (SE = 1.96) eggs per female. Clutch size varied widely from female to female, ranging from 5 to 12 eggs, depending on female SVL. There exists a strong relationship between body size and clutch size (y=0.4281x-14.0325; r=0.822; P<0.05; Ortega & Barbault, 1986). To calculate natality, the female numbers by age class were multiplied by the average clutch size. The estimated number of *S. scalaris* hatched in 10 hectares was 2245 (Table 3). Younger females from the second clutch do not produce a second clutch themselves. This demographic characteristic is significant, because shorter and younger females must wait until their second reproductive season to produce two clutches.

TAIL AUTOTOMY

Tail autotomy rates increase with age. The average values for tail autotomy were: juveniles 9.10%, subadults 11.05%, adults I 39.01% and adults II 50.25%. The minimum average value of caudal autotomy is observed during December, and the maximum during July.

MORTALITY AND SURVIVAL

From the 120 autopsies performed on females during the reproductive seasons, only 25 atrophic eggs were found from a total of 180 oviductal eggs; thus the percentage of embryo failure was relatively low (13.89%), suggesting a low rate of mortality before egg laying (Table 4). The average mortality of individuals estimated by mark-recapture methods over a year was greater than 76% for all age groups and both sexes (Table 4). The minimum mortality occurred amongst juveniles, and the maximum value was for adults II, females.

The *Sceloporus scalaris* population life table (Table 5) indicates a Slobodkin (1962) Type IV survivorship

TABLE 2. Demographic structure for the 1981 population of *S. scalaris* at La Michilía; mean number of individuals (±SD) is calculated for 10 hectares.

	Juveniles	Male subadults	Female subadults	Male adults I	Female adults I	Male adults II	Female adults II
Jan	355±42	402±82	492±45	-	-	154±34	136±28
Feb	-	568±75	497±68	-	-	242±16	232±16
Mar	-	73±23	73±18	339±58	339±123	36±7	49±5
Apr	-	-	-	339±79	310±42	121±31	142±21
May	-	-	-	277±18	298±62	158±123	118±32
Jun	-	-	-	167±39	201±35	36±5	175±22
Jul	-	-	-	118±24	154±21	26±6	81±7
Aug	10±3	-	-	83±7	127±7	127±13	83±12
Sep	41±12	-	-	60±18	85±12	10±25	38±6
Oct	2216±270	-	-	-	-	187±32	213±15
Nov	1954±183	-	-	-	-	150±27	160±22
Dec	1763±207	30±16	20±7	-	-	171±32	249±35
Total	6319	1073	1082	1383	1514	1418	1686

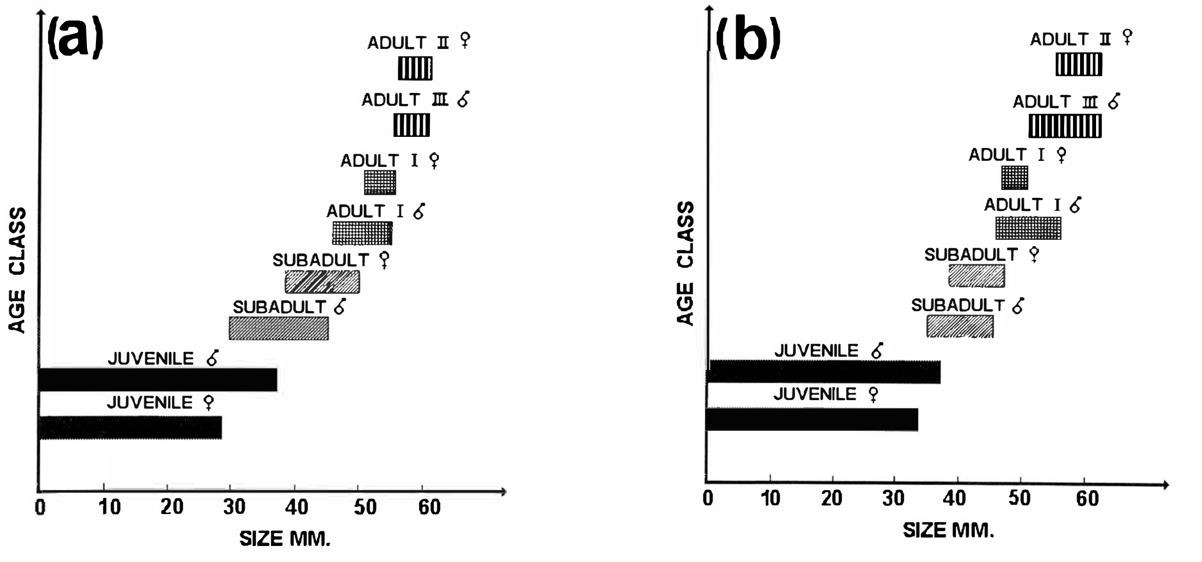

FIG 1. Snout-vent graphs illustrating cohort groupings in La Michilia *S. scalaris* population. (a) First clutch cohort; (b) second clutch cohort.

curve as described by Deevey (1947). The highest mortality occurs in the younger age groups. The population replacement rate (R_0) is 1.059 and the average generation period is 1.19 years.

DISCUSSION

DENSITY

Densities of most common lizard species vary from 10 to 100 adults per hectare (Barbault, 1975) and, according to the calculations of Turner (1977), the average density for lizards is around 51 per hectare. The density for *S. scalaris* at La Michilía (50 per ha) is close to the general average. Ballinger & Congdon (1981), studying a *S. scalaris* population of this species in Arizona, found an adult density of 140 individuals per hectare at the beginning of the summer.

The density found in Arizona is considerably higher than the values found at La Michilía. However, even higher variability occurs in the density figures for different populations of the same lizard species (Darevskij & Terentev, 1967; Grenot, 1976; Pilorge , 1981).

POPULATION STRUCTURE

The age structure of a particular population depends on the length of the hatching period and on the individual's average longevity (Barbault, 1975). *S. scalaris* has a discontinuous, short and well-defined reproductive season (Type II of Barbault, 1975), and it is also relatively short-lived, similar to several temperate and tropical lizard species (Barbault, 1973; 1976). The combination of the two variables, short breeding periods and reduced longevity, determines the age structure observed in the *S. scalaris* population at La Michilía. Age groups were clearly defined, showing the highest density in the groups of juveniles and adults I. In the population studied by Ballinger & Congdon (1981), these authors only provided the composition of the resident individuals for the month of June and only for two age classes, yearlings and adults. The average numbers of individuals per hectare reported by Ballinger and Congdon (1981) were 40 yearling males, 50 yearling females, 20 adult males and 40 adult females. All these numbers are considerably above our estimates for the month of June (Table 2).

TABLE 3. Estimated number of *S. scalaris* hatchlings (mean±SD) produced for both clutches. * = females of the second clutch.

Females	No. in 10 ha	Mean size (mm)	Mean clutch size	Hatchlings produced
Adults I	154±34	47.69±38	6.38±102	983
Adults II	81±7	57.55±5.54	10.60±2.45	859
Adults I*	85±7	46.05±3.07	0	0
Adults II*	38±5	57.55±6.12	10.60±2.07	403

TABLE 4. Mortality and survival percentages of *S. scalaris* individuals.

Class	Mortality	Survival
Embryo	13.89	86.11
Juveniles	76.88	23.12
Male adult	83.82	16.18
Female adult I	82.08	17.92
Male adult II	90.07	9.93
Female adult II	91.29	8.41

The *Sceloporus scalaris* sex ratio at hatching is effectively 1:1, similar to most other lizard species (Barbault, 1975) - with the exception of the very distinctive parthenogenetic species or subspecies (Grassé, 1970). With increasing age, it is common to observe a change in sex ratio, usually in favour of the females (Hirth, 1963; Barbault, 1974), but in some cases favouring the males (Alcala, 1966; Turner, Lannom, Medica & Hoddenbach, 1969). In other cases, numerical equality between males and females (Brooks, 1967; Telford, 1969) remains constant, as is the case with *S. scalaris* at La Michilía (average 54.25% females). In Arizona (Ballinger & Congdon,1981), females also outnumbered males from slightly up to as much as 2:1.

NATALITY

Comparing the average clutch size of the La Michilía *S. scalaris* population (8.79) with other *S. scalaris* populations, we found that the females of La Michilía are only a little more prolific than those studied in Arizona by Newlin (1976; average clutch size 8.38) and Ballinger & Congdon (1981; average clutch size 8.52). At La Michilía the average size of females (54.82±3.88 mm) is slightly larger than the body size of *S. scalaris* females from Arizona (52.36±4.19 mm, Newlin, 1976; 53.62±4.49 mm, Ballinger & Congdon, 1981). However, there are no significant differences between female sizes in La Michilía and in Arizona (t= 0.43, t= 0.02 respectively).

However, the clutch size found at La Michilia is below the clutch size for two *S. scalaris* populations studied by Mathies & Andrews (1995), also in Arizona: 9.4 and 11.2 eggs. In these cases the differences found cannot be explained purely on the basis of female body size; the average female body size for the populations studied by Mathies and Andrews (1995) was smaller than at La Michilia (46.9 and 52.8 mm).

Females of three of the four Arizona *S. scalaris* populations (Newlin, 1976; Ballinger and Congdon, 1981; Mathies and Andrews, 1995) only produce one clutch, whereas 40% of the La Michilía lizard females produce a second clutch (Ortega & Barbault, 1986). An undetermined percentage of females in one of the four Arizona populations also produced a second clutch (Mathies & Andrews, 1995).

MORTALITY AND SURVIVAL

Prenatal mortality varies widely among lizard populations, ranging from less than 5% (Ballinger, 1971) to 90% (Blair, 1960; Barbault, 1973). *Sceloporus scalaris* pre-natal mortality values at La Michilia (13.9%) are similar to the hatchling failure rate found in one Arizona population (12.7%; Ballinger & Congdon, 1981). Pre-natal mortality values at La Michilia are relatively low compared to the most common values found for lizards (40% to 60%; Brooks, 1967; Tinkle, 1969; Barbault, 1974). *S. scalaris* juvenile mortality at La Michilia (76.8%) was close to the values found for the Arizona population (68.7%; Ballinger & Congdon, 1981), and both values were close to the average values found for all lizards (Zweifel & Lowe, 1966; Barbault, 1975). *S. scalaris* adult mortality at La Michilia (86.9%) was greater than the value found in Arizona (74.1%; Ballinger & Congdon, 1981) and close to that of lizard species with high mortality rates (Barbault, 1975).

At La Michilía there were many potential predators of *S. scalaris*, including (Ortega, 1986) 11 bird species, 7 mammal species and 8 reptile species. However, there are no accurate records of the efficiency of these predators in relation to this lizard population. For this

TABLE 5. Life table for the *S. scalaris* population at the Michilía biosphere reserve. x=age in years; l_x= age specific survival proportion; d_x=proportion of the original population death in the age interval; q_x= age specific proportional mortality; m_x=age specific fecundity; $l_x m_x$= age x individual contribution to the net reproductive rate (R_o). R_o=1.059

Age class	x	l_x	d_x	q_x	m_x	$l_x m_x$	$x(l_x m_x)$
Eggs	0	1.0	0.139	0.139	--	--	--
Juveniles	0.17	0.861	0.662	0.769	--	--	--
Adults I	0.67	0.199	0.163	0.820	3.19	0.635	0.425
Adults II	1.67	0.036	0.033	0.916	10.60	0.381	0.637
Adults II	2.67	0.003	0.002	0.916	10.60	0.032	0.085
Adults II	3.67	0.001	0.001	1.000	10.60	0.011	0.039

reason, we cannot accurately discern whether the estimated mortality rates are the result of predator attacks.

The *S. scalaris* population at La Michilía Biosphere Reserve had a replacement rate of 1.059, with an average generation period of 1.19 years. In Arizona, the population studied by Ballinger & Congdon (1981) shows a replacement rate of 1.859, which explained the population increase observed in the area (Ballinger & Congdon, 1981). In Arizona (Ballinger & Congdon, 1981), approximately 44% of the lifetime fertility is the result of the first reproductive year; at La Michilia this value is almost 60%.

This study represents the first contribution, developed in Mexico, to the knowledge of the main population attributes and dynamics of a very common Mexican lizard.

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