

Stochastic population dynamics in populations of western terrestrial garter snakes with divergent life histories

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Abstract. Comparative evaluations of population dynamics in species with temporal and spatial variation in life-history traits are rare because they require long-term demographic time series from multiple populations. We present such an analysis using demographic data collected during the interval 1978–1996 for six populations of western terrestrial garter snakes (*Thamnophis elegans*) from two evolutionarily divergent ecotypes. Three replicate populations from a slow-living ecotype, found in mountain meadows of northeastern California, were characterized by individuals that develop slowly, mature late, reproduce infrequently with small reproductive effort, and live longer than individuals of three populations of a fast-living ecotype found at lakeshore locales. We constructed matrix population models for each of the populations based on 8–13 years of data per population and analyzed both deterministic dynamics based on mean annual vital rates and stochastic dynamics incorporating annual variation in vital rates. (1) Contributions of highly variable vital rates to fitness (λ_s) were buffered against the negative effects of stochastic variation, and this relationship was consistent with differences between the meadow (M-slow) and lakeshore (L-fast) ecotypes. (2) Annual variation in the proportion of gravid females had the greatest negative effect among all vital rates on λ_s . The magnitude of variation in the proportion of gravid females and its effect on λ_s was greater in M-slow than L-fast populations. (3) Variation in the proportion of gravid females, in turn, depended on annual variation in prey availability, and its effect on λ_s was 4–23 times greater in M-slow than L-fast populations. In addition to differences in stochastic dynamics between ecotypes, we also found higher mean mortality rates across all age classes in the L-fast populations. Our results suggest that both deterministic and stochastic selective forces have affected the evolution of divergent life-history traits in the two ecotypes, which, in turn, affect population dynamics. M-slow populations have evolved life-history traits that buffer fitness against direct effects of variation in reproduction and that spread lifetime reproduction across a greater number of reproductive bouts. These results highlight the importance of long-term demographic and environmental monitoring and of incorporating temporal dynamics into empirical studies of life-history evolution.

Key words: *deterministic demography; Eagle Lake, California (USA); garter snake; life history; stochastic demography; Thamnophis elegans.*

INTRODUCTION

Life-history theory focuses on understanding patterns of life-history differences among species and the underlying processes that generate these differences (Roff 1992, Stearns 1992). Empirical examinations of population dynamics in the field have therefore focused on determining the ecological underpinnings of evolved differences in life histories. Central to ecological inference in this area has been the tradition of comparative studies within and among species of differences in mean demographic parameters (e.g., Promislow and Harvey 1990, Martin 1995, Reznick et

al. 1996). Such comparisons of average demographic rates have yielded important insights about the causes of life-history differences such as how predation, a “top-down” agent of selection, and variable resources, a “bottom-up” selective force, are related to evolution in life-history traits (Martin 1995, Bronikowski et al. 2002, Walsh and Reznick 2009). In contrast, empirical examinations of temporal variation in population dynamics are much rarer, owing to limited availability of long-term data sets amenable to testing theoretical predictions (Morris and Doak 2004, Nevoux et al. 2010). Studies that incorporate temporal variability are necessary to extend the bridge between theoretical predictions and empirical observations that has served as the basis for our current understanding of life-history evolution. Evolutionary models suggest that temporal variation in population vital rates and dynamics and in ecological interactions may impose strong selection pressure simultaneously on life-history traits and demo-

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graphic rates and should help explain patterns of life-history evolution (Orzack and Tuljapurkar 1989, Tuljapurkar 1990a, 2010, Benton and Grant 1999, Roff 2002, Horvitz and Tuljapurkar 2008, Koons et al. 2008, Tuljapurkar et al. 2009, Coulson et al. 2010).

Methods used to study empirical population dynamics have recently been expanded to incorporate a stochastic demographic perspective into analyses (Morris and Doak 2002, Lande et al. 2003). Thus, since earlier notable reports (Benton et al. 1995), the empirical literature that utilizes stochastic models has been increasing (Coulson et al. 2001, Ezard et al. 2008, Morris et al. 2008). In addition, applied studies have incorporated stochastic dynamics into population models to guide conservation actions (Fieberg and Ellner 2001, Morris and Doak 2002, Lande et al. 2003) and to predict how changes in environmental variability will affect populations in the future (Boyce et al. 2006, Morris et al. 2008, Jonzén et al. 2010). A rich set of theoretical and methodological resources exists that can improve insights from the analysis of long-term demographic data sets regarding the importance of temporal variation in a third area, that of life-history evolution (Tuljapurkar 1990b, Levin et al. 1996, Pfister 1998, Tuljapurkar et al. 2003, 2009, Morris and Doak 2004, Doak et al. 2005, Haridas and Tuljapurkar 2005). Specific outcomes from empirical analyses of long-term temporal dynamics are expected to advance our understanding of evolution in variable habitats (e.g., Morris et al. 2011). Important outcomes include testing the prediction that life histories should be buffered against the negative effects of variability (Pfister 1998), measures of the selection gradients associated with changes in stochastic variation in individual life-history traits (Lande 1982, Caswell 2001, Tuljapurkar et al. 2009), and measures of the direct relationship between year-to-year environmental variation and the fitness costs resulting from such variation (Davison et al. 2010, Tuljapurkar 2010). Fitness in temporally variable environments for density-independent populations is measured by the geometric mean of growth rates during individual time steps; therefore a cost may be imposed because higher variability decreases the geometric mean (Lewontin and Cohen 1969). Macro-level analyses have supported the view that selection has worked to buffer the fitness cost of variability by selecting for lower sensitivity to life-history traits that are most temporally variable (Pfister 1998, Sæther and Bakke 2000, Gaillard and Yoccoz 2003, Dalglish et al. 2010). Whether buffering of life histories can explain differences among populations within species, and whether buffering occurs at the level of individual vital rates remain open issues. Comparisons of stochastic demography are also needed to test predictions about the sensitivities of different vital rates to changes in temporal variation (e.g., Ezard et al. 2008). Furthermore, investigations that identify the causes of temporal variation in vital

rates (e.g., Coulson et al. 2001), and the ecological context that leads to differences in stochastic dynamics are particularly important in understanding how stochastic processes influence life-history evolution (Koons et al. 2009, Tuljapurkar et al. 2009, Jonzén et al. 2010, Nevoux et al. 2010, Tuljapurkar 2010).

Here we test these predictions about the importance of temporal variation viz. life-history evolution among spatially distinct populations of the western terrestrial garter snake (*Thamnophis elegans*). Study populations in the vicinity of Eagle Lake in northeastern California originated from one ancestral source population that became differentiated into two genetically diverged ecotypes that have evolved distinctive morphologies and life-history strategies (Bronikowski and Arnold 1999, Bronikowski 2000, Manier et al. 2007, Sparkman et al. 2007, Robert and Bronikowski 2010). Populations in this system correspond to either a lakeshore (L-fast) ecotype in which individuals grow fast, mature early, breed frequently with large litter sizes, and die young; or a meadow (M-slow) ecotype where individuals grow slowly, mature late, breed less frequently with smaller litter sizes, and live twice as long as L-fast individuals. These distinctive life-history strategies are maintained despite low levels of gene flow between the two ecotypes (Bronikowski 2000, Manier and Arnold 2005), and common environment experiments support the view that early life-history differences among populations have a genetic basis (Bronikowski 2000). In this report, we compare stochastic population dynamics for M-slow and L-fast populations to evaluate support for a relationship between temporal variability in environmental resources and associated population dynamics, and whether the relationship corresponds to life-history differences among populations.

METHODS

Study populations and field methods

We collected data on six focal populations of western terrestrial garter snakes in the vicinity of Eagle Lake in Lassen County, California, USA, representing three L-fast and three M-slow populations. From 1978 to 1996, demographic data were collected for these populations, corresponding to the lakeshore (L1, L2, and L3) and meadow populations (M1, M2, and M3). There was variation in the specific study years and length of study among populations and we report results from analysis of annual demographic models constructed for: 1980–1987 for L1; 1979–1988, 1994, and 1995 for L2; 1979–1988, 1994, and 1995 for M1; 1978–1988, 1994, and 1995 for M2; and 1980–1988, 1994, and 1995 for M3. A third lakeshore population (L3) was studied intensively between 1979 and 1988. However, limited recaptures of marked animals precluded estimates necessary to generate models with temporal dynamics for this population. Because the data provide an additional lakeshore data point for deterministic dynamics and for

estimates of variance in reproductive parameters we include the population in these analyses.

Snakes were captured during systematic searches of study areas. Areas were repeatedly searched on an annual basis from June to August with additional searches in May and October in some of the years. All snakes were individually marked by scale clipping or with a passive integrated transponder (PIT) tag. Snout-vent length was measured and sex was determined for all individuals. During the summer months, adult females were palpated to determine whether they were gravid and to estimate litter size based on the number of embryos. Accuracy of this method was validated by a strong correlation between litter size estimated by palpation in the field and litter size recorded at birth for the same individuals after being brought into captivity ($n = 78$, $r = 0.88$). To estimate survival rates, capture records for each individual were compiled, including recaptures in subsequent years, and these were used to generate unique capture histories for individuals throughout the study period (Lebreton et al. 1992).

Anurans comprised an annually variable portion of snake diet compared to other prey, and presence of breeding anurans was closely tied to environmental conditions (i.e., precipitation and temperature; Kephart 1982, Kephart and Arnold 1982). In a previous study of the L2 population, Kephart and Arnold (1982) found that anurans comprised the majority of snake diet in years when a low proportion of captured snakes had empty stomachs, demonstrating a strong correlation between anuran presence and general food availability. When available, diet analysis has shown that snakes from both ecotypes eat the tadpoles and metamorphs of *Pseudacris regilla* and *Bufo boreas* but anurans compose a greater proportion of the diet in meadow habitats where fish are largely unavailable (Kephart 1982). Lakeshore snakes feed on *Bufo boreas* when they are available and in years where precipitation is especially high they can comprise more than one-half their diet. However, the majority of L-fast snakes diet is fish (*Rhynchithys osculus*) and leeches (*Erpobdella* spp.), which are abundant in lake habitats and predicted to be relatively consistent in availability among years. Based on these studies we made a number of predictions about how food availability would affect demography. We predicted that the presence of breeding anurans would be a strong predictor of annual variability for both populations, but that the availability of alternative food resources would mean that the effect on annual variability in lakeshore populations would be smaller than in meadow populations. We classified years during the study into those when breeding anurans were present, and tadpoles and metamorphs were abundant at study sites and those when they were not. We used detailed field notes about summer conditions, notes on anuran presence, and stomach contents from snakes captured in the field to classify each of the years.

Overview of analyses

We constructed a set of matrix population models that we used to gain insights into how stochastic population dynamics differed between the two life-history ecotypes. We relied on a combination of deterministic and stochastic techniques as well as prospective and retrospective analyses (Caswell 2001). Our approach to model development, parameterization, and analysis involved the following steps:

- 1) We defined the life cycle graphs and the corresponding Lefkovich matrices (Lefkovich 1965) we used for modeling the population dynamics for each of the populations.
- 2) We generated estimates of five vital rates needed to populate the models: the proportion of adult females that were gravid (PG), litter size (LS), neonate survival (SN), juvenile survival (SJ), and adult survival (SA).
- 3) For each of the populations we conducted a standard prospective matrix model analysis, estimating both deterministic and stochastic growth rates, sensitivities, and elasticities. This allowed us to compare differences in the means and variances of vital rates among populations and the relative strength of selection associated with potential changes in each of the means and variances.
- 4) We determined whether differences in life histories among populations reduced the effects of variation (i.e., buffered) in vital rates on mean fitness (λ_s). We examined the relationship between the coefficient of variation and the elasticity of vital rates for each population, testing for an inverse relationship both within populations and within vital rates.
- 5) We examined the retrospective contribution of temporal variation and covariation in vital rates to annual variation in λ by analyzing a set of life-table response experiments (LTRE; Levin et al. 1996, Caswell 2000, 2001, 2010, Davison et al. 2010). We decomposed the total fitness costs related to annual variation in λ into contributions of variance in each vital rate and covariance among vital rates using a random design LTRE. We then decomposed fitness costs directly related to annual variation in the presence of breeding anurans into contributions from each vital rate using a stochastic LTRE.

Life cycle and matrix model

In developing the population model used in our analyses we placed an emphasis on accurate estimation of temporal variation. To accomplish this goal we constructed a parsimonious structure for the model that allowed us to focus on resolving among-year variation of the components. For both ecotypes, we recognized three stages (neonates, juveniles, and adults). We assumed that the probability of being gravid and litter size were the same for all adult females. In addition, we

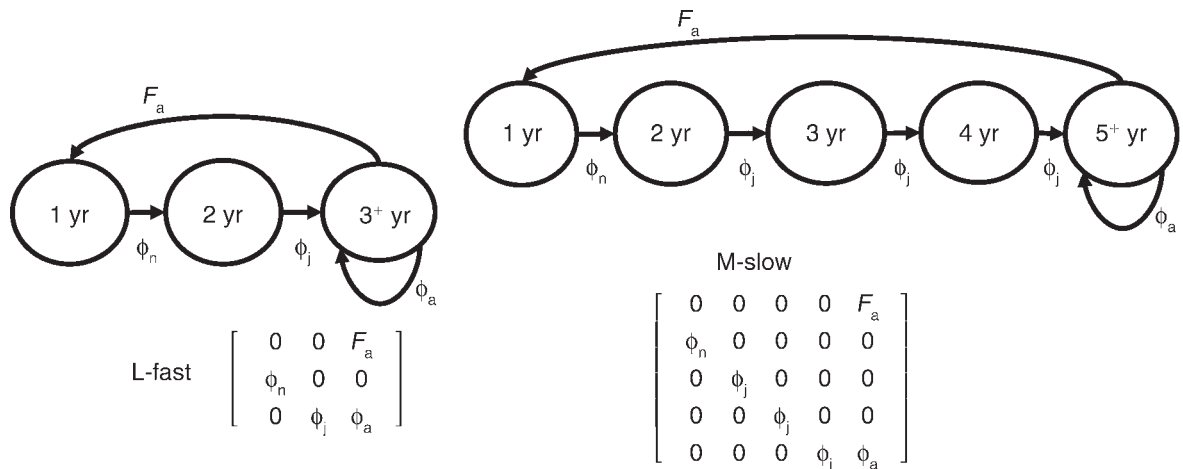


FIG. 1. Life cycle graphs and transition matrices used for modeling the population dynamics of lakeshore (L-fast) and meadow (M-slow) ecotype western terrestrial garter snakes (*Thamnophis elegans*) in the vicinity of Eagle Lake, California, USA. L-fast populations have a fast-paced life history relative to M-slow populations, which have a slow-paced life history. Abbreviations are: n, neonate; j, juvenile; a, adult.

assumed that transitions among stages happened at the same age for all individuals within a population. Individuals were assumed to spend one year in the neonate stage in both ecotypes. Based on previous work we stipulated that individuals spent either one year or three years as juveniles, for the L-fast and M-slow populations, respectively (Bronikowski and Arnold 1999). Finally, we were unable to estimate survival from birth (a late-fall event) to the beginning of the first summer (ϕ_0). Because we were unable to estimate differences in this parameter among years and populations, we used a fixed value of 0.8, picked to approximate the median SN rate for a partial year. Consequently, variation in this parameter was not included in models.

We constructed our models for the female portion of the population based on a pre-breeding census design. We generated life cycle graphs and the corresponding annual transition matrices (\mathbf{A}_t) and a mean annual matrix ($\bar{\mathbf{A}}$) as a function of stage specific survival (ϕ_i) and fecundity (F ; Fig. 1). The life cycle analyzed for L-fast populations was a three-stage model, ages 1, 2, and ≥ 3 years, with each of the stages respectively corresponding with neonate, juvenile, and adults. For M-slow populations the life cycle consisted of five stages: 1-year-olds defined as neonates, 2-, 3-, and 4-year olds as juveniles, and ≥ 5 -year-olds as adults. For both ecotypes, only adults contributed to the neonate stage through fecundity, which was estimated as a function of component vital rates, $F = PG \times LS \times 0.5 \times \phi_0$. The equation for fecundity has the assumption of a 50:50 sex ratio at birth, based on our many years of observed litter sex ratio.

We were unable to estimate annual variability in survival for the L3 population, and so we only estimated the mean matrix, $\bar{\mathbf{A}}$. Thus, analyses for this population

were limited to those based on deterministic growth rates and deterministic perturbation analyses.

Estimation of vital rates

We generated mean annual estimates and estimates of annual variance for the set of vital rates used in our population models, PG, LS, SN, SJ, and SA. Estimating variance based on raw annual estimates of vital rates will overestimate process variation in the rate because of the added variation due to sampling error. To account for this we used standard variance decomposition procedures to separate the sampling from process components of variation (Morris and Doak 2002). This separation was done post hoc for LS and PG and as part of the estimation process using a hierarchical modeling approach for each of the survival rates. Estimates of PG were generated based on the proportion of adult females caught during June–August that were pregnant. LS was estimated from field data of litter size based on palpating adult females for young. We used methodology outlined by White (2000) that accounts for unequal sampling variance among years to estimate process variation in both PG and LS. Our estimation procedure for survival rates drew on standard methodology for mark–recapture estimates of survival (Lebreton et al. 1992) embedded within a hierarchical model and fit using Markov chain Monte Carlo methods (Lukacs et al. 2008, White et al. 2008). This allowed us to directly estimate a random effect for annual variation in survival while accounting for sampling variation. Detailed descriptions of survival estimation methods are found in Appendix A.

Basic matrix model analysis

We focused on the influence of component vital rates v_k rather than individual matrix elements a_{ij} in estimation of matrix sensitivities and elasticities (Morris

and Doak 2004). We estimated the deterministic growth rate (λ_1) and deterministic sensitivities and elasticities of vital rates (\bar{S}_v and \bar{E}_v) based on $\bar{\mathbf{A}}$ for each population (Caswell 2001). Sampling error of λ_1 was calculated as a function of the standard errors of component vital rates. Deterministic sensitivities and elasticities of vital rates, v_k , were calculated directly based on their relationship to the sensitivities for individual matrix elements, a_{ij} :

$$\bar{S}_{v_k} = \frac{\partial \lambda_1}{\partial v_k} = \sum_{i,j} \frac{\partial \lambda_1}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial v_k}$$

$$\bar{E}_{v_k} = \frac{v_k}{\lambda_1} \frac{\partial \lambda_1}{\partial v_k} = \frac{v_k}{\lambda_1} \sum_{i,j} \frac{\partial \lambda_1}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial v_k}.$$

Sensitivities measure the effect of absolute changes in v_k on λ_1 , while elasticities of vital rates measured the effect of proportional changes in v_k on $\log \lambda_1$.

We examined population dynamics based on a stochastic population model for L1, L2, M1, M2, and M3. We calculated the stochastic growth rate (λ_s) using both Tuljapurkar’s (1990b) small variance approximation and stochastic simulation by randomly drawing among annual matrices, \mathbf{A}_t (Morris and Doak 2002). The first method is approximate, while the second is unbiased as the number of simulations increases. Both methods incorporate within-year covariation among vital rates but assume that serial correlation among years does not occur. Initial results showed that differences in estimates of λ_s from the two methods were negligible for all populations, and therefore we used Tuljapurkar’s approximation and analyses based on that approximation for all further analyses. The approximation draws on sensitivities estimated from the deterministic analysis for the m vital rates:

$$\log \lambda_s = \log \lambda_1 - \frac{1}{2\lambda_1^2} \sum_{i=1}^m \sum_{j=1}^m \bar{S}_{v_i} \bar{S}_{v_j} \text{cov}(v_i, v_j). \quad (1)$$

This equation demonstrates the effects of variation on fitness, showing that variance in a vital rate ($\text{var}[v_k] = \text{cov}[v_i, v_j]$, $i = j = k$) and positive covariance among the vital rates decreases λ_s , while negative covariance increases λ_s . These effects result in the constraint $\lambda_s \leq \lambda_1$.

Sensitivity and elasticity of λ_s to changes in vital rates must account for changes in mean values and variance of the vital rates (Eq. 1; Tuljapurkar et al. 2003, Doak et al. 2005, Haridas and Tuljapurkar 2005). Haridas and Tuljapurkar (2005) demonstrate that the sensitivity and elasticity of λ_s to changes in the means for vital rates are proportional to \bar{S}_v and \bar{E}_v from the deterministic analyses. Therefore, we focused on the effects of changes in temporal variation in each of the vital rates on λ_s . The effect on fitness of changes in variation for vital rates is of particular interest for stochastic analyses, and sensitivities can be used as a direct measure of changes in fitness associated with an absolute change in variation in a vital rate. The small variance formulation for λ_s

(Eq. 1) has been used to derive equations for sensitivities and elasticities of λ_s as a function of deterministic sensitivities (Doak et al. 2005, Haridas and Tuljapurkar 2005). Following the formulation by Doak et al. (2005) we calculated sensitivities of λ_s to the standard deviation of annual variation in a vital rate, σ_i , as

$$S_{\sigma_i} \approx -\frac{\bar{S}_{v_i}}{\lambda_1} (\bar{S}_{v_i} \sigma_i + \sum_{j \neq i} \bar{S}_{v_j} \sigma_i \rho_{i,j}). \quad (2)$$

The stochastic sensitivity is not only a function of σ_i for each vital rate but also proportional to the correlation, ρ_{ij} , of each vital rate to each of the other vital rates. The elasticity to λ_s was calculated as

$$E_{\sigma_i} \approx -\frac{\bar{S}_{v_i} \sigma_i}{\lambda_1^2} (\bar{S}_{v_i} \sigma_i + \sum_{j \neq i} \bar{S}_{v_j} \sigma_i \rho_{i,j}). \quad (3)$$

Eqs. 2 and 3 measure the effect of absolute and relative contributions of increased σ_i on λ_s based on the derivative of Eq. 1. Effects on λ_s include those due to increases in variances in the vital rate. In addition, increased variance in a vital rate will increase covariance even when correlation remains constant and Eq. 2 and Eq. 3 account for this associated effect. Note that E_{σ} and S_{σ} are only positive in cases in which negative correlations have a large contribution to Eqs. 2 and 3.

Buffering

Theory suggests an inverse relationship between \bar{E}_v and the coefficients of temporal variation (CV) for a vital rate (Pfister 1998, Morris and Doak 2004, Doak et al. 2005). The prediction of an inverse relationship can be seen as arising directly from Eq. 1 because increasing variation has a negative effect on λ_s , proportional to the effect of changes in that vital rate on λ_1 . Thus, the optimal life history can be seen as one that minimizes overall temporal variation of λ and occurs when the sensitivity of λ_1 to highly variable vital rates is minimized. We examine each of several approaches for testing the buffering prediction for multiple vital rates across multiple populations all based on estimating the linear relationship between \bar{E}_v and CV for a set of vital rates. They included: (1) Plot \bar{E}_v vs. CV for all vital rates from all populations at the same time (hereafter, overall relationship); (2) Plot \bar{E}_v vs. CV for all of the vital rates for a single population (hereafter, within-population relationship); (3) Plot \bar{E}_v vs. CV for all of the populations for a single vital rate (hereafter, within vital rate relationship). All three relationships were useful in examining the buffering hypothesis. Previous studies have focused on the overall and within-population relationships, largely because the within vital rate relationship requires that the same vital rate be measured across all of the populations being compared, which is impossible in comparisons of species with disparate life cycles. The within vital rate relationship, however, is especially informative in understanding whether selection for buffering is evident within a

comparative context. First, changes in temporal variation and selection to increase or decrease the sensitivity of a life-history component can be seen as acting on each of the individual vital rates. Second, the within vital rate relationship, unlike the within-population relationship, measures changes among populations and thus is the relationship that tests for buffering within the comparative context. Finally, phylogenetic constraint is most likely to be seen in repeated within-population comparisons where relative variability and sensitivity among vital rates is likely to be similar across all populations.

We used correlation as a measure to estimate the overall, within-population, and within-vital-rate relationships between \bar{E}_v and CV with the expectation that correlations should be negative if the buffering prediction holds. For all proportional vital rates we calculated the CV relative to the maximum possible CV to account for differences in potential variation among vital rates (Morris and Doak 2004). Sample size limits the power to test whether correlations are significant for individual populations or vital rates when examining within-population and within-vital-rate relationships (Pfister 1998; $n = 5$ in our case). Therefore, we calculated a common correlation coefficient for all populations for the within-population relationship and for all vital rates for the within-vital-rate relationship ($n = 25$) using the procedure described by Graybill (1976). Complete derivation of the calculation of common correlation coefficients is found in Appendix B. We also calculated average ecotype values of \bar{E}_v and CV for L-fast and M-slow populations, to examine whether among ecotype relationships followed overall patterns of correlation.

Life-table response experiment

In addition to prospective analyses, we used a retrospective approach to examine the contribution of variance and covariance of component vital rates to annual variation in λ . Life-table response experiments (LTRE) offer a way to decompose factors contributing to variation in λ among annual projection matrices, \mathbf{A}_t , similar to a traditional analysis of variance (Levin et al. 1996, Caswell 2001). We decomposed the contribution of annual variation in each of the vital rates to (1) the total annual variance in λ and (2) variance in λ related to whether or not breeding anurans were present. For the first we used a standard random design LTRE (Caswell 2001) and for the second we employed recently developed methods for stochastic LTRE analysis (SLTRE).

The random design LTRE can be used to decompose variation in λ among years into the contributions due to variance of individual vital rates and covariance between rates. The method provides insight into vital rates that retrospectively contributed to observed temporal variation in λ and to the relative effect of stochastic variation in vital rates to fitness costs due to stochastic variation on λ_s . The random design LTRE is based on the

relationship of variance in λ to variation in each of the component vital rates where

$$\text{var}(\lambda) \approx \sum_{i=1}^m \sum_{j=1}^m \bar{S}_{v_i} \bar{S}_{v_j} \text{cov}(v_i, v_j). \tag{4}$$

Each term in the summation, therefore, determines the contribution (C) of the covariance or variance terms to variation in λ where

$$C_{ij} = \bar{S}_{v_i} \bar{S}_{v_j} \text{cov}(v_i, v_j).$$

Eq. 4 is inversely proportional to the second term in the equation for $\log \lambda_s$ (Eq. 1), which represents the fitness cost of annual variation in λ . Thus, relative contributions of vital rates to the random design LTRE, quantify the observed negative effects of each individual variance and covariance term on λ_s .

We used an SLTRE analysis to decompose variance in λ that could be attributed to whether breeding anurans were present in the previous year to determine how costs of stochastic prey availability affected each population. We calculated the SLTRE using methods presented by Davison et al. (2010; see Caswell 2010 for an alternative derivation for the SLTRE). The goal of the analysis was to quantify how each vital rate contributed to variance in λ for years following those with and without breeding anurans. The SLTRE analysis estimates the contribution of changes among populations in both mean annual vital rate values and their standard deviation on $\log \lambda_s$. The mean and standard deviations correspond to the two components of Eq. 1 used to calculate $\log \lambda_s$. To isolate variation related to prey availability for each population we compared the actual time series of vital rates for all years (v_{it}) to a hypothetical population where variation attributed to whether or not breeding anurans were present in the previous year was removed (v'_{it}). Means for each of the vital rate were kept equal between the two populations so that differences in $\log \lambda_s$ were solely due to removing the portion of annual variation in each of the vital rates related to anuran availability.

Values for v'_{it} were calculated as follows: For each population we calculated the mean vital rate values for all years (\bar{v}_i^{all}), for years when breeding anurans were present (pres) in the previous year (\bar{v}_i^{pres}), and for years when they were absent (abs) in the previous year (\bar{v}_i^{abs}). For years when breeding anurans were present in the previous year $v'_{it} = v_{it} - (\bar{v}_i^{\text{pres}} - \bar{v}_i^{\text{all}})$ and when absent $v'_{it} = v_{it} - (\bar{v}_i^{\text{abs}} - \bar{v}_i^{\text{all}})$. The standard deviation of vital rates were σ_i for the actual population and σ'_i for the hypothetical population. Using standard methods for LTRE analyses with two groups we constructed a reference population intermediate between any two populations of interest. Values for v_{it}^{ref} , calculated as the mean of v_{it} and v'_{it} in each year, were used to calculate the stochastic elasticity of the reference population. The contribution (C_i) of variance in each vital rate to the change in $\log \lambda_s$ due to annual variation

TABLE 1. Summary of life-history differences between ecotypes based on deterministic and stochastic matrix models of population dynamics for the two ecotypes of western terrestrial garter snake (*Thamnophis elegans*) in the Eagle Lake vicinity, California, USA.

Variable	M-slow (meadow)	L-fast (lakeshore)
Generation time	8 yr	5 yr
Overall survival (all ages)	0.74 yr ⁻¹	0.51 yr ⁻¹
Age-dependent survival	higher juvenile and neonate survival	age/size-dependent increases in survival in the two populations with highest λ
Deterministic sensitivities	lower sensitivity of λ to changes in early life-history traits (PG and SN)	higher sensitivity of λ to changes in early life-history traits (PG and SN)
Annual variability in vital rates	greater variability in PG	lower variability in PG
Stochastic sensitivities	largest negative effect on λ occurs for increases in PG	same
Buffering within populations	vital rates with high CVs have low elasticities	vital rates with high CVs have low elasticities
Buffering within vital rates	higher CV and lower elasticity for PG lower CV and higher elasticity for SA	lower CV and higher elasticity for PG higher CV and lower elasticity for SA
Contribution of each vital rate to annual variability in λ .	majority of annual variation in λ due to variation in PG, greater absolute contribution of PG	majority of annual variation in λ due to variation in PG, smaller absolute contribution of PG
Effects of prey availability	annual variation in prey availability has larger effect on λ_s primarily due to changes in PG	annual variation in prey availability has little effect on annual λ_s

Note: Abbreviations are: proportion gravid (PG), neonate survival (SN), adult survival (SA), and coefficients of temporal variation (CV). L-fast populations have a fast-paced life history relative to M-slow populations, which have a slow-paced life history.

in prey availability is

$$C_i = E_{\sigma_i}^{\text{ref}} \{ \log(\sigma_i) - \log(\sigma_i') \}.$$

The value was calculated for all vital rates in all populations.

RESULTS

Results, which are summarized in Table 1, were consistent with differences along a slow-to-fast continuum and with theoretical predictions from life-history theory. In lakeshore locations, $n = 873, 1108,$ and 147 individuals were marked and released in L1, L2, and L3, respectively. Annual estimates of vital rates for each of the populations can be found in Appendix C. In meadow locations, $n = 1655, 449,$ and 709 individuals were marked and released in M1, M2, and M3, respectively. Both the proportion of gravid females and litter size were higher in L-fast populations than in M-slow populations (Table 2). Survival rates were

higher in M-slow populations than in L-fast populations (Fig. 2). Juvenile survival rates were as high as or higher than adult survival rates in M-slow populations, indicating a limited cost for delayed age of first reproduction in these populations. Likewise, in M2 and M3, neonate survival was similar to survival in older age classes and in M1 it was still higher than in any of the L-fast populations. L-fast populations varied in how survival rates changed with age; L1 had equivalent survival across all ages, L2 survival increased gradually with age, and L3 increased steeply with age. Mean generation time T_c in years calculated from \bar{A} was 8.0 years for the M-slow populations vs. 5.0 years for the L-fast populations (Table 2).

Population growth rates differed among populations, with greater variation among L-fast populations (Table 2). The difference between λ_1 and λ_s was similar among populations, ranging from -0.004 to -0.009 . There were no consistent differences in the effects of stochastic variation in vital rates on λ_s between ecotypes,

TABLE 2. Results from matrix model analyses of six populations of western terrestrial garter snakes from lakeshore (L-fast) or meadow (M-slow) ecotypes in the Eagle Lake vicinity, California, USA.

Variable	L1 (GAL)	L2 (PIK)	L3 (RKY)	M1 (PAP)	M2 (NML)	M3 (MAH)
λ_1	0.809	0.911	1.223	0.954	1.052	0.990
SE(λ_1)	0.045	0.031	0.062	0.031	0.031	0.038
λ_s	0.805	0.905		0.95	1.047	0.981
T_c	4.3	4.3	6.3	8.1	8.6	7.2
Proportion gravid	0.318	0.534	0.655	0.348	0.316	0.326
Litter size	6.521	8.703	10.533	5.216	5.307	5.414

Notes: Site names in parentheses correspond to those used in Manier and Arnold (2005) and Manier et al. (2007). We calculated the deterministic growth rate λ_1 for each population based on average vital rates across all years and the stochastic growth rate λ_s , which incorporated annual variation in vital rates. SE(λ_1) is the standard error of the mean estimate of λ_1 . Generation time T_c is the average age of mothers computed from the deterministic analysis. The proportion of gravid females and litter size are average values for all years.

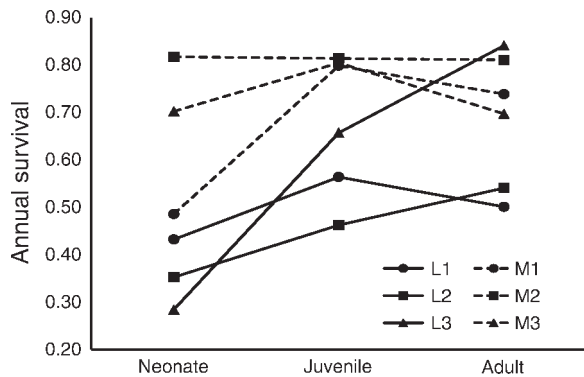


FIG. 2. Annual survival rates estimated from mark-recapture data for garter snakes from six populations in the vicinity of Eagle Lake, California. Snakes from L-fast populations (L1, L2, and L3) had lower overall rates than those from M-slow populations (M1, M2, and M3).

suggesting that the aggregate fitness costs of demographic variability were similar between ecotypes.

Deterministic perturbation analyses showed an overall shift in the relative importance of changes in fecundity vs. adult survival between ecotypes, with fecundity being more influential in L-fast populations than in M-slow populations and vice versa for survival of older age classes. \bar{S}_v was higher for PG and SN in L-fast populations than in M-slow populations and similar for other vital rates (Fig. 3). \bar{E}_v was similar for all vital rates in the L-fast populations, whereas \bar{E}_v for SJ and SA were 2.4 to 3.4 times greater than for PG, LS, and SN in M-slow populations. Comparisons between ecotypes showed that \bar{E}_v for SJ was greater in M-slow populations than L-fast populations, primarily due to the longer juvenile period in meadow populations (3 vs. 1 year in

duration). \bar{E}_v for SA was similar for both ecotypes while \bar{E}_v for PG, LS, and SN were 1.6 to 1.9 times greater in L-fast populations than M-slow populations.

In all populations in both ecotypes, \bar{S}_σ and \bar{E}_σ were greatest for PG (Fig. 4). In four of five populations, SA had the second greatest magnitude, while in L1 changes in σ for SN were predicted to have the second greatest effect on growth rate.

We found support for the hypothesis that life-history differences buffer against negative effects of variation in vital rates. There was a negative correlation between \bar{E}_v and CV for the overall test of all vital rates and all populations combined ($r = -0.452, P = 0.01$). Consistent with predictions of Morris and Doak (2004) there were no combinations where there was both high \bar{E}_v and high CV for a vital rate (Fig. 5A; all values occur in the bottom left half of the figure, none in the top right corner). We did not find support for differences in the correlation between \bar{E}_v and CV among populations ($U = 0.258, P = 0.99$; Appendix B). Therefore, we averaged all populations to estimate a single common correlation coefficient for the within-population relationship between \bar{E}_v and CV. Consistent with predictions, the common correlation coefficient for the within-population relationship was negative ($\hat{R} = -0.383, P = 0.031$). Again we did not find support for differences in correlations between \bar{E}_v and CV among vital rates ($U = 7.91, P = 0.10$). Values for vital rates were combined to estimate the common correlation coefficient for the within vital rate relationship, which was significantly negative ($\hat{R} = -0.677, P = 0.027$).

The within vital rate relationship was consistent with a process driven primarily by ecotype differences. This was supported by four out of five vital rates showing a negative relationship between mean ecotype values of

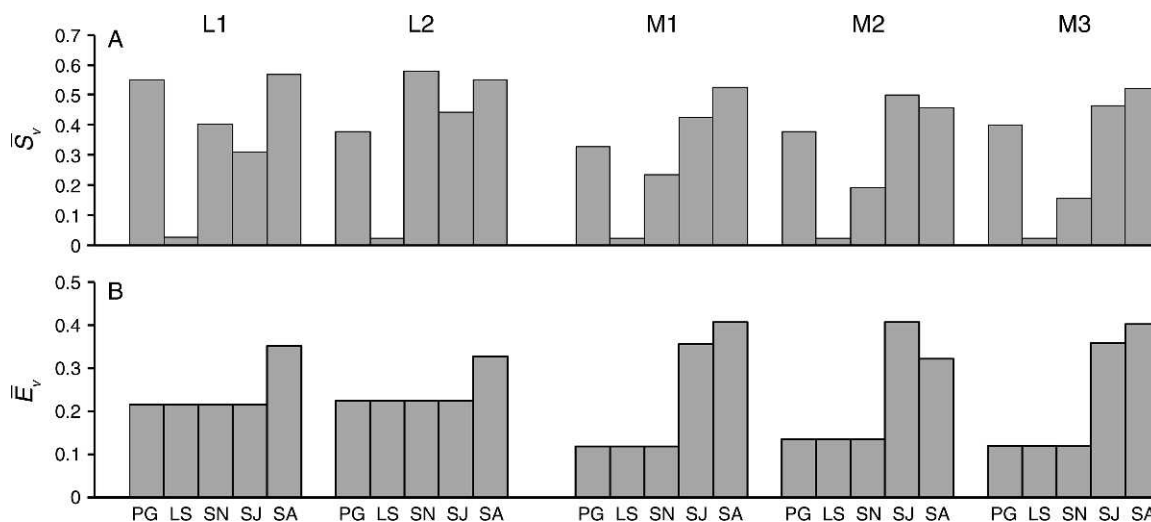


FIG. 3. (A) Sensitivities (\bar{S}_v) and (B) elasticities (\bar{E}_v) of deterministic growth rates (λ_1) to changes in vital rates for garter snakes from two L-fast (L1 and L2) and three M-slow (M1, M2, and M3) populations in the vicinity of Eagle Lake, California. Vital rates measured were proportion gravid females (PG), litter size (LS), neonate survival (SN), juvenile survival (SJ), and adult survival (SA).

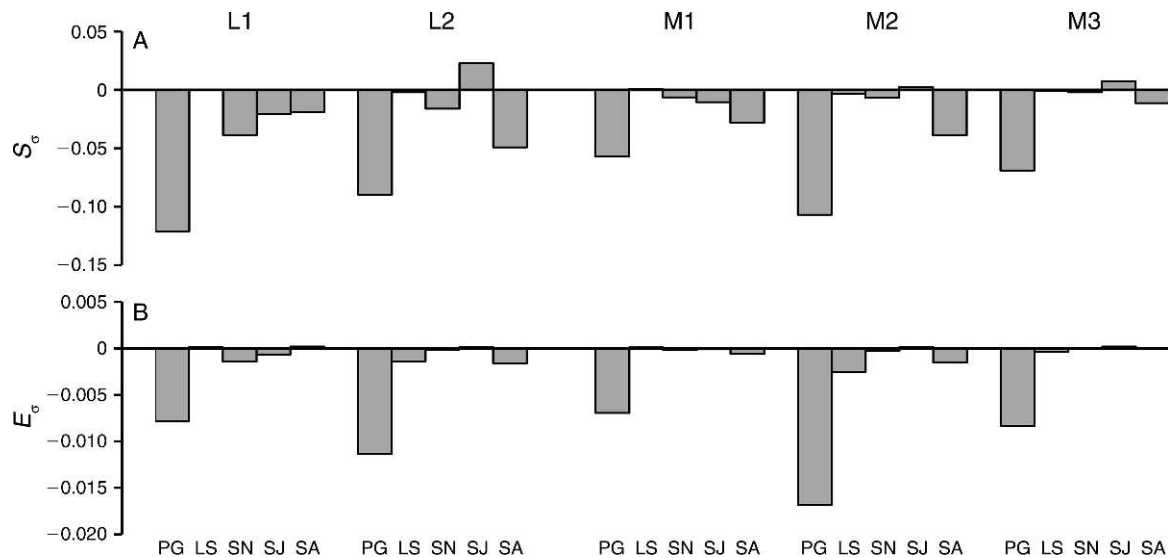


FIG. 4. (A) Sensitivities (S_{σ}) and (B) elasticities (E_{σ}) of stochastic growth rates (λ_s) to changes in the standard deviation of annual variation in vital rates for garter snakes from two L-fast (L1 and L2) and three M-slow (M1, M2, and M3) populations in the vicinity of Eagle Lake, California. Vital rates measured were the proportion of gravid females (PG), litter size (LS), neonate survival (SN), juvenile survival (SJ), and adult survival (SA). Values are generally negative because increases in variation in a vital rate have a negative effect on λ_s .

\bar{E}_v and CV (Fig. 5B). Visual examination suggests that the relationships may be stronger for vital rates near the upper limit of the parameter space (PG and SA), again consistent with the prediction of Morris and Doak (2004). The strongest relationship occurred for PG, suggesting that increased relative variability in this vital rate in M-slow populations has been important in the evolution of lower elasticity to this vital rate.

Results from the random design LTRE demonstrated that annual variation in PG had the greatest contribution to annual variation in λ for all populations (Fig. 6). Variability in gravidity (PG) accounted for 75% and 98% of annual variation in λ depending on the population. The absolute effect of variance in PG was higher in M-slow populations than in L-fast populations, with the greatest absolute effect in M3. SA had the second greatest contribution for variance terms in four of the five populations. Covariance terms had a relatively small contribution in all populations except in M2 where positive covariance of PG to LS and SA increased annual variation in λ for the population.

Results from the SLTRE showed that PG had the largest contribution to annual variation in λ attributable to whether or not breeding anurans were present during the previous year for all populations (Fig. 7). However, the contribution of prey-related variance in PG to $\log \lambda_s$ was 3.7 to 23.2 times greater in M-slow populations than in L-fast populations. This is consistent with a greater fitness cost associated with annual prey availability in M-slow populations due to its influence on the probability that females are gravid in a given year.

DISCUSSION

Temporal variation in reproduction

Compared to other life-history traits, annual variation in the proportion of gravid females had a disproportionate effect on stochastic demography for snakes from both ecotypes. Variability in prey availability in the previous year appeared to synchronize reproduction within years leading to relatively high annual variability in the proportion of females that were gravid. Both litter size and survival rates at all ages were relatively invariable compared to the proportion of gravid females. As a consequence, more than three-quarters of the annual variability in λ in all populations was due to differences in this parameter. This means that the stochastic fitness cost resulted largely from variation in a single life-history trait, despite ample variation in other life-history traits. Changes in annual variance in the proportion of gravid females also had the greatest effect on λ_s as measured by both stochastic sensitivities and elasticities. Vital rate sensitivities are a direct measure of the change in mean fitness (λ) associated with an absolute change in the vital rate (Lande 1982, Caswell 2001, Tuljapurkar et al. 2009). Thus, a similar increase in annual variance in the proportion of gravid females will have a larger fitness cost than that for other vital rates.

The proportion of gravid females not only had a disproportionate effect on stochastic dynamics within populations, but differences in both its magnitude and its relation to prey availability also explained differences in stochastic demography between the M-slow and L-fast ecotypes. Relative variability in gravidity

was greater in the M-slow populations than L-fast populations. Similarly, the random effect life-table response experiment showed that annual variability in gravidity had a greater effect on annual variability in λ in M-slow populations than L-fast populations. The difference between ecotypes in the magnitude and consequence of annual variability in reproduction was related to a strong signature for cross-ecotype buffering in this life-history trait. The shift to later reproduction, smaller litter size, and higher survival rates at all ages in M-slow populations has dampened the negative fitness effects associated with high variability in gravidity. In total, results indicate that environmental variability that affects reproduction through variability in food availability has selected for life-history differences among populations of western terrestrial garter snakes.

Buffering of temporally variable life-history traits

An evolutionary prediction arising from stochastic models of population dynamics is that demographic parameters that have high temporal variability should have a smaller influence on fitness (Stearns and Kawecki 1994, Pfister 1998). This prediction is based on the observation that variation in population growth rates has a negative effect on fitness (Lewontin and Cohen 1969, Gillespie 1977) and that the effect of variation is directly related to elasticity of population growth rates to changes in component vital rates (Tuljapurkar 1990a). The predicted relationship has been referred to as “buffering” because of the expectation of an inverse relationship between variance and sensitivity for vital rates (Pfister 1998). Most recent empirical studies of stochastic environmental variation on life-history evolution have focused on buffering to predict patterns across a range of taxa (Pfister 1998, Sæther and Bakke 2000, Gaillard and Yoccoz 2003, Dalgleish et al. 2010). General patterns in this study are consistent with a predicted inverse relationship between the elasticity and the CV of vital rates within populations in both ecotypes.

Our results also offer novel support for the buffering hypothesis. In addition to previous findings that explain macro-level patterns across taxa that have diverged over long evolutionary periods (e.g., Pfister 1998), we show that life-history differences among populations of a single species are consistent with buffering. More importantly we show that the relationship not only holds among vital rates within populations but also for each of the individual vital rates across populations. We argue that this is a more direct and powerful test of the prediction. The hypothesis that life-history traits should be buffered against the effects of environmental variation is based on the prediction that variance in an individual life-history trait elicits selection to reduce variance in that trait. Thus, comparisons of the same vital rate among multiple populations directly tests for the expected pattern in response to selection. In

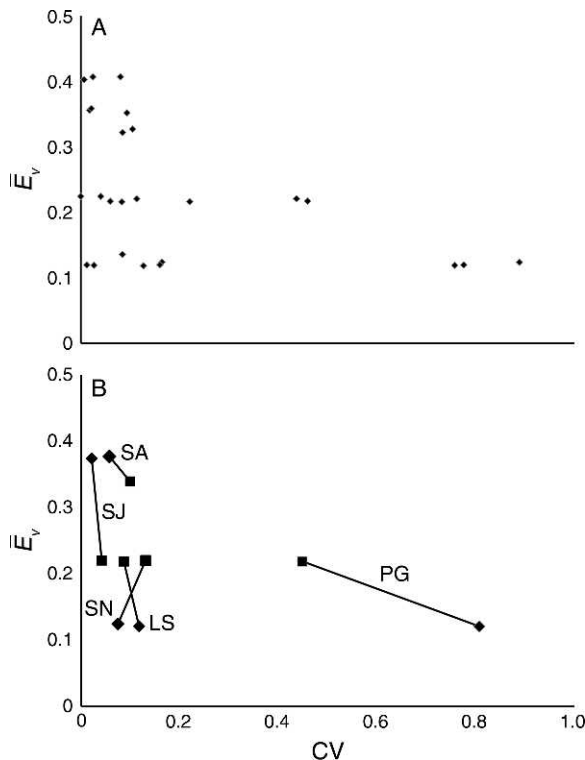


FIG. 5. Comparison of coefficients of variation in vital rates to the elasticity of growth rate to the vital rate for garter snakes from five populations in the vicinity of Eagle Lake, California. (A) All vital rates from all populations are compared and show a general inverse relationship. (B) Inverse relationships in mean differences between ecotypes are also seen in four of five vital rates. Means were calculated for L-fast populations (squares) and M-slow populations (diamonds) and are connected by a solid line for each vital rate. The strongest relationships occurred for vital rates with high variability or sensitivity, including the proportion of gravid females (PG) and adult survival (SA). Juvenile survival (SJ) and litter size (LS) also had negative relationships, while the relationship for neonate survival (SN) was positive and opposite of that predicted.

addition, comparison within a single vital rate avoids the problem of comparing life-history components for which variation may be structured by very different developmental, physiological, and ecological influences. Previous comparisons of life histories across a diverse set of taxa show that survival and growth tend to have consistently greater influence on fitness than fecundity as measured by sensitivities and elasticities (Pfister 1998, Gaillard and Yoccoz 2003). As a result, relationships within a single population can arise if environmental variability has a greater inherent impact on vital rates that affect fecundity over survival and growth, rather than the direct selection of buffering. Directly comparing the same life-history trait across a set of populations avoided this confounding.

Much of the difference among populations as it relates to buffering can be accounted for by differences between the two ecotypes. Comparisons of averages for

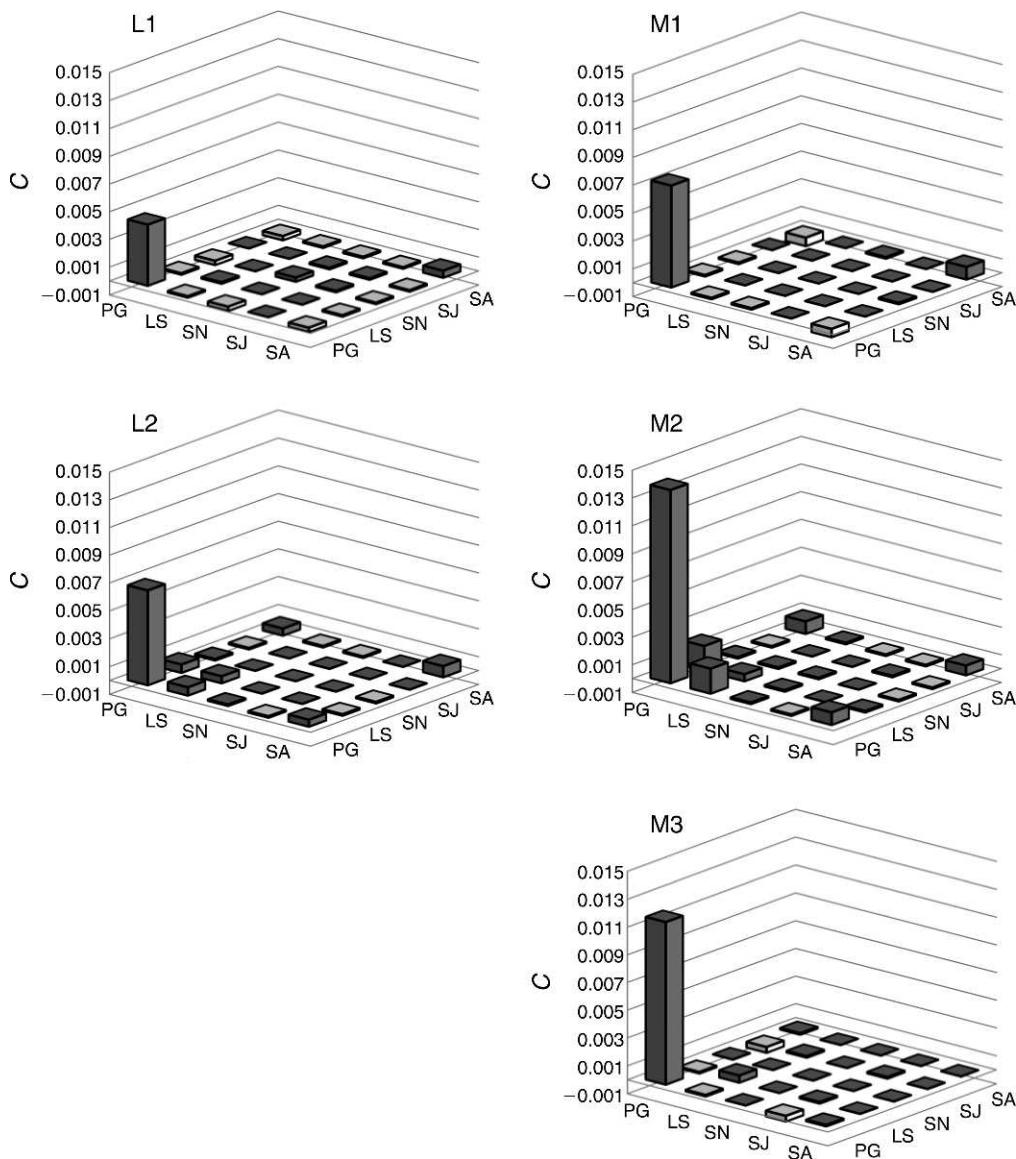


FIG. 6. Random-design life-table response experiment measuring the effects of annual differences in vital rates to variation in growth rate for five garter snake populations in the vicinity of Eagle Lake, California. Values are the contribution (C) of variance or covariance in vital rates to annual variation in λ . Vital rates measured were the proportion of gravid females (PG), litter size (LS), neonate survival (SN), juvenile survival (SJ), and adult survival (SA). In all populations, variability in PG had the largest contribution to variation in λ_1 , with the magnitude of this effect greater, on average, for M-slow populations (M1, M2, and M3) than for L-fast populations (L1 and L2). Positive values are shown in dark gray, and negative values in light gray.

populations within each ecotype show the inverse relationship between elasticity and CV for ecotype comparisons for all vital rates except neonate survival. The strongest relationship occurs for the proportion of gravid females for which average CVs of M-slow populations are doubled and average elasticities are halved relative to fast populations. Elasticity for the proportion of gravid females and other early life vital rates are lowered in M-slow populations as a result of delayed reproduction and high survival rates, which tend to increase the contribution of adult survival rates

to fitness. Even with significant buffering of the proportion of gravid females in M-slow populations, its absolute effect on annual variability in λ is still greater than in L-fast populations. However, if L-fast populations had the same annual variability in the proportion of gravid females as M-slow populations, given their life history the fitness costs attributable to that variability would be greater than that observed for M-slow populations. This observation further bolsters the argument that variation in prey availability, acting through the vital rate PG, has been an important

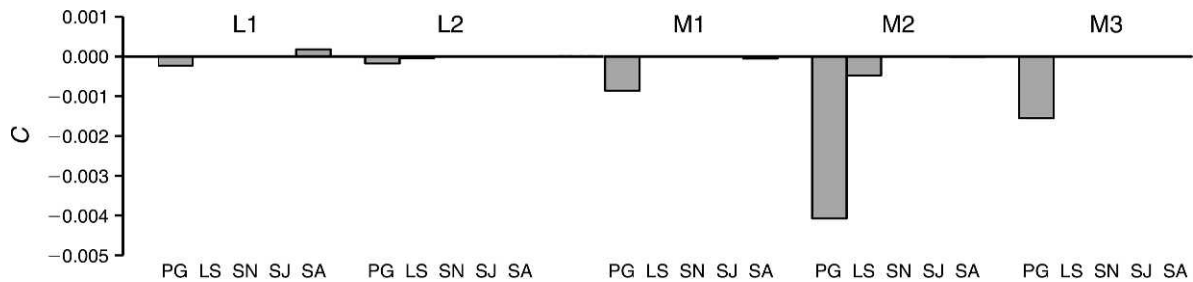


FIG. 7. Fixed-effects life-table response experiment measuring the effect of anuran availability on annual population growth rate for garter snake populations in the vicinity of Eagle Lake, California. Effect sizes for each vital rate measure the effect of changes in that vital rate in years with and without breeding anurans on differences in λ between years with and without breeding anurans. That is, C_i is the contribution in variance in each vital rate to the change in $\log \lambda_s$ due to annual variation in prey availability. Vital rates measured were the proportion of gravid females (PG), litter size (LS), neonate survival (SN), juvenile survival (SJ), and adult survival (SA). In all populations, changes in PG had the largest effect on λ , with the magnitude of this effect greater on average for M-slow populations (M1, M2, and M3) than for L-fast populations (L1 and L2).

selective force in the evolutionary divergence of these two life-history strategies.

Deterministic dynamics

L-fast populations have lower survival across age classes, larger litter sizes, more frequent reproduction, earlier age of first reproduction, faster growth, and shorter generation times (see *Results*; Bronikowski and Arnold 1999). Interestingly, the L1 population shows a number of traits that appear to be intermediate between the rest of the lakeshore populations and meadow populations. This intermediacy is consistent with the spatial position of the population, which is located on the shore of Eagle Lake but is most closely connected by a stream network to adjacent M-slow populations. This population is also intermediate in coloration and morphology (Manier et al. 2007).

Results from this study were consistent with other studies that have suggested that mortality rates have a strong influence on life-history evolution (Reznick et al. 1996, Walsh and Reznick 2009). Age-specific declines in mortality attributable to changes in size are predicted to select for shifts along a slow-to-fast continuum (Abrams and Rowe 1996), an expectation that was realized in our garter snake study system. Estimates of neonate and juvenile survival were consistently lower for L-fast populations than M-slow populations. In addition, in L2 and L3 large age-specific increases in survival were evident. These are the two populations previously found to have much higher individual growth rates than meadow populations, while the L1 population was shown to have intermediate individual growth rates (Bronikowski and Arnold 1999). This result suggests that size-specific predation has a direct role in promoting fast life histories in lakeshore populations.

Ecology of life-history differences

Understanding the ecological processes that generate stochastic dynamics is important to determine the influence that these processes have on the evolution of life histories (Koons et al. 2009, Tuljapurkar 2010).

Ecological context has had an important role in determining how deterministic dynamics influence life-history evolution (Martin 1995, Reznick et al. 1996, Bronikowski and Arnold 1999, Bronikowski et al. 2002). Ecological context may be even more important in understanding the influence of stochastic dynamics on life-history evolution. Quantifying environmental variation and its relationship to component vital rates, is crucial for understanding how temporal variation selects for different life-history traits (Tuljapurkar 2010). Understanding how environmental variation affects individual vital rates is similarly important in conservation biology because of the importance of predicting environmental impacts on demography (Boyce et al. 2006, Morris et al. 2008, Jonzén et al. 2010).

Ecological interactions can select for life-history traits through effects on top-down and bottom-up processes related to predation and food availability (Stearns 1992). This study provides empirical evidence that effects in both directions have been important in determining life-history differences between garter snake ecotypes. Higher mortality rates across all ages in lakeshore habitats suggest that predation in this environment is responsible for high levels of extrinsic mortality (Bronikowski and Arnold 1999). Lakeshore habitats are more open and likely more frequented by avian predators (A. M. Sparkman and S. J. Arnold, *unpublished data*), suggesting that predation has favored cryptic coloration and characteristic morphology in L-fast snakes (Manier et al. 2007). At the same time, bottom-up processes clearly play an important role in our system. The proportion of gravid females had the greatest contribution to stochastic demographic processes, and both temporal and among ecotype variation in this parameter was related to environmentally determined prey availability.

We conclude that a combination of top-down and bottom-up influences, as well as deterministic and stochastic processes, likely work in concert to select for life-history differences between ecotypes. Conditions that favor persistence of the snakes differ between

lakeshore and meadow habitats. L-fast populations benefit from consistent availability of food, and M-slow populations benefit from low predation rates. Adaptation to the contrasting environments experienced by snakes in each of the two ecotypes has resulted in selection for different optimal life histories.

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APPENDIX A

Details for the estimation of annual survival rates in the focal populations of garter snakes (*Ecological Archives* E092-140-A1).

APPENDIX B

Derivation of the common correlation coefficient (*Ecological Archives* E092-140-A2).

APPENDIX C

Annual estimates of vital rates for each population of garter snake (*Ecological Archives* E092-140-A3).