

Demography of the lizard *Sceloporus grammicus*: exploring temporal variation in population dynamics

J.J. Zúñiga-Vega, F.R. Méndez-de la Cruz, and O. Cuellar

Abstract: We conducted a 5 year demographic study in one population of the viviparous lizard *Sceloporus grammicus* Wiegmann, 1828 in central México. The population was structured in three size classes (juveniles, small adults, and asymptotic adults) for which we estimated annual survival and fecundity rates. A population projection matrix was constructed for each annual transition. All of them resulted in finite rates of population growth (λ) that, although variable from year to year (from 0.808 to 1.065), were not significantly different than unity, indicating population stability. Elasticity analysis revealed that survival staying in the same size class was the demographic process that made the greatest contribution to λ values in most years. Similarly, the stasis of large adults was the vital rate with the highest relative importance for population persistence. To incorporate the observed yearly variation in long-term population projections, we used a mean matrix, a stochastic simulation, and a resampling procedure. All these resulted in long-term population growth rates that were not significantly different than unity. Our results indicate overall demographic stability for the studied population of *S. grammicus*.

Résumé : Nous avons mené une étude démographique de 5 ans sur une population du lézard vivipare *Sceloporus grammicus* Wiegmann, 1828 dans le centre du Mexique. La population est structurée en trois classes de taille (jeunes, petits adultes, adultes de taille asymptotique) pour lesquelles nous avons estimé les taux annuels de survie et de fécondité. Nous avons construit une matrice démographique de projection pour chaque transition annuelle. Toutes les matrices donnent des taux réels de croissance de la population (λ) qui, bien que variables d'une année à l'autre (de 0,808 à 1,065), ne diffèrent pas significativement de 1, ce qui indique une population stable. Une analyse d'élasticité montre que la survie des individus qui restent dans la même classe de taille est le processus démographique qui contribue le plus aux valeurs de λ la plupart des années. De même, la stase des grands adultes est le taux vital qui présente l'importance relative la plus grande pour la persistance de la population. Afin d'incorporer les variations annuelles observées dans les projections démographiques à long terme, nous avons utilisé une matrice moyenne, une simulation stochastique et une procédure de ré-échantillonnage. Toutes ces méthodes ont fourni des taux de croissance de population qui ne diffèrent pas significativement de l'unité. Nos résultats indiquent globalement la stabilité démographique de la population de *S. grammicus* que nous avons étudiée.

[Traduit par la Rédaction]

Introduction

Demographic analyses have proven useful in setting up numerical basis for guiding conservation actions of imperiled species (Crouse et al. 1987; Crooks et al. 1998; Heppell et al. 2005). A fundamental part of population viability analysis relies on estimating demographic trends (Beissinger and McCullough 2002; Münzbergová and Ehrlén 2005; Zam-

brano et al. 2007). In addition, research focused on population dynamics also provide insight on the life-history strategies evolved by species and populations under distinct ecological scenarios (Franco and Silvertown 1996, 2004; Metcalf and Pavard 2007). Estimating demographic parameters is the first step when characterizing a life history whose evolutionary and ecological causes of variation want to be understood (Stearns 1992; Roff 2002).

Temporal variation is a relevant factor to take into account when studying demography. The ability of populations to respond to stochastic or predictable changes in the environment can determine their long-term persistence probabilities (Tuljapurkar 1990; Boyce et al. 2006). Therefore, a complete picture of the long-term numerical dynamics experienced by natural populations can only be obtained by taking into account the causes and consequences of temporal demographic variation (Inchausti and Halley 2003; Tuljapurkar et al. 2003).

In the present paper, we analyze the demography of one population of the most abundant and widespread lizard species in México using a matrix model approach (Caswell 2001). The mesquite lizard (*Sceloporus grammicus* Wieg-

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mann, 1828) is a viviparous lizard that inhabits almost every type of habitat present in north and central México, from low-altitude semitropical environments to high-altitude montane sites, through xeric and even urban regions (Sites et al. 1992; Ochoa-Ochoa and Flores-Villela 2006). We document and analyze interannual variation in the demographic parameters of a high-altitude population of the species in an attempt to project the long-term consequences of such temporal variability. We also aim to provide quantitative support to the current conservation status of *S. grammicus* ("under special protection"; Secretaría de Medio Ambiente y Recursos Naturales 2001).

We focused our attention on the following seven questions. (1) What are the size-specific survival rates of these lizards? (2) What is the finite rate of population increase of *S. grammicus* in the studied population? (3) Do survival probabilities, population structure, and population growth rates vary significantly among years? (4) What are the phases of the life cycle that contribute the most to population growth rate? (5) What is the relative importance of fecundity, growth, and stasis for mean fitness? (6) Do these patterns of relative importance vary temporarily? (7) What are the numerical long-term consequences of integrating the observed interannual variation in the estimated demographic parameters?

Materials and methods

Study species

Sceloporus grammicus is a geographically widespread viviparous lizard that exhibits considerable interpopulational variation in life-history traits (Ramírez-Bautista et al. 2004). Mean adult size of females vary from 44.5 to 55.2 mm snout-vent length (SVL), whereas minimum size at maturity ranges from 34.0 to 44.1 mm SVL among populations (Martínez 1985; Méndez-de la Cruz 1988; Ramírez-Bautista et al. 2004). Mean litter size also exhibits considerable intraspecific variation from 3.3 to 6.2 young (Ortega and Barbault 1984; Guillette and Bearce 1986; Lemos-Espinal et al. 1998). Body growth rates are faster at relatively low elevations when compared with those observed in populations at relatively high elevations (Lemos-Espinal and Ballinger 1995; Ortega-Rubio et al. 1999b; Zúñiga-Vega et al. 2008). These differences in life-history attributes appear to result in relevant differences in the population dynamics among the diverse localities that this species inhabit (Lemos-Espinal et al. 1998; Ortega-Rubio et al. 1999a). In our study site (described below), the mean (SE) adult size is 48.5 ± 0.07 mm SVL with a minimum size at maturity of 42.3 mm SVL. Females reach maturity at a mean age of 12.5 months. Matings occur in September, females are pregnant during ~8 months, and births take place during May and June. Mean (SE) litter size is 5.2 ± 0.25 young (Guillette and Casas-Andreu 1980; Zúñiga-Vega et al. 2008).

Study site and field methods

We delimited a 0.5 ha plot within a national park (Parque Nacional Zoquiapan, referred to here as PNZ) located at 19°41'N, 98°42'W and at 3200 m of elevation in the volcanic mountains of central México. Predominant vegetation is pine forest interspersed with abundant grass. Two marked

climatic seasons occur at the study site: a wet and highly cloudy season from June to October (mean total rainfall during these wet months is 470 mm) and a dry one from November to May in which the warmest and coldest temperatures of the year occur (mean total rainfall during these dry months is 138 mm; "Chapingo" weather station from Servicio Meteorológico Nacional, México).

We visited the study site twice a year (in June and November) from June 1991 until June 1997. Each sampling period consisted of ca. 4 weeks of monitoring the population during which we caught all the observed *S. grammicus* individuals by hand or noose. Data from this 4 week period were pooled into a single capture occasion per organism. Upon capture we recorded SVL, body mass, and sex for each lizard. An individual number was assigned on the first capture by toe-clipping with which organisms were identified in further sampling events.

Survival estimates

We used our mark-recapture data to estimate size-specific survival probabilities by means of the standard Cormack-Jolly-Seber (CJS) framework implemented in the software MARK (White and Burnham 1999). This computer program is based on maximum likelihood procedures to get at least two main parameters: survival (ϕ) and recapture (p) probabilities (Lebreton et al. 1992). In this study we focus only on females, given the assumption that female gestation and interbrood interval constrain recruitment (Caswell 2001). Therefore, we structured the population in three size classes that we assume experience different vital rates (growth, fecundity, and survival); thus, survival rates were estimated for females within each of these categories. Juveniles were all those lizards from size at birth to size at maturity (42.3 mm SVL for females of *S. grammicus* in PNZ; Guillette and Casas-Andreu 1980). Small adults were all those individuals from size at maturity to the size at which we began to register rates of body increment equal to zero (48 mm SVL; Zúñiga-Vega et al. 2008). Asymptotic adults were all the reproductive females whose body growth is almost negligible (i.e., >48 mm SVL). Survival rates for these size classes were calculated for each annual transition (from June of any particular year to June of the following).

We implemented 16 different models that differed in the way both survival and recapture probabilities may (or may not) vary across size classes and through time. Thus, these 16 models resulted from all the possible combinations of ϕ and p parameters assumed to be constant (\cdot), time-dependent (t), size-class-dependent (g), and assuming that each size class vary differently through time ($g \times t$ as per MARK; White and Burnham 1999). MARK identifies the best model based on the information-theoretical measure of model parsimony Akaike's information criterion (AIC; Burnham and Anderson 2002) and calculates weighted average estimates for both ϕ and p parameters according to the relative support and likelihood of each competing model. Thus, these model-weighted survival estimates are more robust than those yielded from any single model alone because they take into account the uncertainty in the process of model selection (White and Burnham 1999; Johnson and Omland 2004). We estimated weighted averages for annual survival rates per

size class, which were used as the basis for our demographic analyses described below.

In addition, we used the model selection framework described above to test for differences in the survival rates among the three size categories (Burnham et al. 1995; Burnham and Anderson 2002). We did this simply by comparing the likelihood and support of the models (as measured by the AIC scores) with constant or size-class-dependent survival probabilities. If a model with constant survival shows the greatest support, this would indicate a lack of differences among size classes in this demographic parameter. Alternatively, if a model in which survival probability vary across size classes shows the greatest support, this would provide evidence of actual differences in the survival rates of juveniles, small adults, and asymptotic adults. Model fit was evaluated using AIC scores as described in Johnson and Omland (2004) with the lowest score indicating the best-fitting model and a difference in AIC between models larger than 2 ($\Delta\text{AIC} > 2$) indicating considerable support for a real difference between them.

Fecundity estimates

As we were not able to directly quantify yearly variations in fecundity (i.e., in the litter sizes produced per female per year), we estimated annual variability in this trait as follows. Based on the previously reported positive relationship between female SVL and litter size for *S. grammicus* in PNZ (litter size = $-3.34 + 0.17 \times (\text{female SVL})$; Guillette and Casas-Andreu 1980), we calculated mean litter size for the mean size of females within each size class (L_{SA} is the expected mean litter size of small adults, L_{AA} is the expected mean litter size of asymptotic adults). We multiplied these predicted litter sizes by the number of observed females each year within each adult size class (N_{SA} is the observed small adult females per year, N_{AA} is the observed asymptotic adult females per year). We summed these products to obtain an expected total number of offspring per year (T_{OFF}) according to the expected mean litter sizes ($T_{\text{OFF}} = (L_{\text{SA}} \times N_{\text{SA}}) + (L_{\text{AA}} \times N_{\text{AA}})$). From this expected total number of offspring produced each year, we calculated the proportion that should have been produced by the females within each size class that were actually present in the study plot at the beginning of each annual transition as $\text{POFF}_{\text{SA}} = (L_{\text{SA}} \times N_{\text{SA}})/T_{\text{OFF}}$ and $\text{POFF}_{\text{AA}} = (L_{\text{AA}} \times N_{\text{AA}})/T_{\text{OFF}}$ for small and asymptotic adults, respectively.

As our summer sampling period of each studied year (June) coincided with the end of the birth season (births in PNZ occur during May and early June; Guillette and Casas-Andreu 1980), we obtained a robust annual estimate of the number of newborns present in the study plot immediately after parturition events (N_{OFF}) simply by counting all registered newborns in the study site during each June visit. We multiplied N_{OFF} per year by the corresponding estimated annual POFF_{SA} and POFF_{AA} to calculate how many of these N_{OFF} were produced by the observed females of each size class (SA_{OFF} is the estimated number of offspring produced by small adult females, AA_{OFF} is the estimated number of offspring produced by asymptotic adult females). SA_{OFF} and AA_{OFF} were divided by the observed number of females on each size class each year (N_{SA} and N_{AA}) to obtain a mean litter size per individual per year based on the newborns

and females observed at the beginning of each annual transition. Finally, as our demographic analyses are only based on females, the estimated litter sizes were divided by 2 to account for the assumption that females should be producing equal number of male and female offsprings. We considered these modified size-specific fecundities to be reliable estimates of yearly variation in reproductive output.

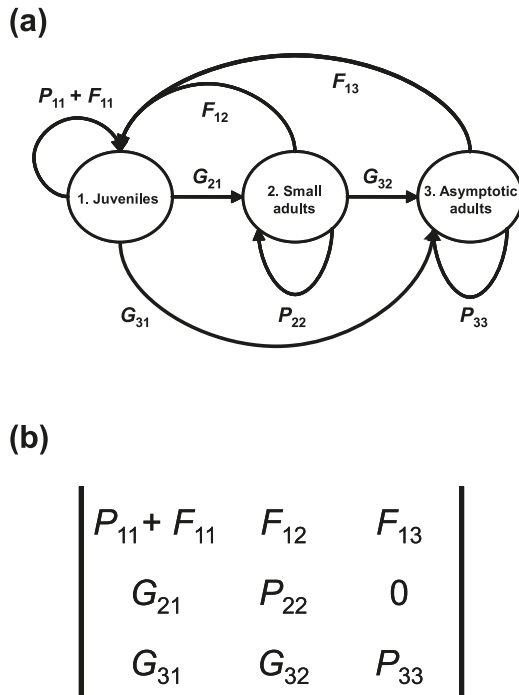
Basic matrix analyses

We constructed five 3×3 population projection matrices (Caswell 2001), each corresponding to one of the following annual transitions: 1991–1992, 1992–1993, 1993–1994, 1994–1995, and 1995–1996. These matrices summarize the survival, growth, and fecundity rates of the different phases of the life cycle of *S. grammicus* represented by the three size classes into which we structured the population (i.e., juveniles, small adults, and asymptotic adults). The life-cycle diagram depicts all the transitions and contributions that can be observed among the size classes from 1 year to the following year (Fig. 1a). When female lizards survive, they can either remain in the same size class (stasis, depicted with a P in both the life-cycle diagram and the transition matrix; Figs. 1a, 1b) or progress to a superior size class (growth, G in Figs. 1a, 1b). In most years (except transition 1994–1995), we observed certain proportion of juveniles surviving and growing more than one size class (to asymptotic adults) from 1 year to the next (transition G_{31} in Figs. 1a, 1b). Both adult categories contribute to juveniles by offspring production (fecundity, F in Figs. 1a, 1b). Matrix entries (a_{ij}), which translate the life-cycle diagram into a numerical and analytical tool, represent survival with stasis (in the main diagonal), survival with growth (in the sub-diagonals), and contribution to juveniles by fecundity (in the first row) of a mean individual in size class j (columns) to size class i (rows) from 1 year to the next (Fig. 1b; Caswell 2001).

Stasis and growth entries of the matrices were derived from the annual survival rates estimated by the program MARK. We partitioned these stage-specific survival probabilities into stasis and growth components using the observed proportion of individuals that remained in the same size class versus those that grew to a larger size class on each corresponding annual transition. Fecundity entries were calculated by multiplying the modified annual litter sizes per size class by the annual survival rate of the corresponding category. This was done to account for the probability that a female survives a whole year to reach the next breeding season to actually produce offspring. This procedure to calculate fecundity entries corresponds to a post-breeding type (Caswell 2001).

In addition, we also took into account the contribution that surviving females in the juvenile size class make to the same juvenile category (matrix entry a_{11}) from 1 year to the following year by means of offspring production. As depicted in Fig. 1a, a proportion of juveniles survive and grow large enough to reach the small adult size class or even the asymptotic adult size class in one annual transition. Some of these “growing” juvenile females at the beginning of any particular annual transition exhibit a size that, although still within the threshold of the juvenile category (i.e., smaller than 42.3 mm SVL), is large enough to reach

Fig. 1. (a) Life-cycle diagram of the mesquite lizard (*Sceloporus grammicus*). Nodes represent size categories, arrows represent transition probabilities (in the case of growth or stasis) or contributions (in the case of fecundities) made by individuals in a particular category to other categories from 1 year to the next. *F*, fecundity; *G*, growth, which is defined as survival with progression to a larger size class; *P*, stasis, which is defined as survival staying in the same size class. Subscripts (*ij*) indicate the direction of the transition or contribution, from size class *j* to size class *i*. (b) Population projection matrix for *S. grammicus*. Terms in the matrix are equivalent to those in the life-cycle diagram. The matrix can be interpreted as a numerical representation of the life-cycle diagram.



sexual maturity soon after our sampling event (i.e., to progress to an adult size class soon after June). This in turn permits them to mate 3 months later in the fall (in PNZ courtship and mating occur in September; Guillette and Casas-Andreu 1980) and to produce young in the late spring of the following year (i.e., at the end of that particular annual transition). Oppositely, females that were just born in the beginning of that particular annual transition are too small to begin vitellogenesis a month after (in July) and to mate during that fall (size at birth is only 20 mm SVL; Guillette and Casas-Andreu 1980). Thus, only some of the juveniles (the largest ones) progressing to an adult size class contribute to that juvenile category by offspring production. We estimated that potentially reproducing proportion simply by quantifying how many of the surviving and growing juveniles began the transition with a size large enough to begin vitellogenesis a month after. We arbitrarily defined such a size as >38 mm SVL. Therefore, the contribution of this year's juveniles to next year's juveniles by offspring production was estimated by the potentially reproducing proportion times the corresponding estimated litter size. In consequence, we calculated the total contribution of juveniles to juveniles (the entry a_{11} in all matrices) as a combination of the stasis of some juvenile females from 1 year to the next and the

offspring produced by those large surviving and growing juveniles that begin reproduction ($P_{11} + F_{11}$ in Figs. 1a, 1b).

We estimated the finite rate of population increase (λ) for each year as the dominant eigenvalue of each annual transition matrix. Similarly, the right (w) and left (v) eigenvectors associated with each λ value represented annual estimates of the projected stable size-class distribution and the size-specific reproductive values, respectively (Caswell 2001). We tested for significant differences between observed and projected (vector w) size-class distributions by means of χ^2 tests. Confidence intervals (95%) for λ values were calculated following the analytical method proposed by Caswell (2001), in which the variance of λ is given by

$$V(\lambda) = \sum_{i,j} (s_{ij})^2 \times V(a_{ij})$$

where $V(a_{ij})$ represents the variance of the matrix entries. For transition probabilities (growth and stasis), $V(a_{ij})$ was calculated as

$$V(a_{ij}) = a_{ij} \times \frac{1 - a_{ij}}{N}$$

where N is the number of individual females with which the corresponding entry was calculated. The variance of fecundity entries was calculated using the information on the natural variability in this parameter (reported in Guillette and Casas-Andreu 1980). The standard error (σ) was calculated as the square root of the variance of λ and the 95% confidence intervals were constructed as $\lambda \pm 2\sigma$.

We used elasticity analysis (de Kroon et al. 1986, 2000) to estimate the proportional change in λ that would result from proportional changes in each vital rate (i.e., in each matrix entry). Therefore, yearly elasticity matrices (whose entries are denoted by e_{ij}) were constructed as follows:

$$e_{ij} = s_{ij} \times \frac{a_{ij}}{\lambda}$$

where s_{ij} is the absolute sensitivity of λ to absolute changes in the matrix entries ($s_{ij} = \partial \lambda / \partial a_{ij}$). As elasticities are standardized sensitivities, they are useful to compare the relative contribution (also interpreted as relative importance; Benton and Grant 1999) of each matrix entry to population growth rate (de Kroon et al. 1986, 2000). In addition, because all the entries in an elasticity matrix sum to unity (Mesterton-Gibbons 1993), we were able to calculate the relative contribution of each size class and of each of the processes that compose the life cycle (fecundity, growth, and stasis) to population growth rate simply by adding all the entries in the elasticity matrices that corresponded to each category or to each process (Silvertown et al. 1993). Nevertheless, as the entry a_{11} in the transition matrices is a combination of juvenile stasis and fecundity (through the offspring produced by some of the growing juveniles; $P_{11} + F_{11}$ in Figs. 1a, 1b), the corresponding elasticity (entry e_{11} in the elasticity matrices) was partitioned into the proportion that is due to stasis and that is due to fecundity. Those proportions were added to the summed elasticity for stasis and fecundity, respectively.

We constructed bootstrap 95% confidence intervals for the elasticities by resampling with replacement our field

data (i.e., the individual encounter histories). For each new random sample, we calculated survival rates, annual matrices, and elasticities. We repeated the process 1000 times generating a bootstrap distribution of elasticities. The 25th and 975th sorted elasticity values for each matrix entry, size class, and demographic process per year were used as the lower and upper confidence limits, respectively (Caswell 2001).

Following Silvertown et al. (1993), we plotted the elasticities for the three main life-cycle components in the demographic triangle, which is a three-way proportional diagram that provides a visual scheme to compare the elasticity value of each of these demographic process. Each axis of the triangle corresponds to the elasticity of each process. To analyze temporal variation in the relative importance of fecundity, growth, and stasis, we plotted one point for each annual transition. Years with a proportionately higher elasticity value for one process (fecundity, growth, or stasis) would tend to be located relatively closer to the corner of the triangle that corresponds to high elasticity values (i.e., close to unity) of such component (Silvertown et al. 1993).

Integrating temporal demographic variation

To assess the long-term effects of temporal variation in the population dynamics of *S. grammicus*, we used distinct methodological tools that would give us complementary insights about the long-term demography of this widespread and abundant lizard species. First, a mean matrix was constructed by averaging the entries of all the annual transition matrices (Caswell 2001). The main assumption of this mean matrix is that the overall numerical trend is simply determined by an averaged effect of the annual demographic responses of the population to annual variations in the environment (Mandujano et al. 2001; Lemos-Espinal et al. 2005). From this mean matrix, we calculated a mean finite rate of population growth (λ_m), its associated w and v eigenvectors, and elasticities for the averaged vital rates, the size classes, and the demographic processes (fecundity, growth, and stasis).

Second, supposing a random interannual variation in the demographic parameters, we conducted a stochastic simulation, which is a method that has been developed to incorporate such temporal variability that is assumed to be stochastic into a long-term demographic projection (Bierzychudek 1982). In this simulation, each iteration in the population projection through time (i.e., multiplication of the transition matrix by a vector that represents the current population structure to obtain population structure in the following year; Caswell 2001) is conducted with a different matrix chosen at random from the five available matrices. In other words, each matrix has the same probability of appearance (0.2) during the iteration process that projects the population size through time.

The simulation consisted of 30 replicates of 1000 iterations each. From each replicate, we calculated the intrinsic rate of population increase (r) as the slope of the regression between projected population size (log-transformed) and time (years). From this r , we obtained a stochastic finite rate of population growth as $\lambda_s = e^r$, where e is the base of natural logarithms. We report the mean λ_s value obtained over the 30 replicates.

Third, we used also a different approach to assess the effects of demographic stochasticity upon the long-term numerical trend of the population. We assumed that our five annual transition matrices are samples from a larger and unknown distribution of matrices for this population. We randomly resampled five matrices with replacement from the five observed annual matrices, calculated their product, obtained a λ value for this 5 year projection, and estimated an overall population growth rate as the fifth root of this 5 year projection λ . This procedure was repeated 1000 times from which we calculated a mean λ value (referred to here as resampled λ or λ_r). From this bootstrapped distribution of λ values, we constructed a 95% confidence interval for λ_r by using the 25th and 975th sorted λ values as the lower and upper limits, respectively.

Results

Survival rates

A model in which survival rate varied across size classes (φ_g) and recapture probability varied through time (p_t) was the best-fitting model with the highest support in our data as indicated by its lowest AIC score (AIC = 1044.8; Table 1). We also report normalized Akaike weights (Burnham and Anderson 2002) for the fitted models, which are measures of their relative plausibility (i.e., likelihood). In this case, also the model with size-class-dependent survival rate and time-dependent recapture rate ($\varphi_g p_t$) showed the greatest likelihood (AIC weight = 0.85; Table 1). As the difference in AIC scores between this and the next best-supported model ($\varphi_g p_t$ is the size-class-dependent survival rate and constant recapture rate) was 4.3 (Δ AIC = 4.3), we concluded that there is considerable evidence of a real difference between these two models.

The three best-fitting models coincided in a size-class-dependent survival rate without any effect of time (i.e., no $g \times t$ effect; Table 1), which indicates a lack of an actual influence of time upon this demographic parameter. Therefore, the model-weighted average estimates of annual size-specific survival probabilities were virtually similar among years for each size category. Mean annual φ value for juveniles was 0.418 in all years, for small adults was 0.522 in all years, and for asymptotic adults was 0.685 in three annual transitions (1991–1992, 1992–1993, and 1995–1996) and 0.686 in the other two annual transitions (1993–1994 and 1994–1995; Fig. 2).

As indicated by our best-fitting model and by the 95% confidence intervals for the model-weighted annual survival rates, there were significant differences among size classes. The annual survival rate of asymptotic adults was higher than that of juveniles and small adults (Fig. 2). These latter two size classes did not appear to differ significantly in their annual probabilities of survival.

Annual and mean matrices

The finite rates of population growth (λ) estimated from the annual transition matrices varied considerably through time ($\lambda_{1991-1992} = 1.061 \pm 0.274$, $\lambda_{1992-1993} = 0.808 \pm 0.200$, $\lambda_{1993-1994} = 1.065 \pm 0.237$, $\lambda_{1994-1995} = 0.853 \pm 0.208$, $\lambda_{1995-1996} = 0.911 \pm 0.226$; Table 2). The mean matrix projected a $\lambda_m = 0.955 \pm 0.130$. However, according

Table 1. Results of fitting 16 competing models to our mark-recapture data of the mesquite lizard (*Sceloporus grammicus*).

Model	AIC	Δ AIC	AIC weight
$\varphi_g P_t$	1044.8	0	0.85
$\varphi_g P \cdot$	1049.1	4.3	0.10
$\varphi_g P_g$	1050.5	5.7	0.05
$\varphi_{g \times t} P_t$	1061.0	16.2	0.0003
$\varphi_{g \times t} P \cdot$	1061.8	17.0	0.0002
$\varphi_t P_t$	1062.6	17.8	0.0001
$\varphi_{g \times t} P_g$	1063.9	19.1	0.00006
$\varphi_t P \cdot$	1064.0	19.2	0.00006
$\varphi_g P_{g \times t}$	1064.5	19.7	0.00004
$\varphi_t P_g$	1068.1	23.3	0.00001

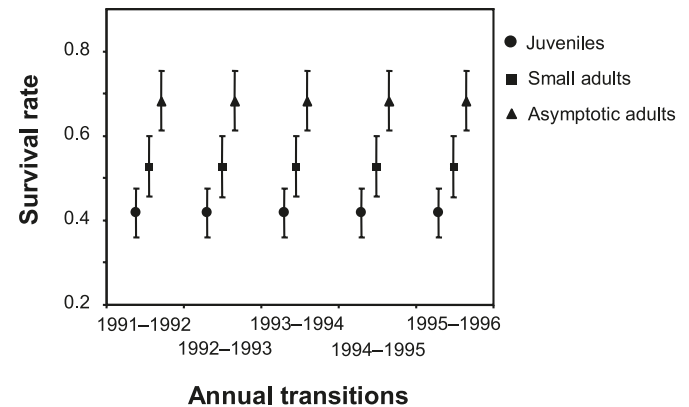
Note: The fitted models represent all the possible combinations of survival (φ) and recapture (p) parameters assumed to be constant (\cdot), time-dependent (t), size-class-dependent (g), and assuming that each size class vary differently through time ($g \times t$). Fit of each model to the observed data was evaluated using Akaike's information criterion (AIC); the model with the lowest AIC score best fits the data. Δ AIC represents the difference between the corresponding model and the best-fitting model. Models with Δ AIC values < 2 are considered to have support comparable with the best model. AIC weight is a measure of the likelihood of the models in our data. We only show here the models with an AIC weight > 0 .

to the 95% confidence intervals for the λ values, none of these was significantly different than unity, which indicates population stability. Even the confidence interval for the annual transition 1992–1993, which resulted in the lowest λ value ($\lambda_{1992-1993} = 0.808 \pm 0.200$), included unity (0.608–1.008). Alternatively, this last result can also be interpreted as the latter λ value being only marginally lower than one. Furthermore, as the confidence intervals for all the calculated λ values, including that for λ_m , showed a considerable overlap, the observed interannual variation does not appear to be significant (Table 2).

Projected stable size-class distributions (vectors w in Table 2) were not different than those observed (columns N_x in Table 2) in the 1991–1992 and 1992–1993 transitions (1991–1992: $\chi^2_{[2]} = 4.26$, $P = 0.12$; 1992–1993: $\chi^2_{[2]} = 4.96$, $P = 0.08$; Fig. 3). Projected and observed size-class distributions for the 1994–1995 transition showed a marginally significant difference ($\chi^2_{[2]} = 6.02$, $P = 0.05$). Statistical differences between projected and observed population structures were detected in the other two annual transitions (1993–1994: $\chi^2_{[2]} = 13.95$, $P < 0.001$; 1995–1996: $\chi^2_{[2]} = 17.38$, $P < 0.001$; Fig. 3). Reproductive values were higher in reproductive size classes in comparison with juveniles, with the highest in the asymptotic adults in all years (Table 2).

Elasticities showed a clear pattern from year to year. First, in all years the stasis of asymptotic adults was the vital rate with the highest elasticity. Except the 1991–1992 transition, this pattern was statistically significant as indicated by the 95% confidence intervals (95% CI; Table 3). In those annual transitions that resulted in a λ value lower than one ($\lambda_{1992-1993} = 0.808$, $\lambda_{1994-1995} = 0.853$, $\lambda_{1995-1996} = 0.911$), this elasticity showed a strikingly high value (≥ 0.50). Second, in those years with a λ value higher than unity ($\lambda_{1991-1992} = 1.061$, $\lambda_{1993-1994} = 1.065$), the progression

Fig. 2. Model-weighted estimates of survival probabilities (φ) obtained from the program MARK for the mesquite lizard (*Sceloporus grammicus*) at our study site. Survival rates and associated 95% confidence intervals are shown per size class and per annual transition.



of juveniles to small adults increased its elasticity in comparison with the remaining annual transitions. Third, in most years, except the transition with the lowest population growth rate ($\lambda_{1992-1993} = 0.808$), fecundity of asymptotic adults showed a relatively high elasticity value (> 0.10 ; Table 3). In the mean matrix ($\lambda_m = 0.955$), the stasis of asymptotic adults (0.402) was the significantly highest vital rate (95% CI = 0.279–0.477) followed by the fecundity of asymptotic adults (0.158, 95% CI = 0.146–0.168) and the progression of juveniles to small adults (0.150, 95% CI = 0.128–0.183; Table 3).

When analyzed at the size-class level, elasticities showed the same pattern in all annual transitions (Table 4). Highest elasticity was observed in asymptotic adults, juveniles were the size class with the second-highest elasticity values, and small adults had the lowest in all years. The difference in the elasticity for asymptotic adults and that for the remaining size classes was significant in all but 1 year as indicated by the 95% confidence intervals. In the 1991–1992 transition, the relative contribution of asymptotic adults to λ (0.432, 95% CI = 0.332–0.498) was not significantly different than that of juveniles (0.345, 95% CI = 0.305–0.398; Table 4). The mean elasticity value (i.e., elasticities calculated from the mean matrix) for asymptotic adults (0.560) was significantly higher (95% CI = 0.445–0.651) than those for juveniles (0.264, 95% CI = 0.227–0.322) and small adults (0.176, 95% CI = 0.143–0.229). In those transitions that resulted in λ values below unity ($\lambda_{1992-1993} = 0.808$, $\lambda_{1994-1995} = 0.853$, $\lambda_{1995-1996} = 0.911$), the elasticities of asymptotic adults were noticeably high (> 0.60 ; Table 4).

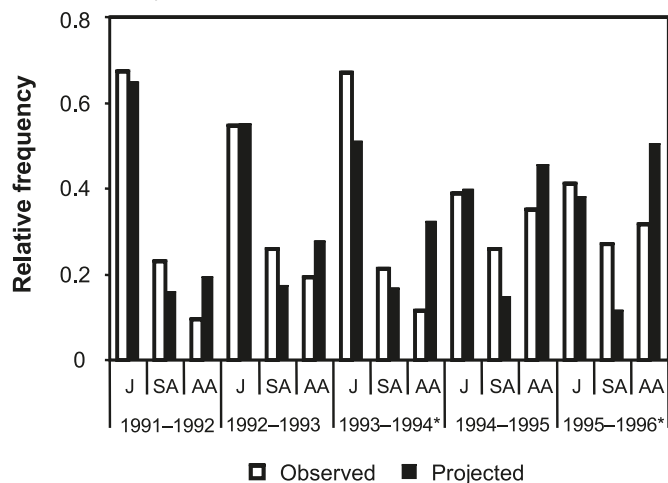
Elasticities per demographic process showed a slightly less clear pattern. In three of the five studied years, the elasticity for stasis was significantly higher than that for growth and fecundity as indicated by the 95% confidence intervals (Table 4). These three annual transitions were the ones that resulted in λ values below unity ($\lambda_{1992-1993} = 0.808$, $\lambda_{1994-1995} = 0.853$, $\lambda_{1995-1996} = 0.911$). In one of the years with λ above unity ($\lambda_{1991-1992} = 1.061$), the elasticity for stasis was also the highest, although not significantly different than that for growth (stasis: 0.380, 95% CI = 0.319–0.435; growth: 0.332, 95% CI = 0.307–0.354). In

Table 2. Population projection matrices (annual and mean) and derived main demographic results for the studied population of the mesquite lizard (*Sceloporus grammicus*).

	Juveniles	Small adults	Asymptotic adults	N_x	w	v
1991–1992 ($\lambda = 1.061 \pm 0.274$)						
Juveniles	0.361	0.935	1.578	35	0.648	0.127
Small adults	0.209	0.209	0	12	0.159	0.337
Asymptotic adults	0.035	0.313	0.685	5	0.193	0.536
1992–1993 ($\lambda = 0.808 \pm 0.200$)						
Juveniles	0.375	0.374	0.631	40	0.551	0.122
Small adults	0.114	0.447	0	19	0.174	0.255
Asymptotic adults	0.038	0.075	0.685	14	0.275	0.624
1993–1994 ($\lambda = 1.065 \pm 0.237$)						
Juveniles	0.171	0.640	1.080	47	0.510	0.171
Small adults	0.348	0	0	15	0.167	0.342
Asymptotic adults	0.070	0.522	0.686	8	0.323	0.487
1994–1995 ($\lambda = 0.853 \pm 0.208$)						
Juveniles	0.136	0.312	0.528	21	0.398	0.156
Small adults	0.314	0	0	14	0.146	0.356
Asymptotic adults	0	0.522	0.686	19	0.455	0.489
1995–1996 ($\lambda = 0.911 \pm 0.226$)						
Juveniles	0.086	0.324	0.547	26	0.380	0.193
Small adults	0.279	0	0	17	0.116	0.338
Asymptotic adults	0.139	0.522	0.685	20	0.504	0.469
Mean matrix ($\lambda = 0.955 \pm 0.130$)						
Juveniles	0.226	0.517	0.873	34	0.510	0.156
Small adults	0.253	0.131	0	15	0.156	0.338
Asymptotic adults	0.056	0.391	0.685	13	0.333	0.506

Note: Corresponding λ values are shown above each matrix ($\pm 95\%$ confidence intervals). N_x is the number of female lizards per size class from which transition probabilities were calculated (observed size-class distribution); w is the projected stable size-class distribution; v is the size-specific reproductive values. N_x for the mean matrix are means of the number of individuals per size class across all years.

Fig. 3. Observed size-class distributions of the mesquite lizard (*Sceloporus grammicus*) compared with those projected by the annual transition matrices. J, juveniles; SA, small adults; AA, asymptotic adults. Annual transitions with a marked significant difference ($P < 0.01$) between observed and projected population structures are indicated by asterisks (see text for χ^2 and P values).



the remaining year, which also resulted in a λ value above unity ($\lambda_{1993-1994} = 1.065$), the elasticity for stasis was lower and not significantly different than that for growth (stasis: 0.336, 95% CI = 0.255–0.391; growth: 0.375, 95% CI = 0.344–0.410; Table 4). Fecundity exhibited the lowest elasticity in most years, except in the year that resulted in the lowest λ value ($\lambda_{1992-1993} = 0.808$), in which fecundity and growth resulted in almost equal elasticity values (0.159 and 0.162, respectively). In the mean matrix, the elasticity for stasis (0.451, 95% CI = 0.366–0.512) was significantly higher than those for growth (0.309, 95% CI = 0.275–0.349) and fecundity (0.240, 95% CI = 0.210–0.282). The elasticity for fecundity increased in those years that resulted in population growth rates above unity ($\lambda_{1991-1992} = 1.061$, $\lambda_{1993-1994} = 1.065$), reaching values of 0.288 and 0.289, respectively, whereas in those years that resulted in λ values below unity ($\lambda_{1992-1993} = 0.808$, $\lambda_{1994-1995} = 0.853$, $\lambda_{1995-1996} = 0.911$), the elasticity for stasis became considerably higher (>0.50). The greatest elasticity for stasis (0.679) was observed in the annual transition with the lowest λ value ($\lambda_{1992-1993} = 0.808$; Table 4). This pattern is graphically depicted in Fig. 4: all matrices had a tendency towards the stasis corner of the triangle (i.e., the corner in which elasticity for stasis equals 1). The annual transition with the lowest λ value ($\lambda_{1992-1993} = 0.808$) was the one among all that exhibited the greatest tendency towards the stasis corner, whereas those with the highest λ value ($\lambda_{1991-1992} =$

Table 3. Elasticity matrices corresponding to the five annual transition matrices and the mean matrix for the studied population of the mesquite lizard (*Sceloporus grammicus*).

	Juveniles	Small adults	Asymptotic adults
1991–1992			
Juveniles	0.117 (0.096–0.150)	0.075 (0.056–0.103)	<i>0.153</i> (0.146–0.159)
Small adults	<i>0.180</i> (0.156–0.207)	0.044 (0.034–0.058)	0
Asymptotic adults	0.048 (0.041–0.053)	0.105 (0.099–0.108)	<i>0.279</i> (0.186–0.347)
1992–1993			
Juveniles	0.110 (0.073–0.174)	0.034 (0.018–0.066)	0.092 (0.079–0.098)
Small adults	0.070 (0.044–0.108)	0.087 (0.042–0.177)	0
Asymptotic adults	0.057 (0.043–0.065)	0.035 (0.026–0.041)	<i>0.514</i> (0.280–0.648)
1993–1994			
Juveniles	0.046 (0.034–0.059)	0.057 (0.043–0.080)	<i>0.186</i> (0.178–0.191)
Small adults	<i>0.189</i> (0.167–0.219)	0	0
Asymptotic adults	0.054 (0.049–0.059)	0.132 (0.123–0.139)	<i>0.336</i> (0.255–0.391)
1994–1995			
Juveniles	0.029 (0.022–0.043)	0.025 (0.016–0.042)	0.130 (0.113–0.150)
Small adults	<i>0.155</i> (0.130–0.190)	0	0
Asymptotic adults	0	0.130 (0.113–0.150)	<i>0.531</i> (0.417–0.599)
1995–1996			
Juveniles	0.020 (0.016–0.028)	0.023 (0.016–0.036)	<i>0.167</i> (0.152–0.185)
Small adults	0.112 (0.091–0.142)	0	0
Asymptotic adults	0.078 (0.068–0.085)	0.089 (0.076–0.106)	<i>0.510</i> (0.419–0.563)
Mean matrix			
Juveniles	0.063 (0.047–0.089)	0.044 (0.031–0.066)	<i>0.158</i> (0.146–0.168)
Small adults	0.150 (0.128–0.183)	0.024 (0.013–0.045)	0
Asymptotic adults	0.051 (0.043–0.056)	0.107 (0.096–0.118)	<i>0.402</i> (0.279–0.477)

Note: Highest elasticities (>0.15) are in italic type. Values within parentheses are the bootstrap 95% confidence intervals.

1.061, $\lambda_{1993-1994} = 1.065$) showed the greatest tendency towards the growth corner (Fig. 4).

Integrating temporal demographic variation

We obtained a mean $\lambda_s = 0.948 \pm 0.052$ in the simulation exercise in which we assigned an equal probability (0.2) to all the annual matrices. According to its 95% confidence interval (0.896–1.00), the λ_s value is only marginally different than unity and not significantly different than the λ_m value ($\lambda_m = 0.955 \pm 0.130$) or than the λ values yielded by all the annual transition matrices, as indicated by the wide overlap in their confidence intervals (see annual λ values in Table 2). Noticeably, in no single replicate among the 30 that we ran, did we obtain a λ_s value above unity. Our bootstrap λ_r resulted in a value of 0.951, which is not significantly different than the λ_m value, λ_s value, or unity, according to its 95% confidence interval (0.853–1.061). This interval also shows that the λ_r value is not statistically distinct from the annual λ values (shown in Table 2).

Discussion

Demographic strategy

Annual survival probabilities of *S. grammicus* at PNZ are relatively high (between 0.418 and 0.685) when compared with those observed in other species of the genus. For instance, Texas spiny lizards (*Sceloporus olivaceus* Smith, 1934), mountain spiny lizards (*Sceloporus jarrovi* Cope in

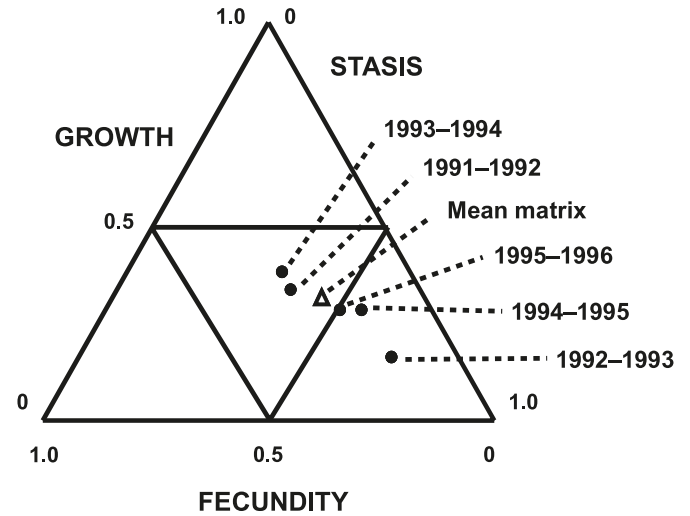
Yarrow, 1875), canyon lizards (*Sceloporus merriami* Stejneger, 1904), rose-bellied lizards (*Sceloporus variabilis* Wiegmann, 1834), and bunch grass lizards (*Sceloporus scalaris* Wiegmann, 1828) exhibit mean annual survival rates of 0.16, 0.36, 0.32, 0.12, and 0.15, respectively (Blair 1960; Ballinger 1973; Dunham 1981; Benabib 1991; Ortega-Rubio et al. 2000). When compared with another population of *S. grammicus* located at a lower altitude (mean survival rate of 0.23 at 2480 m of elevation; Ortega-Rubio et al. 1999a), the high survival rates that we found at PNZ are even more noticeable. This pattern might be explained by the many lines of evidence that have demonstrated a tendency for lizard species (and this might also apply to other ectothermic organisms) to exhibit enhanced annual survival probabilities at high altitudes or latitudes (Adolph and Porter 1993, 1996; Sears 2005). The explanations for this phenomenon have been based on (i) less biological interactions in increased altitudes or latitudes derived by less biological diversity (i.e., less competitors and predators; Tinkle et al. 1970; Ballinger 1979; Dunham 1982) and on (ii) thermal constraints (less thermoregulation opportunities during the year), which reduce the time of activity and thus the total time throughout the year in which individuals are under predation and mortality risk (Rose 1981; Adolph and Porter 1993; Sears 2005). The studied population is located at 3200 m of elevation and thermoregulation opportunities during the year appear to be relatively constrained (e.g., high annual frequency of cloudy days; Zúñiga-Vega et al. 2008). In addi-

Table 4. Elasticities per size class and demographic process corresponding to the five annual transition matrices and the mean matrix for the studied population of the mesquite lizard (*Sceloporus grammicus*).

	1991–1992	1992–1993	1993–1994	1994–1995	1995–1996	Mean matrix
Size class						
Juveniles	0.345 (0.305–0.398)	0.237 (0.173–0.330)	0.289 (0.260–0.330)	0.184 (0.152–0.237)	0.210 (0.186–0.256)	0.264 (0.227–0.322)
Small adults	0.224 (0.192–0.264)	0.156 (0.091–0.285)	0.189 (0.167–0.219)	0.155 (0.130–0.192)	0.112 (0.094–0.143)	0.176 (0.143–0.229)
Asymptotic adults	0.432 (0.332–0.498)	0.607 (0.371–0.730)	0.522 (0.451–0.692)	0.661 (0.569–0.714)	0.677 (0.599–0.717)	0.560 (0.445–0.651)
Demographic process						
Fecundity	0.288 (0.257–0.326)	0.159 (0.120–0.211)	0.289 (0.260–0.330)	0.162 (0.135–0.203)	0.210 (0.184–0.250)	0.240 (0.210–0.282)
Growth	0.332 (0.307–0.354)	0.162 (0.125–0.200)	0.375 (0.344–0.410)	0.285 (0.243–0.340)	0.280 (0.244–0.327)	0.309 (0.275–0.349)
Stasis	0.380 (0.319–0.435)	0.679 (0.587–0.754)	0.336 (0.255–0.391)	0.554 (0.453–0.616)	0.510 (0.419–0.571)	0.451 (0.366–0.512)

Note: Values within parentheses are the bootstrap 95% confidence intervals.

Fig. 4. Ordination of the population projection matrices (annual and mean) of the mesquite lizard (*Sceloporus grammicus*) within the demographic triangle according to their elasticities per demographic process. Mean matrix is denoted by the open triangle.



tion, the number of predators and competitors in this volcanic and high-altitude region of central México should also be relatively reduced (Uribe-Peña et al. 1999). These latter couple of facts should interact to produce the high survival rates in all size classes that we observed in the study site.

Observed annual rates of population growth were quite variable from year to year (λ values between 0.808 and 1.065). However, none of these λ values were significantly different than unity, which indicates numerical equilibrium. In fact, two additional lines of evidence reveal that population density and structure should remain relatively constant across years just as we observed during the course of the study. First, the number of lizards (both male and female) registered in the study site was similar among years (lizards per 0.5 ha: year 1991 = 102, year 1992 = 122, year 1993 = 112, year 1994 = 104, year 1995 = 122). Second, population structure appeared to be relatively stable through time as was indicated by the lack of statistical differences between the projected stable size-class distribution and the observed population structure in two annual transitions (1991–1992 and 1992–1993) and by a marginally significant difference between these in another transition (1994–1995; Fig. 3). The chance of disturbance to the population structure in the field might be quite high, and therefore, it must be difficult to find a perfect match between observed and predicted population structures in every year. Apparently, during early summer of every year, this population consisted of approximately 54% juveniles, 25% small adults, and 21% asymptotic adults as indicated by the mean observed population structure.

According to the results of the elasticity analysis, the demographic strategy of the species in the study site is based on a relatively high contribution of the stasis of large adults for the mean fitness of the population (recall that population growth rates have been interpreted as measures of the mean fitness of populations; van Groenendael et al. 1988; Benton and Grant 1999). Moreover, the size class and demographic process with the highest contribution to the

overall population growth rate were asymptotic adults and stasis, respectively (as indicated by the mean matrix and most of the annual matrices). This sort of elasticity pattern has been previously observed in species and populations under long-term demographic equilibrium or with low potential for numerical increase (Doak et al. 1994; Contreras and Valverde 2002; Schaub et al. 2006). The position of the studied population within the demographic triangle was variable from year to year with a tendency towards the region in which relatively late-maturing and long-lived species of distinct taxa are located, such as mammals that mature at 3 years of age or later (Heppell et al. 2000), iteroparous forest herbs, and woody plants (Silvertown et al. 1993; Franco and Silvertown 1996). In species whose rates of population growth indicate stability or decline, the survival of adults contribute the most to the mean fitness (Silvertown et al. 1996; Caswell 2000), which appears to be the case for the studied population of *S. grammicus*.

Temporal variability in the population dynamics

Even though survival rates did not vary among years, the proportions of individuals staying in the same category or progressing to others from year to year did vary during the course of the study. For instance, during the first two annual transitions of the study (1991–1992 and 1992–1993), a certain proportion of surviving small adults remained in the same category, whereas in the other three transitions (1993–1994, 1994–1995, 1995–1996), all of them progressed to asymptotic adults (Table 2). This variation in growth and stasis rates promoted yearly variation in population growth rates. However, in all years, λ values were not significantly different than unity, which indicates the overall population stability in spite of annual variability in the size-specific vital rates. In an attempt to find possible environmental causes of such yearly variation in the demography, we correlated λ values obtained from the annual matrices with distinct climatic variables such as rainfall and temperature (mean, maximum, and minimum) without success. Neither rainfall nor temperature appeared to be associated with annual variation in the demography of *S. grammicus* at our study site. However, other variables that we failed to measure such as predation intensity or food and moisture availability could have varied among years promoting the observed yearly differences in the vital rates. Several previous studies on demographic patterns of lizard species have shown that survival, reproductive, and population growth rates are strongly correlated with environmental factors such as food availability, rainfall, and temperature (e.g., Tinkle et al. 1993; Dickman et al. 1999; Germano and Williams 2005; Barrows 2006).

In contrast to the size-specific growth and stasis rates, the relative importance of the distinct life-cycle components remained considerably consistent from year to year. Asymptotic adults and stasis as demographic process make the overall greatest contribution to population fitness. However, higher λ values were associated with increased importance of growth and fecundity. An increased proportion of individuals progressing to larger size classes results in more offspring production, because in *S. grammicus* there is a positive relationship between female size and number of young produced (Guillette and Casas-Andreu 1980). The main consequence of more growth and fecundity is a greater

tendency towards population increase. In contrast, decreasing values of λ were associated with higher relative importance for the stasis of individuals in their same size class. In such relatively unfavorable years (1992–1993, 1994–1995, 1995–1996), the persistence of the population is mostly explained by the stasis of adults (i.e., this process contributes with more than 50% of the λ values; see Tables 3, 4). This pattern of variation in the elasticities is consistent with previous studies on diverse taxa which have demonstrated that under relatively unfavorable conditions raw survival as opposed to growth or fecundity increases its relative contribution to mean fitness, whereas during favorable periods fecundity and growth are promoted and thus augment their relative contribution to an enhanced population growth rate (Silvertown et al. 1996; Heppell et al. 2000).

We recognize that our attempts to estimate yearly variations in fecundity might be less accurate than the estimated variation in survival and growth rates. However, we decided to come up with approximations of the actual variability in the mean litter sizes produced per year rather than assuming constant fecundity values across years, which is an even less realistic scenario. Reproductive output is quite plastic among lizard species (e.g., Abts 1987; James 1991; Rohr 1997). Even though the range of natural variability in litter sizes of *S. grammicus* at PNZ is only moderate (between 3 and 7 young; Guillette and Casas-Andreu 1980), our results should be interpreted cautiously as fecundity usually contributes with ca. 24% of the λ values (according to the elasticity for fecundity calculated from the mean matrix).

Long-term population projections and conservation implications

The annual transition matrices and the mean matrix resulted in population growth rates not significantly different than unity. In addition, both the stochastic simulation and the matrix resampling procedure resulted in confidence intervals for λ_s and λ_r that included unity. Moreover, observed population density remained relatively constant through the studied years. All these results appear to indicate long-term population stability of *S. grammicus* at the studied site. If this demographic equilibrium is true, this population might be regulated through density-dependent processes in such a way that if density is reduced, then survival, growth, or fecundity rates could increase. We recognize that this sort of population dynamics can be analyzed using density-dependent matrix models (Grant and Benton 2000; Neubert and Caswell 2000; Caswell 2001). However, we lack information on specific relationships between density and size-specific vital rates required to construct such models. Lacking this information, a density-independent approach can effectively be used to estimate population trends and to determine relative importance of each phase of the life cycle for population persistence (Caswell 2000).

As elasticities indicate the relative contribution of the observed vital rates to the population growth rate (de Kroon et al. 1986, 2000), they have proven useful in pointing out those phases of the life cycle in which conservation efforts would render the greatest benefits (Crouse et al. 1987; Esparza-Olguín et al. 2002; Freedman et al. 2003). In the case of the studied population of *S. grammicus*, the vital rate with the highest elasticity values in all years was the

stasis of asymptotic adults, whereas the most important size class was asymptotic adults as well. To analyze whether changes in the vital rates of asymptotic adults indeed would have the greatest impact on the long-term population fitness in comparison with changes in juveniles and small adults, we simulated increases in survival and fecundity of all size classes and observed their effects on the mean λ ($\lambda_m = 0.955$). A small increase (15%) in the survival (stasis) of the largest size class resulted in a λ_m value above unity (1.016), whereas in other vital rates such as the fecundity or stasis of small adults, a $\lambda_m = 1.00$ would only be obtained with increases >100%. In fact, a 10% simultaneous increase in both survival and fecundity of the asymptotic adults would result in $\lambda_m = 1.01$. A management action that enhances survival of asymptotic adults would yield an increase in the corresponding fecundity entry as well, because we calculated fecundity entries following a postbreeding procedure (Caswell 2001).

However, we recognize that one limitation of elasticities is that they indicate what vital rates contribute the most to the observed population growth rates; they do not implicitly indicate what particular changes in the life cycle would reverse the observed demographic tendency (Silvertown et al. 1996; Mills et al. 1999). A supplementary approach would be to look at the relationship between λ and the relative importance of the life-cycle components (growth, fecundity, and stasis). For *S. grammicus* at PNZ, increases in λ values are associated with increases in the relative contribution of growth and fecundity (see Fig. 4). Thus, for augmenting the overall numerical trend of the population, besides enhancing the survival rate of large adults, it would also be necessary to promote recruitment by the survival (with growth) of juveniles and small adults and by increasing the rate of offspring production.

In conclusion, the demographic evidence that we provide here points out to a demographic equilibrium of the population of *S. grammicus* at PNZ. This might also be the case for other populations of the species as indicated by the population growth rates close to unity observed in previous demographic studies in other localities (Lemos-Espinal et al. 1998; Ortega-Rubio et al. 1999a). Nevertheless, the observed population stasis might be the result of density-dependent processes that in turn might result from habitat limitations. Therefore, *S. grammicus* should be protected from further habitat loss, and hence, we suggest that it maintain its current conservation status (“under special protection”; Secretaría de Medio Ambiente y Recursos Naturales 2001), as central México currently experiences high rates of environmental deterioration.

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