

Demography of *Xenosaurus platyceps* (Squamata: Xenosauridae): a comparison between tropical and temperate populations

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Abstract. There appears to be variation in life-history strategies even between populations of the same species. For ectothermic organisms such as lizards, it has been predicted that demographic and life-history traits should differ consistently between temperate and tropical populations. This study compares the demographic strategies of a temperate and a tropical population of the lizard *Xenosaurus platyceps*. Population growth rates in both types of environments indicated populations in numerical equilibrium. Of the two populations, we found that the temperate population experiences lower adult mortality. The relative importance (estimated as the relative contribution to population growth rate) of permanence and of the adult/reproductive size classes is higher in the temperate population. In contrast, the relative importance for average fitness of fecundity and growth is higher in the tropical population. These results are consistent with the theoretical frameworks about life-historical differences among tropical and temperate lizard populations.

Keywords: demographic tactics, lizard life histories, matrix population models, tropical-temperate variation, *Xenosaurus platyceps*.

Introduction

Demographic and life history traits exhibit variation both between and within species and attempts to understand such variation have resulted in a significant amount of empirical and theoretical literature concerning the evolution of life histories (reviewed in Stearns [1992] and Roff [2002]). Environmental conditions have been shown to affect the expression of demographic and life history traits, always within certain boundaries imposed by physiological, developmental, phylogenetic, and design constraints (Hedderon and Longton, 1996; Sears, 2005; Zamora-Abrego, Zúñiga-Vega and Nieto-Montes de Oca, 2007). Actually, life-historical differences among populations of a single species can have genetic basis that resulted from local adaptations to particular sets of selective factors (Niewiarowski and Roosen-

burg, 1993; Díaz et al., 2007; Roff, 2007). When studying the sources of variation in demography and life history traits, particular emphasis has been placed on the lineage Squamata (Du et al., 2005). Lizards and snakes, as well as other ectothermic organisms, are highly dependent upon climatic conditions, and therefore geographic variation is assumed to be highly determined by the environmental regimes that populations experience (Adolph and Porter, 1993, 1996; Shine, 2005).

Tinkle (1969) and Tinkle, Wilbur and Tilley (1970) argued that lizard species and lizard populations inhabiting tropical environments experience longer favorable periods (for reproduction, metabolism, growth, social activities, etc.) in comparison with those inhabiting temperate environments. Furthermore, Adolph and Porter (1993, 1996) proposed that environments with long favorable periods result in higher mortality rates because lizards spend more time active (both daily and yearly) and are therefore at an increased risk of predation than are lizards inhabiting regions with restricted favorable seasons. As a result, life history traits and demographic strategies in the tropics are predicted to be remarkably different than those observed in temperate habitats. In spite of ex-

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tensive research on lizard life histories (see Clobert, Garland and Barbault [1998] and references therein), most studies have been focused on short-lived species that live in temperate environments. Thus, current conclusions about demographic and life history patterns of lizard species are biased and generalizations are still limited (Widerhecker, 2003; Du et al., 2005; Iverson et al., 2006).

The main objective of this paper is to compare the demographic behavior of one tropical and one temperate population of the long-lived, late-maturing lizard *Xenosaurus platyceps* (King and Thompson, 1968) using a matrix model approach. This species is a flattened knob-scaled lizard that exhibits viviparity and an adult mean snout-vent length (SVL) of 111.7 mm. Its distribution is restricted to the Mexican state of Tamaulipas and it can be found from temperate to tropical forests (Martin, 1958). Like other members of the genus *Xenosaurus*, lizards from this species are thermoconformers and exclusively inhabit rock crevices from which they rarely entirely leave (Lemos-Espinal, Smith and Ballinger, 1997). They are active during the day and exhibit prey chemical discrimination and a sit-and-wait foraging mode (Cooper, Lemos-Espinal and Smith, 1998). *Xenosaurus platyceps* is currently cited as an endemic species under special protection by the Mexican environmental agency (NOM-059-ECOL-2001) due to the scarcity of populations, and for the purposes of this study we were only able to locate one abundant population within each environment type.

Materials and methods

Two 5 ha study plots were delimited in two contrasting environments separated by approximately 60 km in Tamaulipas, México. The temperate site, referred to here as "El Madroño", is located in an oak forest at 1460 m of elevation. Mean annual temperature in this region equals 22.9°C and total annual rainfall is 926.4 mm. The tropical site, referred to here as "Gómez Farías", is located in a sub-perennial tropical forest at 420 m of elevation within the Biosphere Reserve "El Cielo". In this site mean annual temperature is 26.1°C and total annual precipitation

is 1245.2 mm ("Tamatán" and "Sabinas" weather stations, respectively, both from Servicio Meteorológico Nacional).

Field methods

From March 2000 to November 2003 we conducted monthly visits to the study sites. Virtually all crevices in the study plot were examined for lizards on every visit. Upon first capture a permanent individual number was assigned to each lizard by toe-clipping. In this and in every subsequent recapture, snout vent length (SVL), body mass, and sex were recorded for every individual. Lizards were then released in the same microhabitat.

Survival estimates

We calculated survival for three annual transitions at each study site: 2000-2001, 2001-2002, and 2002-2003. Size-specific survival rates were estimated considering only resident lizards (individuals with more than one recapture; Ballinger, 1973). The use of this method for estimating survival probabilities avoids including migratory lizards. The proportion of resident lizards observed in the summer of a given year that were recaptured again in the summer of the following year was considered as an estimate of the annual survival rate. Our confidence on the accuracy of these survival estimates is based upon three main reasons: 1) this method is appropriate for organisms with low mobility or high philopatry such as xenosaurid lizards whose mean distance moved during their whole lifespan is minimal (between 5.47 and 12.26 m) and that remain in the same crevice (or set of three close crevices at the most) during long periods of time (Lemos-Espinal, Smith and Ballinger, 2003; Zamora-Abrego, 2004; Zúñiga-Vega et al., 2007). In consequence, we were able to know with high reliability where to locate individual lizards on each sampling occasion. 2) On each visit to the study plots we extensively sampled virtually all suitable microhabitats (rock crevices) for these lizards which maximized the probability of observing all the individuals alive. 3) After the early stages of our field work every new individual marked was a newborn, which indicated that we have already marked the whole population and that migration is almost null in these lizards; otherwise we would have been frequently finding unmarked juvenile or adult lizards. These exposed facts support the reliability of our survival estimates as it would have been hard to miss resident lizards unless they were actually dead.

To test for differences in mortality between sites we conducted a two-way ANOVA with mortality (calculated as $1 - \text{survival rate}$) as the response variable and site and size class as categorical factors. Since transition probabilities show a binomial distribution, mortalities were transformed to the arcsine of their square root (Zar, 1999). We conducted an additional two-way ANOVA with site and size class as predictors and mortality of adult categories as the response variable. This was done to test for differences in adult mortality between the two contrasting localities.

Matrix analyses

The population dynamics and comparative demographics of *X. platyceps* were evaluated through the construction of six four-by-four matrices: one for each population for each of the three annual periods studied (2000-2001, 2001-2002, and 2002-2003). Lefkovich (1965) matrices were used, in which lizards were placed into four categories according to size. The upper limit for the first size class (yearlings) was 72 mm snout-vent length SVL, the size that corresponds to one year of age (Rojas-González, unpubl.). The distinction between the second and third categories (juveniles and adults I) was based on the reported size at maturity for these lizards which is 100 mm SVL (Ballinger, Lemos-Espinal and Smith, 2000). Finally, the split of adults in two categories (growing and asymptotic adults) was done using the size at which we began to register zero growth rates (114 mm SVL; Rojas-González, unpubl.).

As with the survival rate, the permanence and growth probabilities of individuals (represented by the main diagonal and subdiagonal of the matrices, respectively) in any given stage class were calculated as the frequency at which lizards in that stage class experienced either survival staying in the same category (permanence or stasis) or survival progressing to the following category (growth) when observed from one year to the next. Each size class (with one exception) had a minimum of 10 individuals from which to calculate matrix transitions. The fecundity estimates, found in the first row of the matrices, represent the average contribution of individuals of adult size classes to yearlings. Fecundity was estimated each year for each site by capturing females near (but not within) the study sites and holding them in captivity until they gave birth. We caught 10, 10, and 23 pregnant females in the tropical site in 2000, 2001, and 2002, respectively, and 10, 12, and 28 in the temperate site in 2000, 2001, and 2002, respectively. As we found a significant effect of female size upon fecundity ($F_{1,86} = 22.8$, $P < 0.001$, $n = 93$; Rojas-González et al., in press), we estimated fecundity entries of the matrices as the litter sizes predicted by the statistical relationship between female SVL and litter size for the average size of lizards within each adult category. From these we got 2.22 and 2.84 newborns per female for adults I and adults II, respectively for El Madroño. For Gómez Farías the relationship between female SVL and litter size predicted 1.94 and 2.45 newborns per female for adults I and adults II, respectively. We used these fecundity estimates per site in all years as neither year ($F_{2,86} = 1.4$, $P = 0.26$) nor the interaction between year and locality ($F_{2,86} = 0.2$, $P = 0.81$) had a significant effect upon fecundity (Rojas-González et al., in press). In both populations, marking was done before the breeding season so it was unnecessary to multiply the measured fecundities by the adult survival probabilities; this corresponds to a pre-breeding procedure for estimating fecundity according to Caswell (2001).

From each of the six matrices constructed we obtained the finite population growth rate (λ), the stable size distribution (vector \mathbf{w}) and the size-specific reproductive values (vector \mathbf{v}) using the power method (Caswell, 2001). Observed size class distributions were compared to those expected under equilibrium (vector \mathbf{w}) using chi-squared tests.

Confidence intervals for λ were calculated using the analytical method proposed by Alvarez-Buylla and Slatkin (1991).

Elasticity matrices were constructed to estimate the relative contribution of each matrix entry to population growth rate. Each elasticity matrix entry was calculated as:

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

where s_{ij} is the absolute sensitivity of λ to changes in a_{ij} ($s_{ij} = \partial\lambda/\partial a_{ij}$, de Kroon et al., 1986; Caswell, 2001). Because the sum of all elasticity matrix entries equals unity, the elasticity values for each entry, demographic process (i.e., growth, stasis, and fecundity), or size class may be interpreted as indicative of its relative importance to λ (de Kroon et al., 1986; Silvertown et al., 1993; de Kroon, van Groenendael and Caswell, 2000). Each location's elasticity values for the three main demographic processes – growth, stasis, and fecundity – were summed for each year, yielding six described data points. Each point was plotted in a triangular space defined by the three demographic processes – in other words, a demographic triangle (Silvertown et al., 1993). In addition to allowing us to compare the relative elastic value of each demographic process between the temperate and tropical locations, this demographic triangle graphically frames the life history strategies selected for in either environment.

Results

There was a significant difference between sites in overall mortality ($F_{1,16} = 60.92$, $P < 0.001$), with the highest mortalities in the tropical site. There was also a significant effect of size class on mortality ($F_{3,16} = 11.08$, $P < 0.001$); yearling mortality was significantly higher than that in the other three size classes (average mortality of yearlings = 0.496, in comparison with juveniles = 0.322, adults I = 0.264, adults II = 0.330). In addition, there was a significant interaction between site and size class ($F_{3,16} = 6.99$, $P = 0.003$), with mortalities in the adult categories of the temperate site being the lowest among all (fig. 1). When comparing only adult mortality between sites, a significant effect was also present ($F_{1,8} = 86.35$, $P < 0.001$), with the tropical locality showing again the highest overall adult mortality rate. Mortality was not different between the two adult categories ($F_{1,8} = 2.16$, $P = 0.180$), although an interaction between site and adult size class was evident ($F_{1,8} = 7.57$, $P = 0.025$), in which mortality of adults II (0.545)

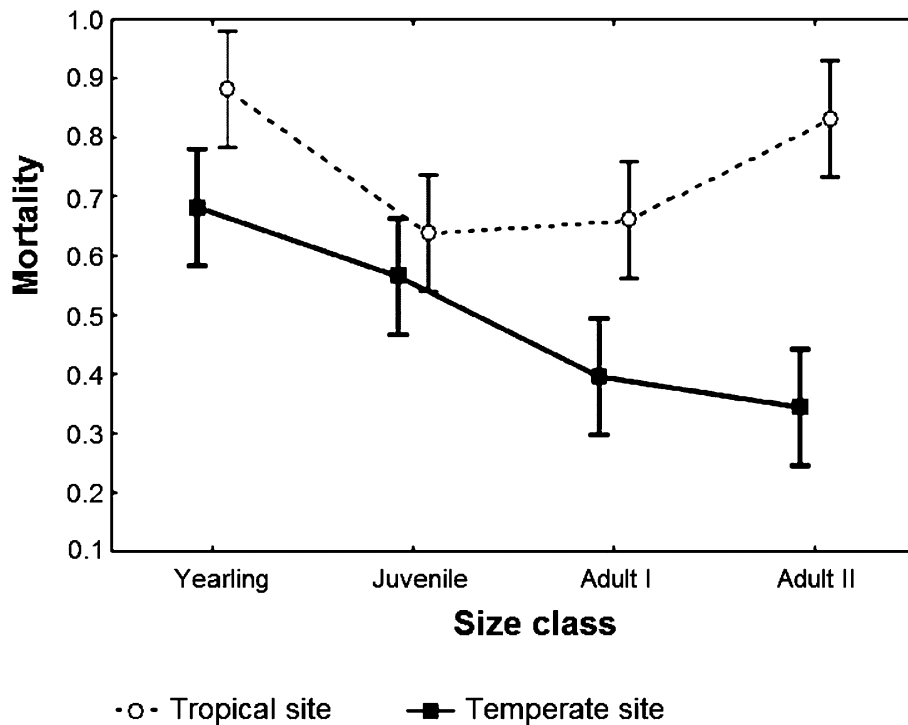


Figure 1. Estimated mortality of each size class for both populations. Note that mortality for yearlings, adults I and adults II are significantly higher in the tropical population.

was relatively higher than that in adults I (0.376) in the tropical population. In the temperate there was no difference between adult size classes in mortality.

Matrix analyses

The three matrices constructed for El Madroño all projected a population growth rate above unity ($\lambda_{00-01} = 1.142$, $\lambda_{01-02} = 1.090$, and $\lambda_{02-03} = 1.021$; table 1). Of the three matrices constructed for Gómez Farías, only one transition matrix projected a population growth rate above unity ($\lambda_{00-01} = 1.047$; table 1) while the other two projected below unity ($\lambda_{01-02} = 0.973$ and $\lambda_{02-03} = 0.932$; table 1). However, there was not a significant difference between the two populations or within either population from year to year, nor were any population growth rates significantly different from unity (fig. 2).

Projected stable size class distributions (vectors \mathbf{w} in table 1) were significantly different than the observed population structure in all an-

nual transitions (El Madroño 2000-2001: $\chi_3^2 = 561.25$, $P < 0.001$; 2001-2002: $\chi_3^2 = 285.33$, $P < 0.001$; 2002-2003: $\chi_3^2 = 241.32$, $P < 0.001$; Gómez Farías 2000-2001: $\chi_3^2 = 113.90$, $P < 0.001$; 2001-2002: $\chi_3^2 = 228.84$, $P < 0.001$; 2002-2003: $\chi_3^2 = 164.72$, $P < 0.001$). Adult size classes showed higher reproductive values (vectors \mathbf{v} in table 1) in comparison with non-reproductive categories in both sites. However, in the temperate site reproductive values of adult size classes are noticeable higher when compared to those observed in the tropical site. In El Madroño reproductive values of adults II were always slightly larger than those of adults I, whereas in Gómez Farías we observed the opposite pattern.

The elasticity matrices constructed (table 2) revealed that the most important size class (in terms of their contributions to population growth rate) for the tropical population was the juvenile class (fig. 3A). Actually, survival with growth of non-reproducing categories were the

Table 1. Population projection matrices and main demographic results for the two *Xenosaurus platyceps* populations studied during three annual transitions. Corresponding λ values are shown above each matrix ($\pm 95\%$ confidence intervals). q_x = mortality per size class, n_x = number of resident lizards per size class from which transition probabilities were calculated, \mathbf{w} = projected stable size class distribution, \mathbf{v} = size-specific reproductive values.

El Madroño 2000-2001					$\lambda = 1.142 \pm 0.179$		
	Yearlings	Juveniles	Adults I	Adults II	n_x	\mathbf{w}	\mathbf{v}
Yearlings	0.39	0	2.22	2.84	18	0.53	1
Juveniles	0.28	0.64	0	0	39	0.30	2.67
Adults I	0	0.13	0.69	0	58	0.09	10.31
Adults II	0	0	0.21	0.90	10	0.08	11.67
q_x	0.33	0.23	0.10	0.10			
El Madroño 2001-2002					$\lambda = 1.090 \pm 0.150$		
	Yearlings	Juveniles	Adults I	Adults II	n_x	\mathbf{w}	\mathbf{v}
Yearlings	0.33	0	2.22	2.84	18	0.54	1
Juveniles	0.28	0.58	0	0	59	0.30	2.72
Adults I	0	0.12	0.76	0	84	0.11	11.59
Adults II	0	0	0.10	0.91	11	0.06	15.91
q_x	0.39	0.30	0.14	0.09			
El Madroño 2002-2003					$\lambda = 1.021 \pm 0.165$		
	Yearlings	Juveniles	Adults I	Adults II	n_x	\mathbf{w}	\mathbf{v}
Yearlings	0.29	0	2.22	2.84	17	0.55	1
Juveniles	0.24	0.57	0	0	46	0.29	3.07
Adults I	0	0.11	0.63	0	63	0.08	12.57
Adults II	0	0	0.16	0.85	13	0.08	16.70
q_x	0.47	0.32	0.21	0.15			
Gómez Farías 2000-2001					$\lambda = 1.047 \pm 0.335$		
	Yearlings	Juveniles	Adults I	Adults II	n_x	\mathbf{w}	\mathbf{v}
Yearlings	0	0	1.94	2.45	4	0.45	1
Juveniles	0.50	0.36	0	0	14	0.33	2.09
Adults I	0	0.36	0.09	0	33	0.12	4.00
Adults II	0	0	0.55	0.33	12	0.10	3.42
q_x	0.50	0.28	0.36	0.67			
Gómez Farías 2001-2002					$\lambda = 0.973 \pm 0.236$		
	Yearlings	Juveniles	Adults I	Adults II	n_x	\mathbf{w}	\mathbf{v}
Yearlings	0	0	1.94	2.45	12	0.49	1
Juveniles	0.33	0.43	0	0	21	0.30	2.96
Adults I	0	0.29	0.13	0	56	0.10	5.54
Adults II	0	0	0.50	0.52	31	0.11	5.43
q_x	0.67	0.28	0.37	0.48			
Gómez Farías 2002-2003					$\lambda = 0.932 \pm 0.266$		
	Yearlings	Juveniles	Adults I	Adults II	n_x	\mathbf{w}	\mathbf{v}
Yearlings	0	0	1.94	2.45	13	0.51	1
Juveniles	0.38	0.20	0	0	10	0.27	2.45
Adults I	0	0.30	0.20	0	41	0.11	5.98
Adults II	0	0	0.41	0.52	31	0.11	5.95
q_x	0.62	0.50	0.39	0.48			

vital rates (i.e., individual matrix entries) with the highest elasticities in this locality (table 2). For the temperate, highest individual elasticities corresponded to stasis of adult categories, which were the most important size classes in

this locality (fig. 3B). The temperate population placed a much higher emphasis on the reproductive classes than on the non-reproductive classes. On the other hand, elasticity analyses revealed that the non-reproductive classes

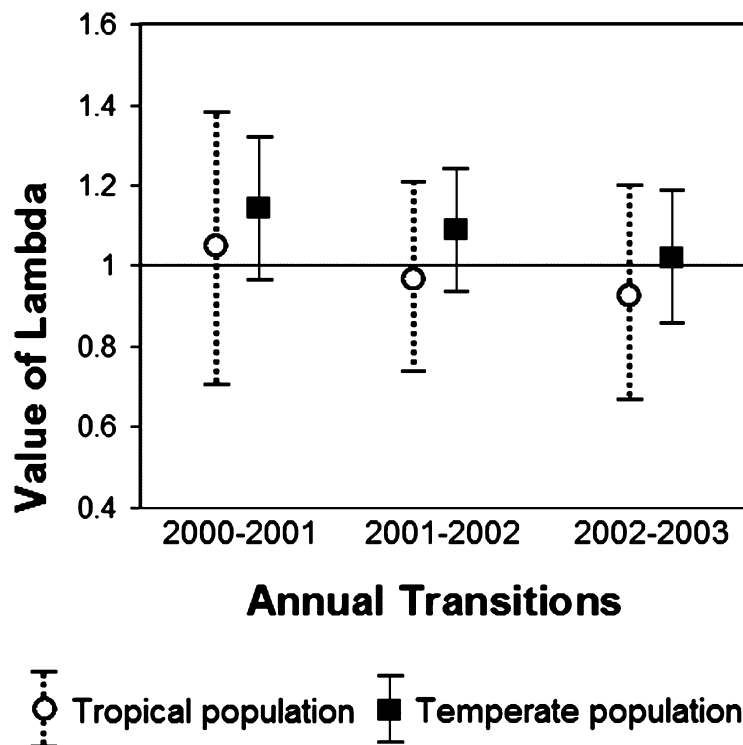


Figure 2. Projected population growth rates (λ) for both study sites and for the three annual transitions studied. None of them was significantly different from unity.

have a higher relative importance in the tropical population when compared to the temperate.

The importance of demographic processes (fecundity, growth, and permanence) between the two populations differed. As the demographic triangle shows (fig. 4), fecundity and growth were of higher importance to Gómez Farías and permanence less so. In contrast, permanence was the most important demographic process to the Madroño population and fecundity and growth were de-emphasized. Little interannual variation was observed in these demographic strategies as indicated by the small temporally-induced variation in the positions of the study sites within the triangle (fig. 4).

Discussion

As we expected, mortality rates were lower in the temperate site. This difference was significant in all size classes except in the juve-

niles (see fig. 1). In temperate regions, the thermal environment places more constraints on ectothermic organisms in comparison with tropical zones (Tinkle, Wilbur and Tilley, 1970; Adolph and Porter, 1993, 1996). The presence and duration of a cold and dry season is common in temperate environments, which reduces the time during the year in which lizards can be active and performing reproductive, social, and foraging activities. Therefore, the amount of time during a year in which lizards are under predation (i.e., mortality) risk is shorter in temperate sites because of the presence of a season of inactivity. Previous studies have shown that mortality in lizards is lower when they are inactive (Rose, 1981).

A shorter activity season in our temperate locality might account for the differences in mortality rates between sites. Climatic information of the studied localities provides evidence that activity (i.e., certain social/reproductive in-

Table 2. Elasticity matrices corresponding to each location for each of the three annual transition matrices for the *Xenosaurus platyceps* populations.

El Madroño 2000-2001				
	Yearlings	Juveniles	Adults I	Adults II
Yearlings	0.06	0	0.05	0.06
Juveniles	0.11	0.14	0	0
Adults I	0	0.11	0.17	0
Adults II	0	0	0.06	0.22
El Madroño 2001-2002				
	Yearlings	Juveniles	Adults I	Adults II
Yearlings	0.05	0	0.06	0.04
Juveniles	0.11	0.12	0	0
Adults I	0	0.11	0.25	0
Adults II	0	0	0.04	0.22
El Madroño 2002-2003				
	Yearlings	Juveniles	Adults I	Adults II
Yearlings	0.04	0	0.05	0.06
Juveniles	0.10	0.13	0	0
Adults I	0	0.10	0.17	0
Adults II	0	0	0.06	0.28
Gómez Farías 2000-2001				
	Yearlings	Juveniles	Adults I	Adults II
Yearlings	0	0	0.12	0.11
Juveniles	0.23	0.12	0	0
Adults I	0	0.23	0.02	0
Adults II	0	0	0.11	0.05
Gómez Farías 2001-2002				
	Yearlings	Juveniles	Adults I	Adults II
Yearlings	0	0	0.08	0.11
Juveniles	0.19	0.15	0	0
Adults I	0	0.19	0.03	0
Adults II	0	0	0.11	0.13
Gómez Farías 2002-2003				
	Yearlings	Juveniles	Adults I	Adults II
Yearlings	0	0	0.09	0.11
Juveniles	0.21	0.06	0	0
Adults I	0	0.21	0.06	0
Adults II	0	0	0.11	0.15

teractions and feeding attempts) of *X. platyceps* is somewhat thermally constrained in El Madroño in comparison with Gomez Farías. For instance, in the former site during the winter minimum temperatures can achieve values below 0°C and snowfall events are relatively common. Furthermore, all throughout the year mean temperatures in El Madroño (mean annual = 22.9°C) are always below mean temperatures in Gómez Farías (mean annual = 26.1°C), with

the highest (44.5°C) and lowest (−1.0°C) always registered in El Madroño (Servicio Meteorológico Nacional – México). These differences in the environmental regimes between sites, along with the fact that *X. platyceps* is a thermoconformer species without a behavioral mechanism to regulate body temperature (Lemos-Espinal, Smith and Ballinger, 1997), strongly suggest that favorable temperatures are less both daily and yearly in the temperate population, which according to theoretical predictions would result in lower activity and mortality in this site, just as we found here (Rose, 1981; Adolph and Porter, 1993, 1996).

Even though the activity pattern of these thermoconformers and strict crevice-dwelling xenosaurid lizards is different than that of actively thermoregulating species (the former just occasionally go out of their crevices; Lemos-Espinal, Smith and Ballinger, 1997, 2004; Zamora-Abrego, 2004), their reproductive, social, and foraging activities should be maximized during the favorable period of the year. As this favorable period appears to be shorter in the temperate zone, the length of the activity season is reduced and consequently annual mortality rates are lower. The lack of such difference in juveniles might be explained by the fact that individuals in this stage do not need to disperse to obtain a territory as do yearlings, nor do they perform activities associated with reproduction as do the adults (e.g. search for mates; Zamora-Abrego, 2004; Zúñiga-Vega, 2005). Therefore, juveniles go out of their crevices less often in both sites resulting in similar mortality risk independent of the type of environment.

Our demographic results indicated that both populations in all years were in quantitative equilibrium (λ values not significantly different from unity). Maintaining this numerical stability might require different demographic strategies, because of the highly contrasting environmental conditions between sites. Such contrasting conditions might promote differences in selection pressures such as the docu-

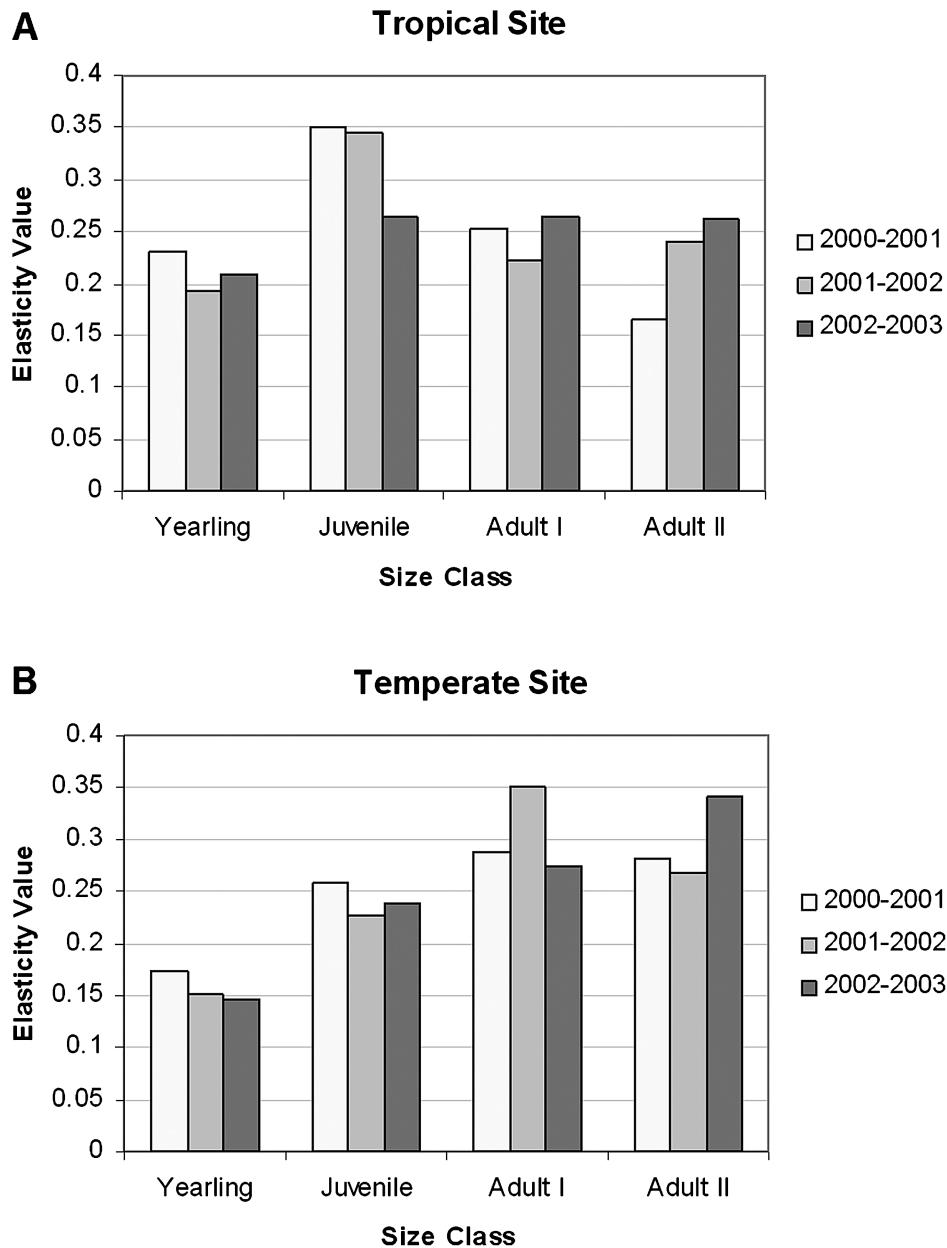


Figure 3. Relative importance of each size class on population fitness as determined by elasticity values. Notice that juveniles are the most important size class in the tropical population while adults are the most important in the temperate population.

mented differences in mortality rates, which in turn might have resulted in the evolution of distinct life histories (Stearns, 1992; Roff, 2002).

Among the main theoretical models that aim to explain the evolution of particular sets of life history traits are the $r - K$ selection model (Dobzhansky, 1950; Mac Arthur and Wilson,

1967) and the “fast-slow” continuum hypothesis (Primislow and Harvey, 1990; Charnov, 1990, 1991). The former suggests that density-dependent mortality and resource availability are two of the main factors that shape the evolution of life history strategies (Boyce, 1984). Unfortunately, our results cannot be discussed

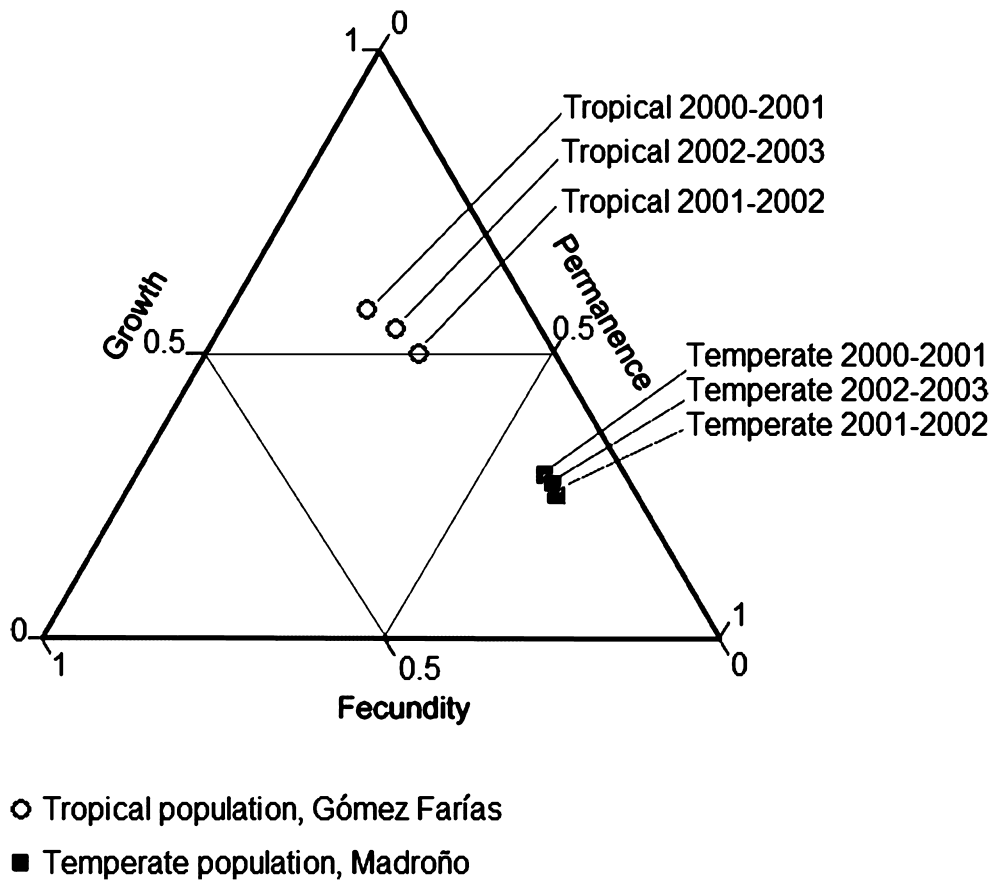


Figure 4. Ordination in the demographic triangle of both populations for each study year. Fecundity and growth are more important to the tropical population while permanence is more important to the temperate population.

in the context of the $r - K$ model because we lack appropriate estimates of resource availability. The “fast-slow” continuum hypothesis, however, is based on variation in adult mortality as the main selective factor for the evolution of life history strategies (Harvey and Zammutto, 1985; Promislow and Harvey, 1990; Charnov, 1990, 1991), and therefore our results can be discussed in the context of this theoretical model. In the temperate locality both reproductive values and elasticities of reproductive categories were higher in comparison with those observed in the tropical locality. This pattern can be explained by the fact that the low adult mortality observed in the temperate population increases the frequency of reproductive events per individual, which results in the production

of a higher number of offspring per lifetime. In contrast, the tropical population’s higher adult mortality results in a lower frequency of reproductive events and thus in a lower number of offspring produced per lifetime (Roff, 1992; Stearns, 1992). Enhanced adult survival with high reproductive values for adult categories, such as in our temperate site, is usually associated with low body growth rates and delayed maturity (“slow” life cycle), whereas poor adult survival with low reproductive values for adult categories such as in our tropical site is associated with fast body growth and early maturation (“fast” life cycle; Promislow and Harvey, 1990; Blackburn, 1991; Saether and Bakke, 2000). Indeed, individuals of *X. platyceps* in the temperate population grow at slower rates (mean

body growth rate of juveniles \pm SE = 0.030 ± 0.002 mm/day, mean growth rate of adults = 0.005 ± 0.0004 mm/day) and reach maturity later (at 50 months) in comparison with those in the tropical population (mean growth rate of juveniles = 0.049 ± 0.004 mm/day, mean growth rate of adults = 0.011 ± 0.001 mm/day, age at maturity = 37 months; Rojas-González, unpubl.), which is consistent with the “fast-slow” continuum hypothesis.

The tropical locality exhibited relatively higher elasticities for non-reproductive categories. The high mortality in this site accounts for this pattern because under poor survival probabilities in the adults, survival and growth to maturity of newborns and juveniles contribute more to the population growth rate, balancing the losses of reproductive individuals (Lewontin, 1965). Thus, the observed high adult mortality might have promoted the evolution of a relatively “fast” life cycle in the tropical site, in comparison with the temperate one, by selecting for those non-reproductive individuals with fast body growth rates and early maturity (Rojas-González, unpubl.).

When analyzing elasticities per demographic process and plotting the populations accordingly in the demographic triangle, we observed that the population with the highest adult mortality (the tropical site) showed relatively higher values for growth and fecundity in all years. In contrast, the population with lower adult mortality rates (the temperate site) had the highest elasticity in stasis and lower elasticities for growth and fecundity in all years. These results are consistent with previous evidence on plants (Franco and Silvertown, 1996), birds (Sæther and Bakke, 2000), and mammals (Hep- pell, Caswell and Crowder, 2000; Oli and Dobson, 2003), which demonstrated that species experiencing high adult mortality and associated “fast” life cycles exhibited a relatively high importance of fecundity for average fitness, whereas species with low adult mortality rates and associated “slow” life cycles showed

a relatively high importance of stasis for their average fitness (Benton and Grant, 1999).

We acknowledge that other confounding factors may play a relevant role in explaining the differences in demographic strategies observed between sites. For example, food availability might be higher in the tropical site, thus yielding higher fecundity and faster growth rates. Further and deeper research should take into account additional environmental factors in order to test their effects on the expression of demographic and life history traits in these lizards. We also acknowledge the necessity of including more sample points (i.e., populations within each environmental type) to conduct a more strict test of theoretical models such as the “fast-slow” continuum hypothesis. Unfortunately, as we previously mentioned, the restricted distribution of *X. platyceps* (Smith, Lemos-Espinal and Ballinger, 2000) only allowed us to locate one abundant population per habitat type.

Despite these possibly confounding variables, our results allow us three main conclusions: (1) temperate and tropical environments exhibit different demographic strategies in *X. platyceps*, feasibly through the effect of differences in the duration of the activity season. (2) Differences between the tropical and temperate populations of this long-lived, late-maturing species agree with the well-recognized theoretical predictions for geographic variation in lizard life histories (Tinkle, Wilbur and Tilley, 1970; Adolph and Porter, 1993, 1996). (3) Our results appear to be consistent with the “fast-slow” continuum hypothesis, in which the degree of adult mortality can account for the covariation of life history traits observed in the two studied populations. Finally, based on our evidence, we suggest that for ectothermic organisms such as amphibians and reptiles there might be a relationship between a “fast-slow” continuum of life-history evolution and a gradient of environments ranging from those with long favorable periods (high adult mortality sites) to those with strongly shortened ones (low adult mortality sites). Further

and taxonomically diverse intra- and interspecific demographic studies are necessary to provide stronger support for this suggested relationship.

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