

# Life history of the Marbled Whiptail Lizard *Aspidoscelis marmorata* from the central Chihuahuan Desert, Mexico

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**Abstract.** The life history of a population of marbled whiptail lizard, *Aspidoscelis marmorata*, was examined from 1989 to 1994 in the sand dunes of the Biosphere Reserve of Mapimí, in Northern México. Lizards were studied using mark-recapture techniques. Reproduction in females occurred between May and August, with birth hatchlings matching the wet season in August. Reproductive activity was highest in the early wet season (July). Males and females reached adult size class at an average age of 1.7 years and 1.8 years, respectively. Body size of males attained an asymptote around 90 mm snout-vent length and females around 82 mm snout-vent length, at an age of approximately 3.6 years and 3.0 years, respectively. The density varied from 7 to 85 individuals / 1.0 ha. The Mexican population had late maturity, relatively long life expectancy, and fewer offspring. Overall, the observed data for *A. marmorata* and the expectations of life history theory for a late maturing species (K-rate selection) are in agreement.

**Keywords.** *Aspidoscelis marmorata*, lizard, Mexico, life history, reproductive cycle, Chihuahuan Desert.

## INTRODUCTION

Four life history traits (age of maturity, clutch size, reproductive effort, and longevity) are used regularly to segregate populations into one of two states generally recognizing but ignoring that a continuum exists between these two. The contrasting states are: short-lived populations characterized by individuals with short lives, early sexual maturity, large broods, and high annual reproductive effort; and long-lived populations characterized by individuals with long lives, delayed sexual maturity, small broods, and low annual reproduction effort. Life history theory provides two opposing models for the evolution of these two population types. The deterministic model postulates that high levels of density-independent mortality result in fluctuating population density, which favors a high intrinsic growth rate ( $r$ ) and produces short-lived populations. In the stochastic model (optimization), high

density-independent mortality produces variable, and usually low, juvenile survivorship, which favors a stable and long-lived adult population. The conflict arises from the generality of the models and their attempt to explain life-histories evolution of diverse organisms (Zug, 1993).

Life history studies within discrete taxonomic groups (e.g., Tinkle et al., 1970; Ballinger, 1973; Dunham, 1980, 1981; James, 1991; Chapple, 2003; Sears and Angilletta Jr., 2004, Mata-Silva et al., 2008, 2010) and among conspecific populations (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, 2000; Niewiarowski et al., 2004; Du et al., 2005; Rojas-González et al., 2008) have been somewhat more successful in revealing the relationships among life-history traits and different environmental regimes. Even in these cases, difficulties are encountered that make conclusions less

robust than desirable. A major difficulty is the discrimination between a trait's variation arising from selection pressures for individuals to adapt to their present habitat / location and variation resulting from a proximate response to current disturbance in local conditions. Awareness of the difficulties in the data and interpretation promotes caution but does not deny the evolution of life-history patterns (Zug, 1993). Life history of a species can be summarized by demographic parameters such as rates of birth and death, migratory movement, and structure of populations through time, as they deal with the interaction between longevity, reproductive age, growth, and age-specific mortality versus the environment (Zug, 1993; Stearns, 2000). Interactions among these parameters through life make demographics of populations subject to constant variation through time. The demography of lizard populations can be influenced by various environmental factors, such as temperature (Adolph and Porter, 1993; Parker, 1994), precipitation (Andrews, 1988; Bull, 1994), food availability (Ballinger, 1977; Howland, 1992; Smith, 1996), as well as morphological and phylogenetic constraints (Ballinger, 1983; Stearns, 1984; Dunham and Miles, 1985).

Some life history patterns can be singled out relating the dynamics and structure of populations (Tinkle, 1969a, Stearns, 2000). For example, lizards with delayed sexual maturity tend to have longer life cycles, along with major energetic investments in maintenance instead of reproduction (Tinkle, 1969a; Tinkle et al., 1970), and lower adult mortality (Hasegawa, 1990; Bull, 1995). Lizards with early sexual maturity have shorter life cycles and higher mortality rates for the young and adults (Ballinger and Congdon, 1981; Andrews and Nichols, 1990), resulting in a higher rate of population turnover (Ferguson et al., 1980; Tinkle et al., 1993). This dichotomy represents the extremes of a life-history gradient, but many intermediate combinations exist (Dunham et al., 1994; Stearns, 2000). The population structure can also be influenced by the mating system. Populations with higher incidence of polygyny tend to have higher male death rates than populations where polygyny is reduced (Schoener and Schoener, 1980; Stamps, 1983), generating a female biased sex-ratio. Life history theory was developed mainly from data of temperate lizard species in the United States (Pianka, 1970; Ballinger, 1983), nevertheless in the vast desert regions of northern Mexico, which has a rich diversity of lizards, long-term studies of life history, population structure and dynamics are limited (e.g., Gadsden et al., 1995; Gadsden et al., 2001b; Gadsden and Estrada-Rodriguez, 2007).

Here we study the life-history of a population of *Aspidoscelis marmorata* from the central Chihuahuan Desert in northern Mexico (Hendricks and Dixon, 1986;

Dixon, 2009). Although there is extensive knowledge of several aspects of the ecology and life history of *A. tigris* from its northern arid distribution (Turner et al., 1969; Pianka, 1970; Parker, 1972; Asplund, 1974; Vitt and Ohmart, 1977; Mitchell, 1979; Hendricks and Dixon, 1984; Anderson, 1994; Sullivan, 2009), little is known about demography and life history of *A. marmorata* from the desert zones of northern México (Gadsden et al., 1995; Díaz-Gómez, 2009; Dixon, 2009; Mata-Silva et al., 2008, 2010).

Herein we identify seasonal patterns of variation in population size, age structure, sex ratio, growth, reproduction, survivorship, and life history attributes of the lizard *A. marmorata* in the central Chihuahuan Desert, and make comparisons with other populations of the same species and *A. tigris*, to evaluate predictions of life history theory.

## MATERIALS AND METHODS

### Study Area

We conducted field work in a 1 ha study plot (26°52'N, 103°32'W) within the Mapimian subprovince of the Chihuahuan Desert in the Mapimí Biosphere Reserve, Chihuahua, Mexico (1250 m elev.) (Barbault and Halffer, 1981). The study plot was gridded with wooden stakes placed 20 m apart over an area of about 100 × 100 m. Data from this study plot were used in the evaluation of demographic characteristics of this population. The habitat was sandy dune, and the vegetation is dominated by desert thornscrub of *Acacia constricta*, *Acacia gregii*, *Larrea tridentata*, *Yucca elata*, and *Lycium berlandieri* (Breimer, 1985).

The climate of this region is seasonal and receives monsoon summer rains, with the highest temperature and rainfall occurring in June through September. Temperatures range from an average winter low of 3.9 °C to an average summer high of 36.1 °C. Mean annual precipitation is 230 mm, but variation between years is high (Cornet, 1988).

### Reproductive Analysis

During 1990 we collected monthly samples of *A. marmorata* from other sand dunes (within several kilometers to the marked population) for analysis of reproductive condition. These were brought into the laboratory and necropsied within 24 h. In total we collected 48 female specimens by noosing or shot with BB rifles, euthanized with Nembutal, preserved in 10% formalin (Gadsden and Palacios-Orona, 1997; Gadsden et al., 2001a), and deposited the samples in the collection of Instituto de Ecología, A. C. (voucher specimens-Inecol-CT-1-48). We used the smallest females that showed vitellogenic follicles or oviductal eggs to estimate the minimum snout-vent length (SVL) at sexual maturity (Ramírez-Bautista and Vitt, 1997). We recorded number of non-vitellogenic follicles, vitellogenic follicles and oviductal eggs

for females. We determined litter size by counting oviductal eggs of adult females during reproductive season.

#### Population Structure and Dynamics

In the staked study plot we caught individual lizards of *A. marmorata* using pitfall cans (100 traps of two gallons volume each one) and funnel traps in spring (4-8 May 1989, 6-12 May 1990, 20-27 Apr. 1991, 13-21 May 1992, 8-11 May 1993, and 20-24 Apr. 1994), summer (11-17 Sep. 1989, 7-16 Jul. 1990, 15-23 Jul. 1991, 21-25 Aug. 1992, 18-22 Jul. 1993, and 21-24 Sep. 1994), and fall (4-14 Nov. 1989, 27-30 Oct. and 1-3 Nov. 1990, 3-11 Nov. 1991, 13-17 Nov. 1992, 10-16 Nov. 1993, and 1-5 Dec. 1994). Traps were checked every day in the morning during different periods of study and were removed after each sampling period.

Each individual was permanently marked by toe-clipping, and a number was painted on the back for quick identification (Tinkle, 1967). 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, abdomens of females were carefully palpated to determine whether oviductal eggs were present. Once data was acquired, lizards were released immediately at the exact point of capture (James, 1991).

In order to increase recapture data with individuals previously marked on the back, the site searches followed a standardized procedure. On each sampling date, each person (3 people) chose one row of quadrants (100 × 20 m) and walked slowly across the entire area remaining at all times between two rows of stakes (Tinkle, 1967; Howland, 1992). Each bush and other hiding places were disturbed when necessary to locate and capture each lizard. Field work was conducted between 9:00 and 14:00 h every day.

We recorded SVL, weight and sex for marked and recaptured lizards and estimated the growth curves of females and males. The changes in length ( $dSVL$ ) and time intervals ( $dT$ ) were used to estimate body growth rates ( $GR = dSVL/dT$ ). Data were analyzed considering the following recapture time interval > 60 and < 460 days. Additionally, averages of growth and snout-vent length of lizards recaptured more than once were used to estimate rates of growth representative of the population. Average length during the interval for each lizard (mean snout-vent length) was the average of the first and last snout-vent length observed for each. We used the von Bertalanffy model to evaluate growth rate of *A. marmorata* (von Bertalanffy, 1951, 1957; Fabens, 1965; Lemos-Espinal et al., 2005). This model predicts that growth rate will be maximal for small body size (juveniles) and will

decrease as the size increases (Lemos-Espinal and Ballinger, 1995) following the linear function:

$$GR = a - b\text{MeanSVL} \quad (1)$$

where  $a$  is the initial growth rate and  $b$  is the decrease coefficient.  $\text{MeanSVL}$  is used instead of original size because growth is measured over a limited period and may overestimate the  $GR$  for initial SVL (Van Devender, 1978).

Asymptotic size is predicted as  $Z = -a/b$ . Equation (1) can be expressed as follows:

$$a - b\text{MeanSVL} = a [1 - \text{SVL}/Z]$$

which is the derivation of Fabens (1965) of differential equation model of von Bertalanffy growth. Knowing the size of lizards at birth ( $SVL_0$ ), and using the  $Z$  and  $b$  values obtained from  $GR = a - b\text{MeanSVL}$ , the growth curve can be obtained from:

$$SVL = Z (1 - ke^{-bT})$$

where SVL is length reached by a lizard after a time  $T$  (from birth),  $k$  is a constant that can be calculated if  $SVL_0$  is known, and  $T$  is the number of days elapsed (age of lizard). The estimate of  $k$  is performed as follows:

$$k = 1 - SVL_0/Z$$

We used the following Fabens (1965) equation to estimate SVL of a lizard at time  $t + d$  ( $SVL_2$ ) in terms of the SVL at time  $t$  ( $SVL_1$ ):

$$SVL_2 = Z - (Z - SVL_1) e^{-bd}$$

where  $d$  is the time interval for growth.

To test how well this model fits the real growth of *A. marmorata*, lizards of known age were compared with sizes predicted by the model. Linear regressions were used to determine the relationship between  $GR$  and SVL. The regressions were calculated separately for each sex and were compared using analysis of covariance (ANCOVA), using SVL as a covariate. For all statistical analysis we used only one observation per individual, which was selected at random. All values are given as means  $\pm 1$  SE.

Densities were estimated from lizards caught in pitfall cans and from visual sightings. We estimated seasonal density (1989-1991) using Jolly-Seber method (Jolly, 1965; Seber, 1982) for open populations; therefore we did not need to assume the absence of recruitment and mortality. The estimation of population size was obtained from the simple relationship:

Population size = Size of marked population / Proportion of lizards marked.

Random sampling becomes the crucial assumption, and we assume that: 1) Every individual has the same probability ( $\alpha_t$ ) of being caught in the  $t$ th sample, where it is marked or unmarked. The critical assumption of equal catchability was tested for Leslie, Chitty, and Chitty Test of Equal Catchability (Leslie et al., 1953). 2) Every marked individual has the same probability of survivorship ( $\phi_t$ ) from the  $t$ th to the  $(t + 1)$ st sample. 3) Individuals do not lose their marks, and marks are not overlooked at capture. 4) Sampling time is negligible in relation to intervals between samples.

Density estimates using Jolly-Seber method did not include data for period 1992-1994. The population abundance of this species declined dramatically during this last period (likely due to a prolonged regional drought) and the data were not suitable for this method.

## RESULTS

### Reproductive Cycle

Body size (SVL) of adult females averaged 78.2 mm (SE = 0.62, range 70-90 mm,  $n = 48$ ). The mean SVL of gravid females was 80.0 mm (SE = 0.84,  $n = 9$ ). Gravid females represented 28% of all sexually mature females caught during the reproductive season ( $n = 32$ ). Reproductive activity in females (Fig. 1) began in May and declined in middle Aug., with oviductal eggs present

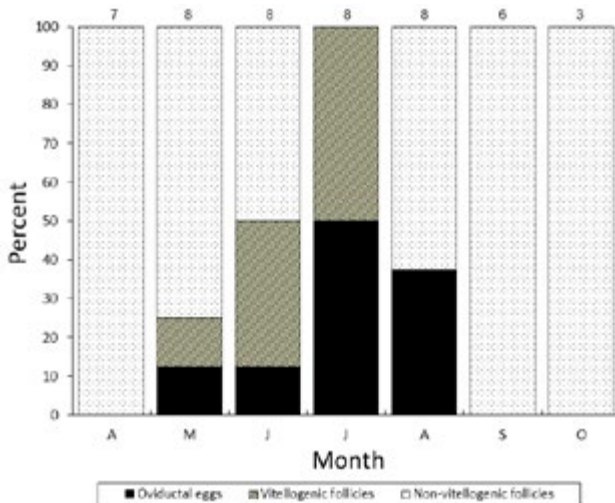


Fig. 1. Percentage of *Aspidoscelis marmorata* in various reproductive stages in each month of the year. Sample sizes appear above bars.

from May to August. We observed hatchlings from Aug. to Sep., when most of the annual precipitation occurred and food was abundant. In Jul. and Aug., 50% and 38% of females respectively had eggs in utero. The embryonic developmental period was estimated from the date at which the first female had freshly ovulated eggs in utero (early-May) to when the first hatchling was found (late-Aug.). These data suggest a gestation of ca. 75 days and incubation was ca. 45 days.

### Morphometric Data Field

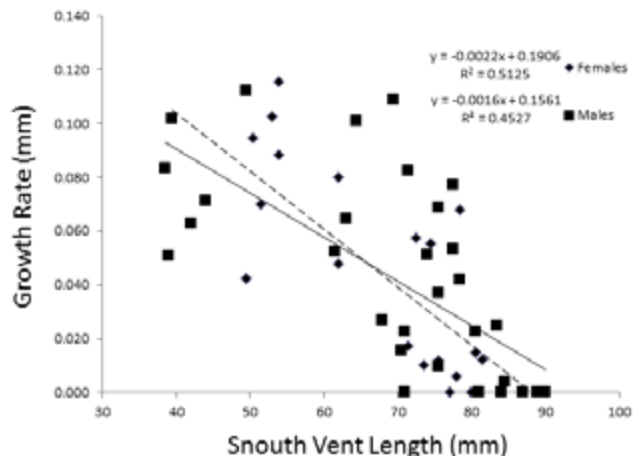
Mean SVL in adult males was 80.95 mm (SE = 0.73, range 70-92 mm,  $n = 70$ ) and in adult females was 76.80 mm (SE = 0.70, range 70-90 mm,  $n = 36$ ). Average body mass of males was 14.67 g (SE = 0.42, range, 8.0-26.5 g,  $n = 69$ ) and in females was 12.00 g (SE = 0.53, range 8.0-22.00 g,  $n = 36$ ). Based on comparisons of males and females, males attained a significantly greater SVL and body mass than females ( $F_{1, 105} = 13.29$ ,  $P < 0.0001$  and  $F_{1, 104} = 14.49$ ,  $P < 0.0001$ , respectively).

### Population Structure and Dynamics

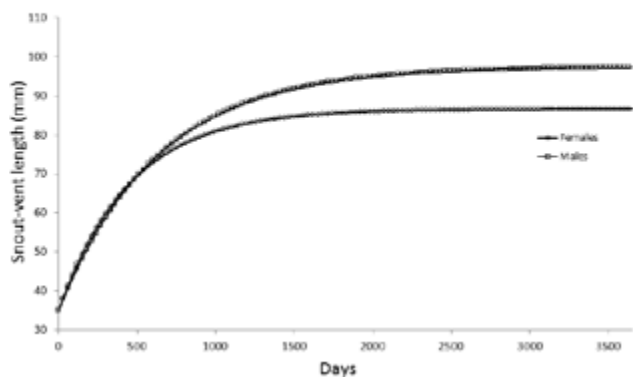
Growth was significantly higher (ANOVA,  $F_{4, 82} = 19.6$ ,  $P < 0.0001$ ) in juveniles and subadults ( $x = 0.12 \pm 0.01$  mm  $\times$  day $^{-1}$ ,  $n = 13$  and  $x = 0.10 \pm 0.01$  mm  $\times$  day $^{-1}$ ,  $n = 22$ , respectively) than hatchlings ( $x = 0.06 \pm 0.01$  mm  $\times$  day $^{-1}$ ,  $n = 5$ ), adults ( $x = 0.02 \pm 0.003$  mm  $\times$  day $^{-1}$ ,  $n = 36$ ), and old adults ( $x = 0.005 \pm 0.003$  mm  $\times$  day $^{-1}$ ,  $n = 7$ ). Females grew faster than males ( $0.046 \pm 0.008$  mm/day and  $0.040 \pm 0.006$  mm/day, respectively), however this difference is not significant (ANCOVA  $F_{1, 52} = 0.012$ ,  $P = 0.91$ ). The growth rate decreased significantly with respect to SVL ( $F_{1, 52} = 45.09$ ,  $P < 0.0001$ ), suggesting a growth curve of von Bertalanffy type. Growth rates varied inversely with the average SVL for males and females (Fig. 2).

The values used to estimate constants of the growth curves were the same for females and males, corresponding to an SVL of 37.9 mm, with an estimated age of 30.0 days. Using these constants in the equation of Fabens (1965), provides longevity for females of approximately 3.0 yr and 3.6 yr for males, at an SVL of 82 mm and 90 mm, respectively (Fig. 3). Longevity for males larger than 90 mm and females larger than 82 mm was very high and may not be representing reality.

The age of an individual can be estimated from data on the earliest date of hatchling emergence, the mean growth rate of individuals in different size classes, and the date of capture. Based on the growth curves of both sexes

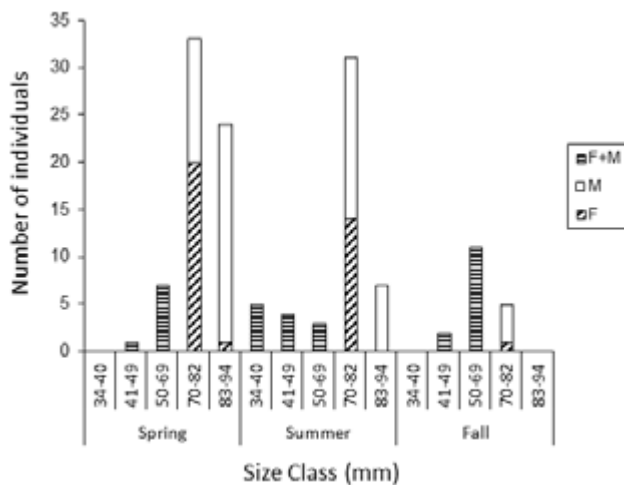


**Fig. 2.** Growth in males and females of the lizard *Aspidoscelis marmorata* in Mapimi, Durango. Each point represents the body growth rate per day which has a given average SVL.



**Fig. 3.** Growth curves of von Bertalanffy model for females and males of the lizard *Aspidoscelis marmorata* in Mapimi, Durango. Abscissa shows age (days); ordinate shows SVL (mm). Estimated from the equation of Fabens (1965), with an initial SVL = 37.9 mm vs. 30 days old. The values used were  $a = -0.0022$  and  $b = 0.190$  for females, and  $a = -0.0016$  and  $b = 0.156$  for males. Open rectangles and open diamonds represent means.

es, males reached the adult size class around 76 mm SVL and females around 75 mm SVL, at an average age of 1.7 yr and 1.8 yr, respectively. Comparing this estimate with the data obtained from the reproduction data (i.e., the data obtained from 1990), the smallest sexually mature female with oviductal eggs was 75 mm SVL, whereas the smallest male measured with enlarged testes was 74 mm SVL. Body size of males attained an asymptote around of 90 mm SVL and females around of 82 mm SVL, at an age of approximately 3.6 yr and 3.0 yr, respectively (Fig. 3).



**Fig. 4.** Number of individuals of *Aspidoscelis marmorata* in different size classes in spring, summer, and fall. 34-40 mm = Hatchlings, 41-49 mm = Juveniles, 50-69 mm = Subadults, 70-82 mm = Adults, and 83-94 mm = Old adults. Open bar represents adult males; diagonal-lined bar represents adult females; and horizontal lines represent females and males of hatchlings, juveniles, and subadults.

The population structure of *A. marmorata* (Fig. 4) in spring and fall were similar but not in summer ( $\chi^2 = 50.44$ ,  $df = 8$ ,  $P < 0.005$ ). A notable feature of summer is the presence of hatchlings and juveniles. The relative number of adult females and males (SVL  $\geq 70$  mm) did not differ significantly among the six years ( $\chi^2 = 1.19$ ,  $df = 5$ ,  $P > 0.25$ ). Lizards in the 70-82 mm SVL size class were the most numerous in spring and summer.

The seasonal sex ratio (1989-1994 pooled) was heavily biased toward males in spring, summer and fall (1.7, 1.6 and 4.0, respectively). In fact, the overall sex ratio (3 seasons pooled) was 1.75 (63 males and 36 females), which is significantly different from 1:1 ( $\chi^2 = 7.3$ ,  $df = 1$ ,  $P = 0.0068$ ).

The mean density in summer, fall, and spring (1989-1991) of *A. marmorata* (Table 1) was 32.0 animals/1.0 ha (SE = 7.5, range 24.5-39.6,  $n = 2$ ), 40.6 animals/1.0 ha (SE = 19.3, range 21.3-60.0,  $n = 2$ ), and 46.0 animals/1.0 ha (SE = 39.1, range 6.9-85.1,  $n = 2$ ), respectively. The mean total density (summer, fall, and spring combined) was 39.5 animals/1.0 ha (SE = 11.7, range 6.9-85.1,  $n = 6$ ). Relationship existed between precipitation and density ( $r = 0.82$ ,  $P < 0.04$ ,  $n = 6$ ). Seasonal density estimates did not include data for the period 1992-1994. The abundance of this population declined dramatically during this last period probably caused by a prolonged regional drought.

Estimates of probability of survival ( $\emptyset$ ) from sample time  $t$  to sample time  $t + 1$  (Table 1) indicated higher survival in 1989 than in other years. We estimated the total

**Table 1.** Population estimates by used of Jolly-Seber model of population estimation. Seasonal samples (1989-1991) of *Aspidoscelis marmorata* from Mapimí Biosphere Reserve, Chihuahua, Mexico. SP=Spring, SU=Summer, FA=Fall.

Population sample	Proportion marked ( $\alpha$ )	Total number (N)	Probability of survival ( $\phi$ )	SE N	SE $\phi$
SP-1989	0.00	0.0	0.38	-	0.09
SU-1989	0.57	24.5	0.98	5.4	0.52
FA-1989	0.53	60.0	0.90	24.7	0.62
SP-1990	0.47	85.1	0.27	48.0	0.19
SU-1990	0.36	39.6	0.28	21.2	0.28
FA-1990	0.40	21.3	0.47	20.5	0.47
SP-1991	0.80	6.9	-	4.8	-
SU-1991	0.33	-	-	-	-

number of new additions to the marked population that were made at sampling  $t$  (called  $Z'_t$ ). Thus, over this period (1989-1991) we observed a total of 47 new individuals entering the marked population and we predicted ( $Z'_t$  values) a total of nine new individuals, and a 19% underestimate. This result is probably biased, and it suggests unequal catchability for the animals within the marked population. This sort of bias could arise if socially dominant individuals are easier to trap.

## DISCUSSION

### Reproductive Cycle

The reproductive season for *A. marmorata* in sand dunes of the Mapimí Biosphere Reserve, began in May (spring) and declined in Aug. (middle summer) during the dry season in May.-Jun. and wet season in Jul.-Aug. Most of the annual rainfall occurs during summer (particularly Aug. and Sep.), and we suggest that hatching emergence (between Aug. and Sep.) corresponds to the wet season when food abundance is high in order to promote juvenile growth and survivorship, as occurs in populations of *A. tigris* in Arizona (Parker, 1972), and Nevada (Tanner and Jorgensen 1963), and *A. marmorata* in Texas (Milstead, 1957). Gadsden and Palacios-Orona (2000) found in the same dune area in Mexico that *A. marmorata* eats insects in abundance during the fall season, mainly isopters, lepidopters, and coleopters. This could increase the reproductive potential of this species of lizard in the spring to emerge from its winter dormancy, due to an increase of fat stored in their fat bodies.

The reproductive cycle peaks in summer and is different to that previously reported for *A. marmorata* in spring (Mata-Silva et al. 2010) and similar to that registered for *A. tigris* and *A. marmorata* (McCoy and Hoddenbach, 1966; Goldberg and Lowe, 1966; Goldberg, 1976; Vitt and Ohmart, 1977), see Table 2. Nevertheless the known differences in reproductive traits among populations of *A. marmorata* and *A. tigris* may be manifesting proximate environmental effects. The smallest females of *A. marmorata* probably reach early sexual maturity at approximately 20 mo of age. Likewise, data available for other female *A. tigris* from low elevations (530-1176 m, see Burkholder and Walker, 1973), females reach sexual maturity after emerging from their second hibernation in 22-24 mo at 70 mm SVL. Burkholder and Walker (1973) estimated size at sexual maturity of *A. tigris* females to be 67-70 mm SVL. In the northeast of the Sonoran Desert in Arizona, some individuals of *A. tigris* reached mature size in their first spring at ages of about 8-11 mo, but many others did not do so until their second spring at ages of 20-23 mo. This is similar to ages at first breeding reported for other areas (Turner et al., 1969; Tinkle, 1969a).

### Population Structure and Dynamics

In this study, *A. marmorata* was observed in the dunes from early spring (Apr.) to early fall (Oct.), as recorded by Hendricks and Dixon (1984) for *A. marmorata* (cited as *Cnemidophorus tigris*) in Texas. According to these authors, juveniles and subadults represent the majority of the population by early fall, probably because the older adults have already begun torpor. Young *A. marmorata* may emerge during warm weather throughout the winter, as evidence by several specimens observed in early winter.

Growth in reptiles is influenced by both phylogenetic and environmental factors (Andrews, 1982). *Aspidoscelis marmorata* exhibits differences in growth rates from *A. tigris* populations possibly related to proximate environmental influences, such as temperature, photoperiod, rainfall and food availability (Tinkle, 1967, Andrews, 1982). Cuellar (1993) studied one high-latitude *A. tigris* population in Utah, which had lower growth rates (0.07 mm  $\times$  d<sup>-1</sup> subadults and 0.008 mm  $\times$  d<sup>-1</sup> adults) than this study. However Parker (1972) studied a daily growth rate of *A. tigris* populations in Arizona, which had higher growth rates for adults (0.04 mm  $\times$  d<sup>-1</sup>) than this study. In Mapimí Biosphere Reserve the mean growth rates for *A. marmorata* was 0.1 mm  $\times$  d<sup>-1</sup> subadults and 0.01 mm  $\times$  d<sup>-1</sup> adults. The discrepancy may represent the inclusion of many immature individuals in the constructed size classes (Cuellar, 1993), whereas all adult *A. marmorata*

**Table 2.** Comparison of life history data between *Aspidoscelis marmorata* (this study, Texas1, and Texas 2) and *Aspidoscelis tigris* (Arizona, California, Colorado and Idaho). M-S = Mata-Silva et al. (2010), MH = McCoy and Hoddenbach (1966), S = Schall (1978), T = Taylor et al. (2001), Pi = Pianka (1970), P = Parker (1972), M = Mitchell (1979), G = Goldberg (1976), VO = Vitt and Ohmarth (1977), BW = Burkholder and Walker (1973).

	Chihuahua	Texas1	Texas2	New Mexico	Arizona	California	Colorado	Idaho
Elevation (m)	1129	1215	500-1845	1059	450-500	1585-1830	432	530-1176
Length of growing season (days)	240	-	-	-	210	130	-	165
Length of reproductive season (days)	120	100	-	-	130	75	100	90
Density (individuals/ha)	7-85	-	-	-	1-36	1-12	-	4-5
Hatchling size (mm SVL)	34-37	48	-	-	37-41	-	-	32-35
Size range mature males (mm)	70-92	68-94	-	-	71-96	-	-	63-97
Size range mature females (mm)	70-90	75-87	60-93	70-80	71-93	-	-	69-102
Average size adult males (mm)	80.2	83.7	-	-	83.5	-	-	81.5
Average size adult females (mm)	76.8	80.9	-	-	76.7	-	-	81.2
Clutch size	2.6	3.3	2.0-2.2	2.2	2.0-2.2	2.3-4.1	2.9-3.4	2.6
Clutch frequency	2	2	2	-	2	2	1	1
Date hatchling appear	August	June	June	-	14-June	Mid-August	July	Mid-August
Source	This study	M-S	MH, S	T	Pi, P, M	Pi, G	VO	BW, Pi

mentioned above were reproductive. However, reciprocal transplant experiments could be useful for examining the relative importance of genetic vs. proximate environmental effects as sources of variation among *A. marmorata* and *A. tigris* rates to identify whether differences in rates are adaptatives. Furthermore, according to Tinkle (1967) and Lemos-Espinal et al. (2003), like other lizards, growth rates of this species possibly fluctuate with the proximate environment on both seasonal and annual timescale.

Numerous population density data exist for *A. tigris*, Pianka (1970) found lower densities for *A. tigris* located in high-latitudes (4-5 individuals per hectare) than in our low-latitudes (mean 39 individuals per hectare), see Table 1 and Table 2. Nevertheless, these density values are within the ranges for other areas summarized by Turner et al. (1969) and are also similar to census estimations by Pianka (1970). The density of adult individuals *A. marmorata* in Mapimí Biosphere Reserve was similar to that found in a population of *A. tigris* in Nevada, fluctuating between 1 to 49 individuals per hectare (Turner et al., 1969); 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). Instead lizard density is influenced by a complex variety of factors, including availability of food resources and thermal environment (Pianka, 1970; Rose, 1982; Christian and Tracy, 1985; Sinervo, 1990).

The density of *A. marmorata* was higher in spring 1990 when compared to the others six seasons (Table 1). This large increase may be due to a larger adult recruitment in spring 1990 in response to previous above nor-

mal precipitation. Pianka (1970) and 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 change according to the distribution and amount of rain throughout the year (Maury, 1995). Although the availability of arthropods was not evaluated in this study, we found a relationship between rainfall and density of lizards.

Mean probability of survival ( $\emptyset = 0.55$ ) obtained in this study (Table 1) was similar to rates registered in a high-latitude population of *A. tigris* in southern Nevada ( $\emptyset = 0.57$ ), see Turner et al. (1969). During summer 1990 in Mapimí Biosphere Reserve (*i.e.*, Aug. through Sep.) high precipitation increased the availability of insect prey. In sand dunes of Mapimí, lizards showed an abrupt prey shift in fall, eating many more Isoptera and Hemiptera and fewer other insects (Gadsden-Esparza and Palacios-Orona, 1997). Increase in food abundance has been shown to affect food utilization in *A. tigris* (Anderson, 1994), and apparently appear to affect reproductive output (Whitford and Creusere, 1977; Dunham, 1981). Therefore, the autoecological and population responses of *A. marmorata* to environmental variation may be regarded as normal.

Life-history characteristics of populations in *A. marmorata* (Table 2) did not deviate from estimates of Fitch (1985), and Burkholder and Walker (1973). In fact, Burkholder and Walker (1973) suggest that southern populations of *A. tigris* produce a minimum of two clutches per season. According to these authors the difference in

clutch size of northern and southern populations and number of clutches laid per year pose some unique problem to be considered. The first factor worth considering is the length of activity period. McCoy and Hoddenbach (1966) suggested that in northern populations the activity period is too short to allow the production of two clutches. Therefore, northern populations partially make up for this by producing one large clutch in each season. The second possibility is that northern populations are larger in average body size and greater longevity, which allows them to produce a larger clutch than those in southern areas. This would again be related to latitude and elevation, and possibly to other factors such as food abundance. However the clutch size varies erratically and geographic trends are not consistent. In most instances, at least, clutch size is probably proportional to body size (Fitch, 1985).

In other lizard species, Tanner (1972) suggest that with increasing elevation *Uta* populations live longer, attain larger size, and have more eggs per clutch. Alternatively, Nussbaum and Diller (1967) predicted that high latitude and/or high altitude *Uta* populations show shorter growing season, shorter reproductive season, reduced per season fecundity (clutch frequency is reduced) and greater survivorship than low altitude and/or low latitude populations. These two life history patterns may be significant in *A. marmorata*, and would be another way of adapting to a short or longer activity season. Pianka (1970) propose that reduced predation, reduced time exposed to predation (shorter active season) in northern populations of *A. tigris* could explain in part the higher average clutch size and lower clutch frequency in these populations. Tinkle (1969b) has reached similar results in his studies on *Uta stansburiana*.

The studied population of *A. marmorata* had a late maturity, a long life expectancy, and few offspring. Overall, the observed data and the expectations of current life history theory for a late maturing species (Ballinger, 1983; Dunham et al., 1994; Stearns, 2000) are in agreement with K-rate selection.

Further studies on other *A. marmorata* populations in Mexico are needed to define latitudinal and elevational tendencies. Intraspecific variations of *A. marmorata* from dissimilar geographic and climatic locations would amplify the understanding of differing environmental conditions and their influence on the life history of the Marbled Whiptail Lizard. These studies will need to gather data on body size, longevity, temperature, moisture, predator pressure, parasites, and availability of food, which potentially affect life history parameters of lizards.

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