Analysis of the Population Dynamics of an Endangered Lizard (*Xenosaurus grandis*) through the Use of Projection Matrices

J. Jaime Zúñiga-Vega, Teresa Valverde, R. Isaac Rojas-González, and Julio A. Lemos-Espinal

We conducted a demographic analysis from 2000 to 2004 of a population of the crevice-dwelling lizard, *Xenosaurus grandis*, in Veracruz, México. We used population projection matrices to model its population dynamics. Three of the four annual matrices projected an actively growing population, whereas the matrix corresponding to 2003–2004 projected a declining population, apparently associated with a higher-than-average environmental temperature during this period. Observed population structure differed from that expected at equilibrium, according to the four matrices. Highest reproductive values corresponded to adult categories. The transition of newborns and juveniles to larger categories, as well as adult stasis, were the vital rates that made the largest contribution to population growth rate (λ). Growth from one size class to the next was the demographic process that contributed the most to λ, and all size classes had similar elasticities in all years. Stochastic simulations integrating interannual demographic variability projected population growth rates above unity, even under an ecological scenario that consisted of 50% of unfavorable years. Despite this trend toward positive population growth, this *X. grandis* population faces an imminent threat due to the growing industrial development in the region in which it is endemic. Thus, we suggest this population as a primary target for conservation efforts, as well as a change in the conservation category of this species from "special protection" to "threatened."

Llevamos a cabo un análisis demográfico de 2000 a 2004 de una población de la lagartija habitante de grietas *Xenosaurus grandis*, en Veracruz, México. Utilizamos matrices de proyección poblacional para modelar su dinámica poblacional. Tres de las cuatro matrices anuales proyectaron una población creciendo activamente, mientras que la matriz correspondiente a 2003–2004 proyectó una población en declive, aparentemente asociada a un incremento en la temperatura ambiental durante este periodo. La estructura poblacional observada fue diferente de la que se esperaba en el equilibrio de acuerdo con las cuatro matrices. Los valores reproductivos más altos correspondieron a las categorías adultas. La transición de las crías y de los juveniles a categorías superiores, así como la permanencia de los adultos, fueron las fases del ciclo de vida que realizaron la mayor contribución a la tasa de crecimiento poblacional (λ). El crecimiento desde cierta categoría de talla a la siguiente fue el proceso demográfico con la mayor contribución a λ y todas las categorías de talla tuvieron elasticidades similares en todos los años. Las simulaciones estocásticas que integraron la variabilidad demográfica entre años proyectaron tasas de crecimiento poblacional por encima de la unidad, aún bajo un escenario ecológico que consistió de 50% de años desfavorables. A pesar de esta tendencia hacia un crecimiento poblacional positivo, esta población de *X. grandis* enfrenta una amenaza inminente debido al creciente desarrollo industrial que se observa en esta región de la cual es endémica. Por lo tanto, sugerimos que esta población sea considerada como un foco de futuros esfuerzos de conservación, así como que la categoría de conservación de la especie se modifique de estar "sujeta a protección especial" a "amenazada."

D EMOGRAPHIC studies provide basic information to evaluate the current status of extant populations for conservation, management, and control purposes (Caswell, 2000; Williams et al., 2002). Matrix population models have been used to address different aspects of the biology of populations, including evolutionary processes (Franco and Silvertown, 1996), demographic patterns (Golubov et al., 1999), and conservation issues (Contreras and Valverde, 2002). Due to their broad potential applications, these matrix models are currently being used in a wide variety of plant (Esparza-Olguín et al., 2002; Franco and Silvertown, 2004; Hansen and Wilson, 2006) and animal systems (Govindarajulu et al., 2005; Jenouvrier et al., 2005; Ripley and Caswell, 2006). Although the life history and population dynamics of many reptiles are well-

documented (Dunham et al., 1988; Clobert et al., 1998), few studies have related demographic analyses to the evaluation of their extinction probabilities and conservation status (Crouse et al., 1987; Webb et al., 2002; Mitro, 2003).

The genus *Xenosaurus* is the only representative of the family Xenosauridae (Squamata: Sauria; Macey et al., 1999). Species in this genus have a restricted and patchy distribution along the western and southern mountain chains in México, with one subspecies reaching out to Guatemala (Ballinger et al., 2000c). At present, six species have been described (Ballinger et al., 2000c; Pérez-Ramos et al., 2000; Nieto-Montes de Oca et al., 2001), and one of them, *Xenosaurus grandis*, was defined as polytypic, with five subspecies (Ballinger et al., 2000a, 2000c). In general, populations of xenosaurid species are usually restricted to small and often fragmented areas. Consequently, most of them face severe threats that may eventually lead to extinction. Although the mentioned characteristics place xenosaurid species as targets for quantitative analyses with conservation purposes, only *X. newmanorum* has been demographically studied (Lemos-Espinal et al., 2003a). In addition, only three species (*X. grandis*, *X. newmanorum*, and *X. platyceps*) have a current conservation category (''under special protection'') according to the Mexican environmental agency (NOM-059-ECOL-2001). This category is usually assigned to species without enough quantitative information that could support their assignment to a more precise conservation status.

The use of demographic models such as population projection matrices have proved useful in evaluating the conservation status of natural populations (Crouse et al., 1987; Contreras and Valverde, 2002). However, it has been emphasized that the deterministic, time-invariant matrix model has an important limitation: it projects the current population behavior into the future without considering demographic variation (Bierzychudek, 1999; Caswell, 2001). Thus, basing conservation decisions on the analysis of single population projection matrices, which underestimate the effect of temporal variation in the population dynamics, may not lead to the desired results such as recovering populations from declining patterns or maintaining them in quantitative equilibrium. Therefore, it is necessary to document and understand the way in which the demography of populations varies through time and to evaluate the long-term consequences of such variation to have a more realistic picture of the actual conservation status of a species. Stochastic matrix models are a theoretical tool that has been devised to address this problem by incorporating yearly variation in population dynamics (Bierzychudek, 1982; Caswell, 2001; Mandujano et al., 2001). In this study we use this approach to address the demography of a population of *X. grandis*.

Xenosaurus grandis is a medium-sized, knob-scaled lizard that exclusively inhabits rock crevices (Ballinger et al., 1995). It shares most of its ecological and physiological traits with other species of the genus, such as low metabolic rates, ''sit-and-wait'' foraging behavior, a diet composed mainly of arthropods, low ability to actively thermoregulate, and viviparity (Ballinger et al., 1995; Lemos-Espinal et al., 1997, 2003b). Its reproductive cycle is biennial with a nine-month gestation period and an average clutch size of 5.1 (Ballinger et al., 2000b). Females mature at ca. 100 mm snout–vent length (SVL) and an average age of 32 months, whereas males mature at ca. 95 mm SVL and an average age of 28 months (Ballinger et al., 2000b; Smith et al., 2000; Zúñiga-Vega et al., 2005).

Subspecies *Xenosaurus grandis grandis* is endemic to the surroundings of the town of Cuautlapan between the cities of Orizaba and Córdoba in the state of Veracruz, México (Ballinger et al., 2000a, 2000c). The category of subspecies will change to specific status as *Xenosaurus grandis* according to a current taxonomic revision (A. Nieto-Montes de Oca, unpubl. data). Intensive monitoring in the region has led us to conclude that this species may have been reduced to only two populations, mostly because the area that surrounds Orizaba and Córdoba is highly deteriorated due to human activities. Therefore, the present study pursued three main objectives: (1) to describe and analyze the main demographic features of one population of *X. grandis* through the use of population projection matrices; (2) to document the extent of temporal variation in the demographic behavior of this population; and (3) to integrate this demographic variability using stochastic simulations to evaluate the long-term persistence probabilities of this population under different ecological scenarios.

MATERIALS AND METHODS

Study site.—We delimited a 5-ha plot in the eastern slope of the Buena Vista mountain (18°52′N, 97°01′W) near the town of Cuautlapan between the cities of Orizaba and Córdoba, in the Mexican state of Veracruz. Vegetation in the area corresponds to a semi-deciduous tropical forest (*sensu* Rzedowski, 1978). The study plot occurred within a coffee–orange–mango plantation established among dense secondary vegetation; this habitat, although not pristine, is typical

of the kind of environment usually occupied by this species. Limestone rocks were abundant under the canopy, which in turn provided microhabitats (rock crevices) for individual *X. grandis*. The climate in the region is markedly seasonal, with a wet season from May to October (rainfall ca. 2100 mm) and a relatively dry season from November through April (rainfall ca. 360 mm; Zúñiga-Vega et al., 2005). Mean annual temperature is 21.8 C, with a maximum in April (39.5 C) and a minimum in January (4 C). Buena Vista mountain, as well as most of the hills and mountains near Orizaba and Córdoba, is currently experiencing rapid environmental deterioration due to intense human activities in the region (industry, cattle breeding, and agriculture).

Field methods.—We visited the study site once per month from May 2000 to October 2004. A capture consisted of locating and extracting a lizard from a rock crevice. On each visit we surveyed all the rock crevices within the study plot. This resulted in equal capture probability across the whole year, given that these lizards spend most (ca. 95%) of their time completely inside such microhabitats, regardless of the time of the day or the time of the year (Ballinger et al., 1995). Demographic data were obtained from marking and recapturing lizards. Each individual lizard was marked with a specific number by toe-clipping. From each lizard captured during a monthly visit, we registered snout–vent length (SVL), body mass, and sex. Lizards were released into the same crevice that they were occupying.

Survival estimates.—To calculate survival rates from one year to the following, we considered only resident individuals (lizards with two or more recaptures; Ballinger, 1973), thus avoiding the inclusion of migratory animals. We estimated survival rate as the proportion of resident lizards originally registered in the wet season of any year that were recaptured during the following wet season. Because individual *X. grandis* appear to be highly loyal to one or two crevices during their entire life and because during the study period we extensively sampled virtually all suitable microhabitats (rock crevices) for these lizards, we assumed that we marked and followed a considerable fraction of the population (if not the entire population), yielding accurate survival estimates. In addition, during the final stages of the field work, almost every new mark corresponded to newborn animals, which provided extra support for our assumption that our survival estimates were derived from resident lizards. We obtained survivorship data for four

annual transitions: 2000–2001, 2001–2002, 2002–2003, and 2003–2004.

Matrix analyses.—The *X. grandis* population was subdivided into four size classes: (1) yearlings, which included all individuals from birth to 71 mm snout–vent length (SVL), the size that corresponds to one year of age (Zúñiga-Vega et al., 2005); (2) juveniles, which included >71 mm SVL to 100 mm SVL in females and to 95 mm SVL in males (minimum size at maturity for each sex; Ballinger et al., 2000b; Smith et al., 2000); (3) adults I, which included all those lizards between >100 or >95 mm SVL (for females and males, respectively) and 112 mm SVL; and (4) adults II or ''asymptotic adults,'' which were lizards larger than 112 mm SVL, at which size we began to register zero growth rates (Zúñiga-Vega et al., 2005). Data from males and females were pooled because we did not find significant differences in survival rates between sexes at any size class according to a two-way ANOVA with sex and size class as categorical factors (sex: $F_{1,24}$ = 0.05, P = 0.83; size class: $F_{3,24}$ = 2.20, P = 0.12).

Four 4 × 4 transition matrices were constructed, each corresponding to one of the four studied annual periods. The entries in these matrices summarized the survival, growth, and fecundity rates of the different life-cycle phases represented by the four size classes. Each matrix entry (a_{ij}) represents the transition probability or the mean contribution of an average individual in size class j (columns) to size class i (rows) as per Caswell (2001). Entries corresponding to permanence of individuals in their same size class (i.e., ''stasis,'' represented in the main diagonal of the matrices) or to the growth of individuals to the following category (represented by the subdiagonal of the matrices) were derived from the estimated survival rates. Therefore, annual survival rates were partitioned into two processes: surviving and remaining in the same size class (stasis), and surviving and growing to a superior size class (growth).

We could not estimate variation in fecundity among years, although we collected 15 presumably pregnant females each year. Of these, only seven gave birth in the laboratory during the entire study period. We hypothesize that the remaining females either retained and reabsorbed their embryos due to stress or were simply mistakenly considered pregnant. Thus, we used only two litter size estimates to calculate fecundity entries (first row of the matrices) for the four annual transition matrices. Fecundity of adults I was calculated by multiplying litter size estimated in the laboratory (4.5 neonates per female, n = 7

females) by the product of the proportion of reproductive females each year (0.5; Ballinger et al., 2000b) and the survival rate of adults I in the corresponding annual transition. We considered survival rate in the fecundity entries because it was necessary to account for the survival probability of females before they can reach birth season (late summer; Zúñiga-Vega et al., 2005). This fecundity estimate corresponds to a post-breeding type (Caswell, 2001). Fecundity of adults II was calculated by multiplying previously reported litter size (5.1 neonates per female; Ballinger et al., 2000b) by the product of 0.5 and the survival rate of adults II. We arbitrarily assigned the larger clutch size estimate (5.1) to the superior reproductive size class to reflect the positive relationship between SVL and fecundity in *X. grandis* (Ballinger et al., 2000b).

We used the power method to obtain the dominant eigenvalue of each matrix, which represents the finite rate of population increase (λ) for the corresponding annual transition. We also obtained the right (w) and left (v) eigenvectors associated with each λ, which represent the stable size class distribution and the size-specific reproductive values, respectively (Caswell, 2001). Confidence intervals for the λ values were constructed according to the analytical method proposed by Alvarez-Buylla and Slatkin (1991). We tested for differences between projected (w eigenvectors) and observed size class distributions using χ^2 tests.

We calculated elasticity matrices (de Kroon et al., 1986, 2000; Caswell, 2001) to estimate the relative change in λ that would result from relative changes in matrix entries. Entries in the elasticity matrices were calculated as:

$$e_{ij} = s_{ij} \times (a_{ij} / \lambda)$$

where s_{ij} is the absolute sensitivity of λ to absolute changes in the corresponding matrix entry ($s_{ij} = \partial \lambda / \partial a_{ij}$). Elasticities are standardized sensitivities, and thus, are useful to compare the relative contribution of each matrix entry to population growth rate (de Kroon et al., 1986, 2000). Entries in an elasticity matrix sum to unity (Mesterton-Gibbons, 1993), which allowed us to quantify the relative contribution of different demographic processes (i.e., growth, stasis, and fecundity) and of different size classes to population growth rate by simply adding elasticity values corresponding to each process or category (Silvertown et al., 1993).

Stochastic simulations.—Bierzychudek (1982) developed a method to incorporate stochastic interannual demographic variation into the projection of the long-term numerical behavior of a population. According to this method, each iteration in the population projection through time (i.e., multiplication of the matrix by a vector representing current population structure to obtain population structure in the following year), is carried out with a different matrix chosen at random from the available matrices representing the demographic behavior of the population in different years. In this case, we used the four annual transition matrices of the *X. grandis* population.

Different stochastic simulations were conducted, representing distinct ecological scenarios, which differed in the probability of choosing each of the four matrices during the iteration process. In the first simulation, we assigned the same probability (0.25) to the four matrices. In the rest of the simulations, we assigned different probabilities to each matrix depending on the probability of occurrence of years with different climatic conditions. To do this, we first evaluated the correlation between estimated population growth rates and different climatic variables for the corresponding years, using monthly climate data obtained for the period 1970–2003 (precipitation, mean, maximum and minimum temperatures, and temperature range) from the weather station "El Naranjal" (Comisión Federal de Electricidad), located seven km southeast of the study site. The λ values obtained from matrix analysis showed marginally significant negative correlations with both mean annual temperature ($r = -0.942$, $t_2 = -3.97$, $P = 0.058$) and mean temperature during the rainy season ($r = -0.946$, $t_2 = -4.13$, $P = 0.054$). Therefore, we assumed that high temperatures have a negative impact on λ in this population (2003–2004 was the warmest annual transition and yielded a λ below unity).

We used the above information to assign different probabilities of occurrence to the four annual matrices for conducting the rest of the stochastic simulations. Thus, for the second simulation we used probabilities of occurrence of 0.3088, 0.3088, 0.2647, and 0.1176. These probabilities correspond to the relative frequencies of years ($n = 34$ years, from 1970 to 2003) with temperatures similar to those observed in the studied years. In other words, the relative frequency of years with mean temperature of the wet months below 24 C was 0.6176; as transitions 2000–2001 and 2001–2002 showed mean temperatures of the wet months below 24 C, we split up the corresponding relative frequency into two (0.6176/2 = 0.3088) and assigned this value to the probability of such matrices. The relative frequency of years with mean temperature of the

TABLE 1. POPULATION PROJECTION MATRICES AND MAIN DEMOGRAPHIC RESULTS FOR THE *Xenosaurus grandis* POPULATION STUDIED DURING FOUR ANNUAL TRANSITIONS. q_x = mortality per size class, n_x = number of resident lizards per size class from which transition probabilities were calculated, w = projected stable size class distribution, v = size-specific reproductive values.

	Yearlings	Juveniles	Adults I	Adults II	n_x	w	v
2000–2001							
Yearlings	0.4	0	2.1316	2.0132	10	0.575	1
Juveniles	0.3	0.3125	0	0	16	0.178	2.98
Adults I	0	0.625	0.2105	0	19	0.101	4.68
Adults II	0	0	0.7368	0.7895	19	0.148	3.99
q_x	0.3	0.0625	0.0527	0.2105			
2001–2002							
Yearlings	0.0571	0	1.7561	2.0306	35	0.408	1
Juveniles	0.7429	0.3714	0	0	35	0.319	1.7
Adults I	0	0.4571	0.2439	0	41	0.135	3.55
Adults II	0	0	0.5366	0.7963	54	0.138	3.86
q_x	0.2	0.1715	0.2195	0.2037			
2002–2003							
Yearlings	0.2308	0	1.2434	1.5412	26	0.454	1
Juveniles	0.5769	0.0833	0	0	60	0.251	1.55
Adults I	0	0.65	0.1316	0	38	0.164	2.5
Adults II	0	0	0.4211	0.6044	91	0.132	2.95
q_x	0.1923	0.2667	0.4473	0.3956			
2003–2004							
Yearlings	0.069	0	1.148	1.1027	29	0.474	1
Juveniles	0.2759	0.1875	0	0	32	0.197	2.83
Adults I	0	0.625	0.1837	0	49	0.185	3.01
Adults II	0	0	0.3265	0.4324	74	0.144	2.63
q_x	0.6551	0.1875	0.4898	0.5676			

wet months between 24 C and 24.3 C was 0.2647; thus, we used this value as the probability of occurrence of matrix 2002–2003, because this transition showed a mean temperature of the wet months of 24.08 C. The relative frequency of years with mean temperature of the wet months above 24.3 C was 0.1176, the value that we used as the probability of occurrence of matrix 2003–2004, because this transition showed a mean temperature of the wet months of 24.38 C. Finally, we conducted other simulations increasing the probability of occurrence of warm years (i.e., increasing the probability assigned to the 2003–2004 matrix, which was associated with the lowest λ) to estimate the frequency of ''unfavorable'' years that would cause a significant local extinction risk.

Each simulation consisted of 30 replicates (runs) of 1000 iterations each. On each run, the slope of the regression between natural logarithm of projected population size against time (years) was considered a measure of the intrinsic rate of population increase (r), from which a λ value under these stochastic conditions (λ_s) could then be calculated ($\lambda_s = e^r$; Bierzychu-

dek, 1982). We report mean λ_s values obtained over the 30 runs for each simulation, as well as the relative frequency of λ_s values below unity within the 30 runs, which was considered an estimate of local extinction probability (Mondragón et al., 2004; Valverde et al., 2004).

RESULTS

A total of 521 lizards was marked during the study period, from which 259 were females and 262 were males. This sex ratio was not significantly different from 1:1 ($\chi^2_1 = 0.5543$, $P = 0.45$). Average survival rate across all size classes and all annual transitions was 0.705. Mortality was not notably higher in any size class when considering data for all annual transitions together (yearlings = 0.337, juveniles = 0.172, adults I = 0.302, adults II = 0.344). However, annual transition 2003–2004 resulted in the highest overall mortality (0.495) and the highest mortalities for yearlings, adults I, and adults II (Table 1).

Matrix analyses.—The matrices of the first three annual periods projected a population growth
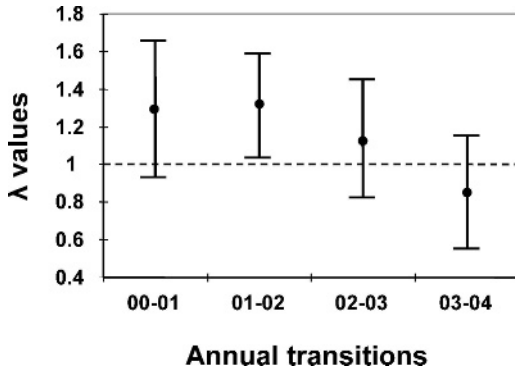
Fig. 1. Projected population growth rates (λ) with their respective 95% confidence intervals for each of the four constructed transition matrices.

rate above unity ($\lambda_{00-01} = 1.29 \pm 0.36$, $\lambda_{01-02} = 1.32 \pm 0.28$, and $\lambda_{02-03} = 1.13 \pm 0.31$; Fig. 1), whereas the matrix corresponding to the period 2003–2004 yielded a population growth rate below unity ($\lambda_{03-04} = 0.85 \pm 0.30$; Fig. 1). Although the first three annual transitions projected population increases, only the λ value from matrix 2001–2002 ($\lambda_{01-02} = 1.323 \pm 0.278$) was greater than unity with 95% confidence (Fig. 1). According to the confidence intervals for λ, the projected population growth rates for the first two annual transitions (λ_{00-01} and λ_{01-02}) differed significantly from that obtained in 2003–2004 (λ_{03-04}) because the former values were higher than the upper limit of the confidence interval of the latter (Fig. 1).

Projected stable-size class distributions (vectors w in Table 1) were significantly different than observed population structure in all annual transitions (2000–2001: $\chi^2_3 = 77.64$, $P < 0.0001$; 2001–2002: $\chi^2_3 = 75.71$, $P < 0.0001$; 2002–2003: $\chi^2_3 = 200.83$, $P < 0.0001$; 2003–2004: $\chi^2_3 = 131.1$, $P < 0.0001$). Size-specific reproductive values (vectors v in Table 1) showed a general pattern: the highest reproductive values were observed in the adult categories, with the exception of transition 2003–2004, where juveniles exhibited a greater value (2.83) than adults II (2.63; Table 1).

Highest elasticity values generally corresponded to growth of yearlings and juveniles as well as to permanence (i.e., stasis) of adults II (Table 2). However, the 2002–2003 and 2003–2004 matrices, which yielded the lowest λ values (1.127 and 0.851, respectively), resulted in relatively lower elasticities for the stasis of adults II. The lowest elasticity values corresponded to stasis of yearlings, juveniles, and adults I in all annual transitions (Table 2). Summing up the elasticity entries corresponding to different de-

TABLE 2. ELASTICITY MATRICES CORRESPONDING TO EACH OF THE FOUR ANNUAL TRANSITION MATRICES FOR THE *Xenosaurus grandis* POPULATION. Highest elasticities are shown in bold type.

	Yearlings	Juveniles	Adults I	Adults II
2000–2001				
Yearlings	0.08	0	0.08	0.11
Juveniles	**0.18**	0.06	0	0
Adults I	0	**0.18**	0.04	0
Adults II	0	0	0.11	**0.17**
2001–2002				
Yearlings	0.01	0	0.09	0.11
Juveniles	**0.20**	0.08	0	0
Adults I	0	**0.20**	0.05	0
Adults II	0	0	0.11	**0.16**
2002–2003				
Yearlings	0.06	0	0.11	0.11
Juveniles	**0.22**	0.02	0	0
Adults I	0	**0.22**	0.03	0
Adults II	0	0	0.11	0.13
2003–2004				
Yearlings	0.02	0	0.13	0.09
Juveniles	**0.22**	0.06	0	0
Adults I	0	**0.22**	0.06	0
Adults II	0	0	0.09	0.10

mographic processes, growth was the demographic process with the highest relative contribution to population growth rate in all annual periods (Table 3). Fecundity and stasis had lower and similar summed elasticities (between 0.2 and 0.29), except in transition 2000–2001, for which stasis had 0.34 and fecundity had 0.19. Analyzing elasticity values per size class, it was noticeable that the summed elasticities per size classes had a similar pattern. No size class could be singled

TABLE 3. ELASTICITIES PER DEMOGRAPHIC PROCESS AND SIZE CLASS CORRESPONDING TO EACH OF THE FOUR ANNUAL TRANSITION MATRICES FOR THE *Xenosaurus grandis* POPULATION.

	2000–2001	2001–2002	2002–2003	2003–2004
Demographic process				
Fecundity	0.19	0.20	0.22	0.22
Growth	0.47	0.51	0.55	0.54
Stasis	0.34	0.29	0.23	0.24
Size class				
Yearlings	0.27	0.21	0.28	0.25
Juveniles	0.24	0.28	0.24	0.28
Adults I	0.22	0.24	0.25	0.28
Adults II	0.27	0.27	0.23	0.19

out for its high contribution to population growth rate in any particular year; elasticity values per size class varied between 0.19 and 0.28 (Table 3).

Stochastic simulations.—The first simulation exercise, assuming that all matrices had the same probability of representing the demographic behavior of the population in any particular year (i.e., 0.25), resulted in a λ_s value that indicated a considerable potential for population increase ($\lambda_s = 1.154$; Fig. 2A, Table 4), although wide fluctuations in population size were projected (Fig. 2B). Similarly, the second simulation exercise, which incorporated the relative frequencies of years with temperature patterns corresponding to those of the four study years, also yielded a λ_s value markedly above unity ($\lambda_s = 1.22$; Fig. 2C; Table 4) with potential for faster population growth through time (Fig. 2D). In the following simulation exercises, we gradually increased the probability of ''unfavorable'' years (represented by the matrix 2003–2004, $\lambda_{03-04} = 0.851$). We did not obtain λ values below unity from the population projections when increasing the relative frequency of such years to 0.4 and 0.5 (Fig. 2E, 2G; Table 4), although considerable population fluctuations were projected (Fig. 2F, 2H). However, when we assigned a probability of 0.6 to the occurrence of unfavorable years, we obtained a considerable frequency of λ values below unity (30%), which was interpreted as the probability of local extinction under this last scenario (Fig. 2I, 2J; Table 4).

DISCUSSION

Average survival rate observed for *Xenosaurus grandis* lizards is relatively high (0.705) when compared to similar-sized lizard species from other genera and families (Turner, 1977; James, 1991; Germano and Williams, 2005) and even higher when contrasting it with survival values reported for smaller species, such as some representative members from the genera *Anolis* and *Sceloporus* (Roughgarden, 1995; Clobert et al., 1998). This difference can be attributed, at least partially, to phylogenetic effects. All members of Anguimorph families, such as Xenosauridae, are late-maturing, long-lived species, whereas most iguanians and small skinks are early-maturing, short-lived species (Dunham et al., 1988; Pianka and Vitt, 2003). Additionally, the strictly crevice-dwelling habit of *X. grandis* could contribute to the high survival probability of these organisms. These lizards spend most (ca. 95%) of their time completely inside rock crevices (Ballinger et al., 1995), which appear to be safe refuges. In fact, high survival rates occur in other members of the genus *Xenosaurus*, all of which are strictly crevice-dwellers (Lemos-Espinal et al., 1997, 2003c, 2004). For instance, *X. newmanorum* exhibited an average annual survival rate of 0.73 (Lemos-Espinal et al., 2003a), that of *X. platyceps* was 0.67 (I. Rojas-González, unpubl. data), and that of a still undescribed species from northeastern Querétaro, México, was 0.7 (G. Zamora-Abrego, unpubl. data).

The demographic results from our first three annual periods (2000–2001, 2001–2002, and 2002–2003) indicated considerable potential for population growth. However, the 2003–2004 transition yielded a λ value below unity, which suggests that yearly demographic variation may be substantial in this population. In addition, in all years, observed size class distributions were different from those expected at equilibrium. These results suggest that this population may be experiencing considerable fluctuations among years, responding demographically to the occurrence of favorable or unfavorable years. This temporal demographic variation is presumably correlated with interannual environmental variation and may be leading the population far from a stable stage distribution.

The lowest projected population growth rate ($\lambda_{03-04} = 0.851$) appeared to be associated with an increase in the annual temperature because that year had a mean temperature of the wet months above 24.3 C and less than 12% of the last 34 years had shown such warm conditions. This high temperature should have exerted a negative impact mainly on lizard survival because we registered considerably higher mortalities in almost all size classes during this year (Table 1). Unfortunately, we could not estimate temporal variation in fecundity or the effect that increase in annual temperature may have upon offspring production.

Highest elasticities corresponded to growth of yearlings and juveniles, as well as to the stasis of the largest reproductive size class. As elasticities can be interpreted as measurements of the intensity of natural selection acting on different life-cycle phases (Benton and Grant, 1999; van Tienderen, 2000), these results suggest the existence of high selection pressures for rapid size increase during early life-cycle stages and for high adult survival. The long time period elapsed between birth and first reproduction in *X. grandis* (28–32 months; Zúñiga-Vega et al., 2005) can account for the high relative importance of newborn and juvenile growth. Meanwhile, a high survival probability combined with a high reproductive value can account for the high contribution of adult stasis to population growth rate.
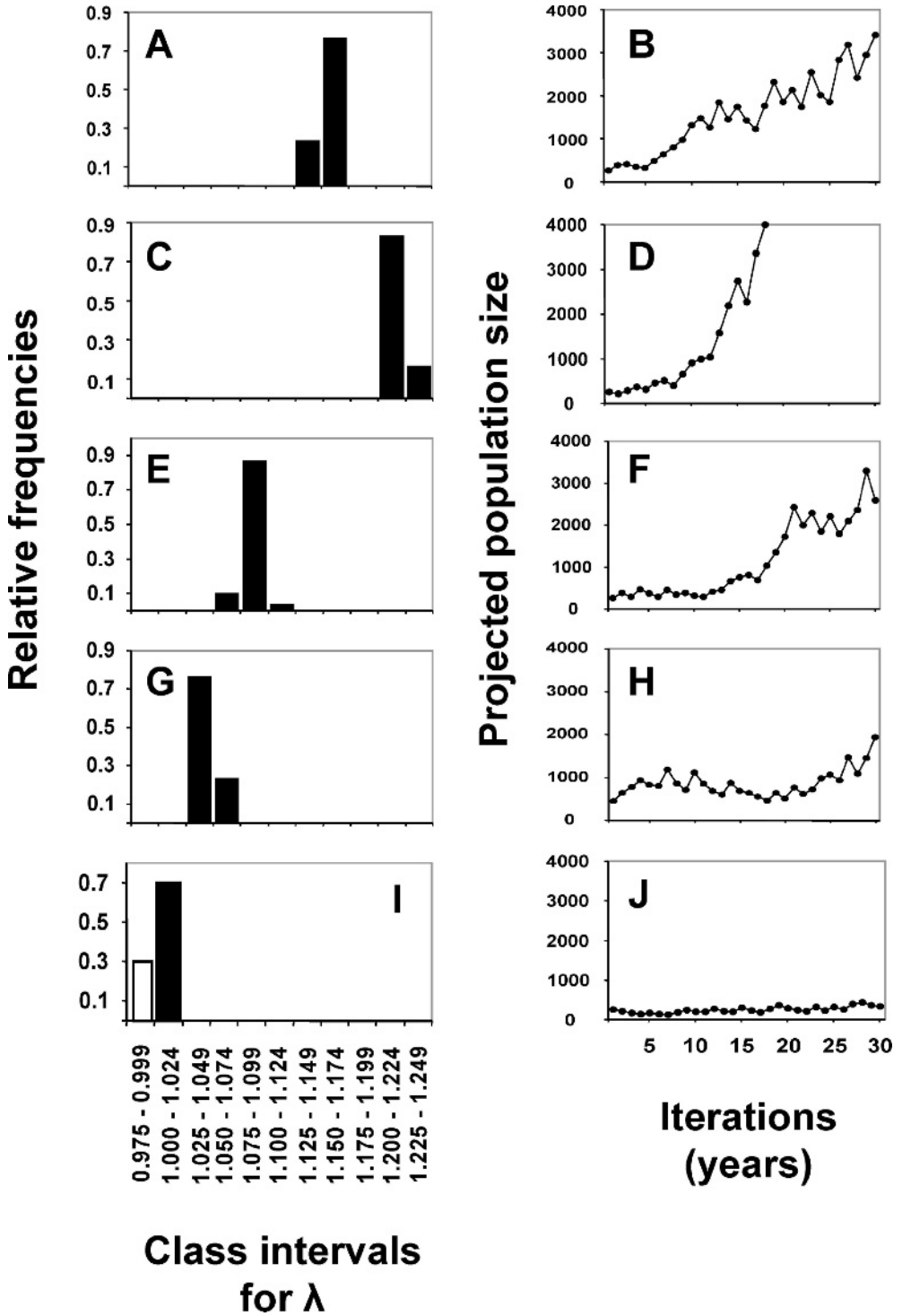
Fig. 2. Relative frequencies of λ_s values obtained in each simulation exercise (left column) and examples of population numerical behavior for the first 30 years for each simulated scenario (right column): (A, B) all matrices with equal probability; (C, D) matrices 00–01 and 01–02 = 0.3088, matrix 02–03 = 0.2647, matrix 03–04 = 0.1176; (E, F) 40% of unfavorable years; (G, H) 50% of unfavorable years; (I, J) 60% of unfavorable years. White bar in (I) represents relative frequency of λ_s values below unity.

TABLE 4.   MAIN RESULTS OF THE STOCHASTIC SIMULATIONS. We show probabilities assigned to each matrix on each simulation exercise, resultant average stochastic population growth rates (λ_s), and estimated extinction probabilities.

	Simulation exercise	Average λ_s	Extinction probability
1.	All matrices with equal probability = 0.25	1.154	0.0
2.	Matrices 00–01 and 01–02 = 0.3088 Matrix 02–03 = 0.2647 Matrix 03–04 = 0.1176	1.22	0.0
3.	Matrices 00–01, 01–02, and 02–03 = 0.2 Matrix 03–04 = 0.4	1.086	0.0
4.	Matrices 00–01, 01–02, and 02–03 = 0.1666 Matrix 03–04 = 0.5	1.045	0.0
5.	Matrices 00–01, 01–02, and 02–03 = 0.1333 Matrix 03–04 = 0.6	1.003	0.3

Growth, defined as survival to the next size class, was the demographic process with the greatest relative contribution to population growth rate. This pattern is common in populations with λ values above unity and can be explained by considering that growing individuals eventually move to reproductive categories where their contribution to the population growth rate is evident (Valverde and Silvertown, 1998). All size classes exhibited similar relative contributions to λ in all years in spite of the observed interannual variation in λ values, which suggests that this pattern may be characteristic of the species. The similar relative importance of all the phases of the life cycle indicates that conservation efforts should be focused on the whole life cycle in order to ensure the persistence of this population.

It is important to recognize that our failure in estimating interannual variation in fecundity could have biased our overall results and conclusions. If fecundity is highly variable in response to the same environmental factors as the rest of the vital rates, we could expect that the resulting variation in λ would be more dramatic than that observed. However, if fecundity varies in response to different environmental variables, a buffering of the observed variation could have taken place. The accuracy of fecundity values used in all matrices (4.5 and 5.1 newborns per female) remains to be tested. If they were too high compared to the actual ones, population growth rates could have resulted closer to unity, indicating a more stable population. We addressed this issue by running an average matrix (obtained by averaging the elements of each of the four yearly matrices) in which we modified the value of the fecundity entries. Figure 3 shows that population growth rates close to unity or

lower were obtained when average fecundity was reduced to approximately two newborns per female (5.1 and 4.5 minus ca. three newborns) or to less than that. This reduction does not seem to reflect a realistic situation because we never observed clutches of less than four and the minimum clutch size reported is precisely two (n = 68 females; Ballinger et al., 2000b). Nevertheless, average values of two young per female could be achieved if an even lower proportion of the females in the population reproduce in a given year. Thus, a deeper exploration of the reproductive patterns of this population would be necessary before reaching more conclusive results in relation to its potential long-term fate.

When integrating the effect of interannual demographic variation through the stochastic
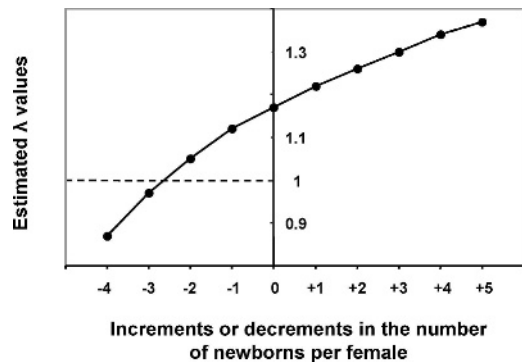

Fig. 3.   Estimated λ values from running average matrices where we modified the fecundity entries by decreasing and increasing them in the number of offspring per female. Notice that the zero in the x-axis corresponds to the values used in the original analyses: 4.5 and 5.1 newborns for adults I and adults II, respectively. Therefore, -1 corresponds to 3.5 and 4.1, -2 to 2.5 and 3.1, etc.

simulations, we observed considerable potential for population growth, even when the frequency of unfavorable years approached 50%. However, a higher frequency of occurrence of warm years would result in drastic population fluctuations, and further increases (i.e., beyond 50%) would place this population under significant extinction risk. Although current trends in global climate change predict yearly temperature increases (Houghton, 2004), 50–60% of warm years in the near future at the study site seem to be an unrealistic scenario. On the other hand, the growing industrial development currently taking place between the cities of Orizaba and Córdoba poses a serious actual threat for this population. In fact, Buena Vista mountain belongs to a cement factory, whose activities include mountain demolition to obtain raw materials for the production of construction cement.

The Mexican environmental agency (Secretaría de Medio Ambiente y Recursos Naturales) has given *Xenosaurus grandis* the category ''under special protection'' (NOM-059-ECOL-2001). This category is often assigned to taxa for which the lack of information regarding their actual status does not allow a more accurate classification. However, considering the highly restricted distribution range of this species, the scarcity of abundant populations, and its highly-specific microhabitat requirements (i.e., abundant rock crevices under the vegetation canopy), in addition to the potentially great impact of local human activities upon this population, we strongly suggest that the appropriate category for *Xenosaurus grandis* should be ''threatened.'' Additionally, given the apparent stability and viability of the studied population, we also suggest that it should be a primary target for conservation efforts.

LITERATURE CITED

ALVAREZ-BUYLLA, E. R., AND M. SLATKIN. 1991. Finding confidence limits on population growth rates. Trends in Ecology and Evolution 6:221–224.

BALLINGER, R. E. 1973. Comparative demography of two viviparous iguanid lizards (*Sceloporus jarrovi* and *Sceloporus poinsetti*). Ecology 54:269–283.

BALLINGER, R. E., J. A. LEMOS-ESPINAL, S. SANOJA-SARABIA, AND N. R. COADY. 1995. Ecological observations of the lizard, *Xenosaurus grandis* in Cuautlapan, Veracruz, México. Biotropica 27:128–132.

BALLINGER, R. E., J. A. LEMOS-ESPINAL, AND G. R. SMITH. 2000a. *Xenosaurus grandis* (Gray). Knob-scaled lizard. Catalogue of American Amphibians and Reptiles 713:1–4.

BALLINGER, R. E., J. A. LEMOS-ESPINAL, AND G. R. SMITH. 2000b. Reproduction in females of three species of crevice-dwelling lizards (genus *Xenosaurus*) from Mexico. Studies on Neotropical Fauna and Environment 35:179–183.

BALLINGER, R. E., G. R. SMITH, AND J. A. LEMOS-ESPINAL. 2000c. *Xenosaurus*. Catalogue of American Amphibians and Reptiles 712:1–3.

BENTON, T. G., AND A. GRANT. 1999. Elasticity analysis as an important tool in evolutionary and population ecology. Trends in Ecology and Evolution 14:467–471.

BIERZYCHUDEK, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes sex. Ecological Monographs 52:335–351.

BIERZYCHUDEK, P. 1999. Looking backwards: assessing the projections of a transition matrix model. Ecological Applications 9:1278–1287.

CASWELL, H. 2000. Prospective and retrospective perturbation analysis: their roles in conservation biology. Ecology 81:619–627.

CASWELL, H. 2001. Matrix Populations Models, 2nd Edition. Sinauer, Sunderland, Massachusetts.

CLOBERT, J., T. GARLAND, AND R. BARBAULT. 1998. The evolution of demographic tactics in lizards: a test of some hypotheses concerning life history evolution. Journal of Evolutionary Biology 11:329–364.

CONTRERAS, C., AND T. VALVERDE. 2002. Evaluation of the conservation status of a rare cactus (*Mammillaria crucigera*) through the analysis of its population dynamics. Journal of Arid Environments 51:89–102.

CROUSE, D. T., L. B. CROWDER, AND H. CASWELL. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412–1423.

DE KROON, H., A. PLAISIER, J. M. VAN GROENENDAEL, AND H. CASWELL. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67:1427–1431.

DE KROON, H., J. M. VAN GROENENDAEL, AND J. EHRLÉN. 2000. Elasticities: a review of methods and model limitations. Ecology 81:607–618.

DUNHAM, A. E., D. B. MILES, AND D. N. REZNICK. 1988. Life history patterns in squamate reptiles, p. 441–

522. *In*: Biology of the Reptilia, Vol. 15. C. Gans and R. B. Huey (eds.). Academic Press, New York.

ESPARZA-OLGUÍN, L., T. VALVERDE, AND E. VILCHIS-ANAYA. 2002. Demographic analysis of a rare columnar cactus (*Neobuxbaumia macrocephala*) in the Tehuacan Valley, México. Biological Conservation 103:349–359.

FRANCO, M., AND J. SILVERTOWN. 1996. Life history variation in plants: an exploration of the fast-slow continuum hypothesis. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 351:1341–1348.

FRANCO, M., AND J. SILVERTOWN. 2004. A comparative demography of plants based upon elasticities of vital rates. Ecology 85:531–538.

GERMANO, D. J., AND D. F. WILLIAMS. 2005. Population ecology of blunt-nosed leopard lizards in high elevation foothill habitat. Journal of Herpetology 39:1–18.

GOLUBOV, J., M. C. MANDUJANO, M. FRANCO, C. MONTAÑA, L. E. EGUIARTE, AND J. LÓPEZ-PORTILLO. 1999. Demography of the invasive woody perennial *Prosopis glandulosa* (honey mesquite). Journal of Ecology 87:955–962.

GOVINDARAJULU, P., R. ALTWEGG, AND B. R. ANHOLT. 2005. Matrix model investigation of invasive species control: bullfrogs on Vancouver island. Ecological Applications 15:2161–2170.

HANSEN, M. J., AND S. D. WILSON. 2006. Is management of an invasive grass *Agropyron cristatum* contingent on environmental variation? Journal of Applied Ecology 43:269–280.

HOUGHTON, J. T. 2004. Global Warming: The Complete Briefing, 3rd Edition. Cambridge University Press, Cambridge, U.K.

JAMES, C. D. 1991. Population dynamics, demography, and life history of sympatric scincid lizards (*Ctenotus*) in central Australia. Herpetologica 47:194–210.

JENOUVRIER, S., C. BARBRAUD, AND H. WEIMERSKIRCH. 2005. Long-term contrasted responses to climate of two Antarctic seabird species. Ecology 86:2889–2903.

LEMOS-ESPINAL, J. A., G. R. SMITH, AND R. E. BALLINGER. 1997. Natural history of *Xenosaurus platyceps*, a crevice dwelling lizard from Tamaulipas, Mexico. Herpetological Natural History 5:181–186.

LEMOS-ESPINAL, J. A., G. R. SMITH, AND R. E. BALLINGER. 2003a. Variation in growth and demography of a knob-scaled lizard (*Xenosaurus newmanorum*: Xenosauridae) from a seasonal tropical environment in Mexico. Biotropica 35:240–249.

LEMOS-ESPINAL, J. A., G. R. SMITH, AND R. E. BALLINGER. 2003b. Diets of three species of knob-scaled lizards (genus *Xenosaurus*) from México. Southwestern Naturalist 48:119–122.

LEMOS-ESPINAL, J. A., G. R. SMITH, AND R. E. BALLINGER. 2003c. Ecology of *Xenosaurus grandis agrenon*, a knob-scaled lizard from Oaxaca, México. Journal of Herpetology 37:192–196.

LEMOS-ESPINAL, J. A., G. R. SMITH, AND R. E. BALLINGER. 2004. Aspects of the ecology of a distinct population of *Xenosaurus platyceps* from Querétaro, México. Amphibia–Reptilia 25:204–210.

MACEY, J. R., J. A. SCHULTE II, A. LARSON, B. S. TUNIYEV, N. ORLOV, AND T. J. PAPENFUSS. 1999. Molecular phylogenetics, tRNA evolution, and historical biogeography in anguid lizards and related taxonomic families. Molecular Phylogenetics and Evolution 12:250–272.

MANDUJANO, M. C., C. MONTAÑA, M. FRANCO, J. GOLUBOV, AND A. FLORES-MARTÍNEZ. 2001. Integration of demographic annual variability in a clonal desert cactus. Ecology 82:344–359.

MESTERTON-GIBBONS, M. 1993. Why demographic elasticities sum to one: a postscript to de Kroon et al. Ecology 74:2467–2468.

MITRO, M. G. 2003. Demography and viability analyses of a diamondback terrapin population. Canadian Journal of Zoology 81:716–726.

MONDRAGÓN, D., R. DURÁN, I. RAMÍREZ, AND T. VALVERDE. 2004. Temporal variation in the demography of the clonal epiphyte *Tillandsia brachycaulos* (Bromeliaceae) in the Yucatán Península, Mexico. Journal of Tropical Ecology 20:189–200.

NIETO-MONTES DE OCA, A., J. A. CAMPBELL, AND O. FLORES-VILLELA. 2001. A new species of *Xenosaurus* (Squamata: Xenosauridae) from the Sierra Madre del Sur of Oaxaca, México. Herpetologica 57:32–47.

NORMA OFICIAL MEXICANA. 2001. (NOM-059-ECOL-2001). Protección ambiental. Especies nativas de México de flora y fauna silvestres. Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio. Lista de especies en riesgo. Diario Oficial de la Federación, Instituto Nacional de Ecología, México.

PÉREZ-RAMOS, E., L. SALDAÑA DE LA RIVA, AND J. A. CAMPBELL. 2000. A new allopatric species of *Xenosaurus* (Squamata: Xenosauridae) from Guerrero, México. Herpetologica 56:500–506.

PIANKA, E. R., AND L. J. VITT. 2003. Lizards: Windows to the Evolution of Diversity. University of California Press, Berkeley, California.

RIPLEY, B. J., AND H. CASWELL. 2006. Recruitment variability and stochastic population growth of the soft-shell clam, *Mya arenaria*. Ecological Modelling 193:517–530.

ROUGHGARDEN, J. 1995. *Anolis* Lizards of the Caribbean. Ecology, Evolution and Plate Tectonics. Oxford University Press, New York.

RZEDOWSKI, J. 1978. Vegetación de México. Limusa, Distrito Federal, México.

SILVERTOWN, J., M. FRANCO, I. PISANTY, AND A. MENDOZA. 1993. Comparative plant demography—relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. Journal of Ecology 81:465–476.

SMITH, G. R., R. E. BALLINGER, AND J. A. LEMOS-ESPINAL. 2000. Male reproductive cycle of the knob-scaled lizard, *Xenosaurus grandis*. Southwestern Naturalist 45:356–357.

TURNER, F. B. 1977. The dynamics of populations of squamates, crocodilians, and rhyncocephalians, p. 157–264. *In*: Biology of the Reptilia, Vol. 7. C. Gans and D. W. Tinkle (eds.). Academic Press, New York.

VALVERDE, T., S. QUIJAS, M. LÓPEZ-VILLAVICENCIO, AND S. CASTILLO. 2004. Population dynamics of *Mammillaria magnimamma* Haworth (Cactaceae) in a lava-field in central Mexico. Plant Ecology 170:167–184.

VALVERDE, T., AND J. SILVERTOWN. 1998. Variation in the demography of a woodland understorey herb (*Primula vulgaris*) along the forest regeneration cycle: projection matrix analysis. Journal of Ecology 86:545–562.

VAN TIENDEREN, P. H. 2000. Elasticities and the link between demographic and evolutionary dynamics. Ecology 81:666–679.

WEBB, J. K., B. W. BROOK, AND R. SHINE. 2002. What makes a species vulnerable to extinction? Comparative life history traits of two sympatric snakes. Ecological Research 17:59–67.

WILLIAMS, B. K., J. D. NICHOLS, AND M. J. CONROY. 2002. Analysis and Management of Animal Populations. Academic Press, San Diego, California.

ZÚÑIGA-VEGA, J. J., R. I. ROJAS-GONZÁLEZ, J. A. LEMOS-ESPINAL, AND M. E. PÉREZ-TREJO. 2005. Growth ecology of the lizard *Xenosaurus grandis* in Veracruz, México. Journal of Herpetology 39:433–443.

(JJZV, RIRG, JALE) LABORATORIO DE ECOLOGÍA, UNIDAD DE BIOLOGÍA, TECNOLOGÍA Y PROTOTIPOS, FACULTAD DE ESTUDIOS SUPERIORES IZTACALA, UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO, LOS REYES IZTACALA, TLALNEPANTLA, ESTADO DE MÉXICO 54090, MÉXICO; AND (TV) DEPARTAMENTO DE ECOLOGÍA Y RECURSOS NATURALES, FACULTAD DE CIENCIAS, UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO, CIUDAD UNIVERSITARIA, DISTRITO FEDERAL 04510, MÉXICO. PRESENT ADDRESS: (JJZV) EVOLUTIONARY ECOLOGY LABORATORIES, DEPARTMENT OF INTEGRATIVE BIOLOGY, BRIGHAM YOUNG UNIVERSITY, PROVO, UTAH 84602. E-mail: (JJZV) jzuniga@correo1.com. Send reprint requests to JZV. Submitted: 3 Feb. 2006. Accepted: 18 Dec. 2006. Section editor: S. F. Fox.