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REVIEW

Stochastic matrix models for conservation and management: a comparative review of methods

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Abstract

Stochastic matrix models are frequently used by conservation biologists to measure the viability of species and to explore various management actions. Models are typically parameterized using two or more sets of estimated transition rates between age/size/stage classes. While standard methods exist for analyzing a single set of transition rates, a variety of methods have been employed to analyze multiple sets of transition rates. We review applications of stochastic matrix models to problems in conservation and use simulation studies to compare the performance of different analytic methods currently in use. We find that model conclusions are likely to be robust to the choice of parametric distribution used to model vital rate fluctuations over time. However, conclusions can be highly sensitive to the within-year correlation structure among vital rates, and therefore we suggest using analytical methods that provide a means of conducting a sensitivity analysis with respect to correlation parameters. Our simulation results also suggest that the precision of population viability estimates can be improved by using matrix models that incorporate environmental covariates in conjunction with experiments to estimate transition rates under a range of environmental conditions.

Keywords

conservation biology, correlated vital rates, environmental stochasticity, population viability analysis, sensitivity analysis, stochastic matrix models, transition matrices.

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INTRODUCTION

Population viability analyses (PVAs) have become increasingly common in the conservation literature as mathematical modeling tools have become more widely accessible to wildlife managers and conservation biologists (e.g. Boyce 1992; Beissinger & Westphal 1998; Groom & Pascual 1998; Reed *et al.* 1998; Morris *et al.* 1999; Menges 2000). While a wide variety of mathematical and statistical tools are available to conduct PVAs, matrix models remain popular because of their relative simplicity and their potential for linking vital rates directly to population dynamics. The goal of this paper is to provide a review of statistical issues concerning the formulation and analysis of stochastic matrix models in conservation biology. Readers are encouraged to consult the review papers cited above for a more general discussion of the strengths and limitations of the various tools available for conducting PVAs, and the practical issues associated with conducting PVAs for a population in the wild.

Estimates of transition rates require at minimum $N+1$ years of data in order to estimate N transition matrices. Frequently, time and monetary constraints limit the researcher to two consecutive years of data collection resulting in one set of transition rate estimates. In these cases, one can conduct a deterministic analysis including: calculation of the dominant eigenvalue to assess the viability of the population, calculation of sensitivities and elasticities to assess the relative importance of each transition rate, and calculation of the stable age structure and reproductive values associated with the estimated transition matrix (Caswell 1989). Demographic data collected for three or more consecutive years allow calculation of multiple transition matrices, differing from each other as a result of sampling variation and variation in environmental conditions. A deterministic analysis based on each estimated matrix will therefore often result in very different conclusions (Bierzychudek 1999). However, a more typical approach to analyzing multiple sets of transition estimates is to formulate a stochastic matrix model under the assumption that the variation in vital rates among matrices is due to fluctuating environmental conditions.

Stochastic matrix models are useful for exploring the same types of questions addressed by a deterministic matrix model. Simulation of population projections provides a means of estimating a stochastic growth rate and other measures associated with the viability of the population, such as the probability of extinction. Similarly, one can conduct a sensitivity analysis to determine which rates have the greatest influence on the population's growth rate. Despite the popularity of stochastic matrix models among conservation biologists, a review of the literature indicates that several methods are currently being used to formulate and analyze stochastic matrix models without much thought being given to the relative accuracy and precision of competing methods. Theoretical or simulation studies comparing methods are rare.

In this paper, we review applications of stochastic matrix models to problems in conservation, with a focus on the methods used to formulate and analyze models. We compare the performance of the different analytical methods currently in use via simulation studies. Based on our results, we offer recommendations concerning data analysis methods that may depend on the quality, quantity and nature of the available data. Models that explicitly relate variability in vital rates to environmental variables are suggested as a potentially more powerful alternative to the descriptive statistical approach that most studies to date have used.

MODEL CONSIDERATIONS

Long-term population dynamics

The basic form of a stochastic matrix model is given by:

$$N(t+1) = A(t)N(t) \qquad (1)$$

where $N(t)$ is a vector of age/size/stage classes, and $A(t)$, $t = 0, 1, 2, \ldots$ is a set of transition or projection matrices assumed to vary according to environmental fluctuations. The resulting dynamics of the model depend on the assumptions regarding the stochastic process generating these transition matrices (Caswell 1989). Most applications in conservation biology assume that the stochastic process generating $A(t)$ is a stationary (time-invariant) ergodic Markov chain. In this case, the long-term dynamics of $N(t)$ will be independent of the initial state of the population, $N(0)$. As t becomes large, the log population size, $\log\{N(t)\}$, will be approximately Gaussian distributed with mean $\log\{N(0)\} + \mu t$ and variance $\sigma^2 t$ (Tuljapurkar & Orzack 1980; Heyde & Cohen 1985). Here, μ is the long-term stochastic growth rate of the population and σ^2 is the "infinitesimal variance" of the process.

If important environmental variables fluctuate in a cyclical manner, a periodic matrix model may be appropriate (see, for example, Golubov *et al.* 1999). While similar convergence properties apply in this case (Caswell 1989), the model is not inherently stochastic. Another important consideration is whether or not to include density dependence in the model. The long-term convergence results discussed above do not apply for density-dependent populations. Density-independent models are often justified for populations that have been reduced to levels well below their carrying capacity and are therefore of concern to population managers. However, density-independent models may not be appropriate for small populations that are limited by habitat availability or for populations that have become endangered as a result of habitat fragmentation. In such cases, where habitat destruction is the main cause of population decline, predictors of future habitat utilization (e.g. current and projected economic growth and zoning regulations) may provide an alternative to demographic population modeling for assessing long-term population viability (C. Wilcox, personal communication). Throughout the rest of this paper, we will assume the underlying population model is density independent, with transition matrices generated by a stationary ergodic Markov chain.

Number of age/stage classes

The first step in formulating a stochastic matrix model is to determine an appropriate number of age/stage classes. Ideally, stage/age classes should only group individuals with similar demographic rates. This can be accomplished by subdividing the population into many classes. However, increasing the number of classes decreases the amount of data per class for estimating the class's transition rates. Vandermeer (1979) and Moloney (1986) offer objective methods for balancing these two conflicting goals. Alternatively, Easterling *et al.* (2000) have developed a continuous state-discrete time modeling approach that does not require specification of size/stage classes. We will not give further consideration to this problem here.

Correlation among vital rates within years

Correlation among vital rates arises when environmental variation affects multiple vital rates simultaneously. For example, severe winter snowfall may decrease both adult and juvenile survival rates, resulting in a positive correlation between these parameters. Several recent studies of populations across time and space have shown significant, and mostly positive, within-year correlations among transition rates (Horvitz & Schemske 1995; Oostermeijer *et al.* 1996). Tuljapurkar's approximation (1990) to the stochastic growth rate, μ, provides a means for investigating the effect of within-year correlation. In the case of temporally independent fluctuations, the stochastic growth rate is approximately given by:

$$\mu \approx \log(\lambda_0) - \frac{1}{2}\sigma^2;$$

$$\sigma^2 \approx \frac{1}{\lambda_0^2}\sum_{ij,kl}\left(\frac{\partial\lambda}{\partial a_{ij}}\right)\left(\frac{\partial\lambda}{\partial a_{kl}}\right)\mathrm{Cov}(a_{ij}, a_{kl}) \qquad (2)$$

where λ_0 is the dominant eigenvalue of the matrix of mean rates,

$$\left(\frac{\partial\lambda}{\partial a_{ij}}\right)$$

is the sensitivity of λ to parameter a_{ij}, and the sum is over $1 \leqslant i, j, k, l \leqslant n$, where n is the dimension of $N(t)$. Clearly, positive correlation has a negative effect on the long-term growth rate of the population, while negative correlation tends to dampen the effect of vital rate fluctuations. Positive correlation among parameters can significantly alter even short-term population projections, and therefore incorrect assumptions regarding the degree of correlation can have far-reaching consequences for viability calculations (Ferson & Burgman 1995; Cisneros-Mata *et al.* 1997). Furthermore, since positive correlation increases σ^2, the variance of the asymptotic distribution of log population sizes, correlation can affect the degree to which one can expect to predict future dynamics.

Autocorrelation

If environmental variables associated with vital rates are correlated over time (e.g. fluctuations in food supply may be correlated from one year to the next), then one may expect vital rates to exhibit autocorrelation. Long time series are required to determine if autocorrelation exists. Swanson (1998) analyzed 175 vertebrate and 88 precipitation data sets and found using resampling techniques that 15 years of data were necessary to stabilize estimates of the autocorrelation present in the data set. Since data are rarely sufficient to determine the degree to which vital rates are temporally correlated, most stochastic matrix models assume vital rates are uncorrelated over time. Those studies that have included autocorrelation have typically done so using an autocorrelation matrix that defines the probability of choosing any given matrix in terms of the previously chosen matrix (Silva *et al.* 1991; Canales *et al.* 1994; Dixon *et al.* 1997). Including autocorrelation did not severely affect the conclusions of these studies, indicating that temporal correlations are probably less important than within-year correlations among rates. These results support theoretical studies that have shown that μ is typically not affected much by autocorrelation (Tuljapurkar 1982). On the other hand, studies have shown that positive autocorrelation can have a large effect on σ^2 and on the rate of convergence of the total population size to a lognormal distribution (Tuljapurker & Orzak 1980; Tuljapurkar 1982; Runge & Moen 1998).

ESTIMATION OF μ AND THE PROBABILITY OF EXTINCTION, P_{EXT}

Demographic data collected for $N+1$ years lead to estimated transition matrices $A_1, A_2, \ldots, A_N$. Stochastic matrix models parameterized from such data are typically used to estimate μ, σ^2, extinction probabilities and sensitivities or elasticities of μ to changes in demographic rates. Several analytical methods have been proposed to calculate these quantities. However, it is unclear which of these methods provide the most accurate and precise estimates.

A population's long-term growth rate and its probability of extinction can be estimated by simulating equation 1 on the computer. The simplest method of simulating population trajectories is to randomly sample from the N estimated transition matrices to project the population for each simulated year. We will refer to this approach as the "random transition matrix" (RTM) approach. Most early analyses of empirical data sets [eight out of 11 applications of matrix models reviewed by Nakaoka (1996)] used this approach.

Alternatively, one can formulate a multivariate distribution to describe how vital rates vary over time and then randomly draw values from this distribution to simulate population dynamics. We refer to this method as the "parametric matrix method" (PMM). This approach has become popular with the availability of several population viability analysis software packages that allow the user to select from a limited menu of distributions [e.g. RAMAS/Stage (Ferson 1994), RAMAS/Metapop (Akçakaya 1997), INMAT (Mills & Smouse 1994), ALEX (Possingham & Davies 1995), VORTEX (Lacy 1993), and GAPPS (Harris *et al.* 1986)]. It should be noted that the above programs differ in their underlying structure and capabilities; see, for example, Mills *et al.* (1996), Brook *et al.* (1999) and Brook *et al.* (2000a,b) for a comparison of different PVA packages. In particular, several of the packages use an individual-based formulation of the transition matrix model to implement demographic stochasticity.

Finally, one can estimate μ and σ^2 analytically using Tuljapurkar's "small fluctuations approximation" (SFA), given by equation 2, and an estimate of extinction risk can then be calculated using these estimated parameters and a diffusion approximation (Lande & Orzack 1988; Dennis *et al.* 1991; Cisneros-Mata *et al.* 1997). All three of these methods have been applied to problems in conservation (Table 1).

Table 1 A selection of stochastic matrix models applied to problems in conservation biology, to illustrate the diversity of methods and assumptions that have been used.

Species (references)	Type of matrix (number of classes)	Number of sets of transition estimates	Purpose of the model	Methods used	Autocorrelation included (Y/N)	Distribution/correlation (if PMM used)	Covariates	Comments
Semibalanus balanoides (barnacle); Wethey (1985)	Age (4)	4 (fecundity) 2 (survival – with and withiout ice) Collected in 4 habitat types	Estimate μ, P_{ext} Assess the importance of catastrophic mortality due to ice scouring. Sensitivity analysis (by using a range of parameter values).	RTM	No	NA	Ice Year (Y/N)	Metapopulation model incorporating different habitat types.
Plantago lanceolata (plant); van Groenendael and Slim (1988)	Size and Age (12) habitat 1 (18) habitat 2	3 (in each of two habitat types)	Estimate P_{ext}, sensitivity analysis. Assess the effect of habitat type on life history characteristics.	RTM, deterministic elasticity analysis	No	NA	No	
Furbish's lousewort *Pedicularis furbishiae* (perennial plant); Menges (1990)	Size/Stage (6)	3 pooled across 3–15 sites.	Estimate P_{ext}, μ. Assess the importance of vegetative cover, substrate type, substrate disturbance class, dominant vegetation, light and soil water potential on transition rates and population viability	RTM, also included natural catastrophes (with varying probability)	No	NA	Covariates collected (see purpose) but not directly included in stochastic model	
Yoldia notabilis (marine bivalve); Nakaoka (1997)	Size (10)	18 (recruitment) 9 (individual growth); sampled at 2 sites.	Estimate μ and sensitivities. Examine the effect of recruitment distribution (normal vs. lognormal) on μ	PMM, stochastic sensitivity analysis (calculated through numerical differentiation)	No	Lognormal & truncated normal (recruitment), normal (individual growth). Rates vary independently	No	

Table 1 continued.

Species (references)	Type of matrix (number of classes)	Number of sets of transition estimates	Purpose of the model	Methods used	Autocorrelation included (Y/N)	Distribution/correlation (if PMM used)	Covariates	Comments
Gopherus agassizii (Desert tortoise); Doak *et al.* (1994)	Size (8)	2 to 4 (sampled at 8 sites).	Estimate μ, sensitivity analysis	PMM, deterministic elasticities calculated from mean matrix.	No	Beta (growth and survivorship). Reproduction held constant. Rates correlated	No	Combined spatial and temporal variability
Umbonium costatum (subtidal snail); Noda & Nakao (1996)	Age (6)	8	Estimate μ	RTM (recruitment)	No	NA	No	
Leptogorgia virgulata (Marine gorgonian coral); Gotelli (1991)	Size (5)	23 (monthly)	Estimate μ, sensitivity analysis.	RTM (varying matrices), RTM (individually varying recruitment, growth, and survival rates).	No	NA	No	Estimated correlation among rates and found negative correlation between survival, growth and recruitment
Haliaeetus leucocephalus (bald eagle); Wood & Collopy (1993)	Age () size of matrix not given in text	Not provided (used means and variances)	Estimate population size after 25 years for population in which eggs were removed vs. control population.	PMM using RAMAS/stage	No	Distribution not given	No	
Arisaema tyiphyllum (perennial herb); Bierzychudek (1982)	Size (7)	2 (sampled at 2 sites)	Estimate μ, sensitivity analysis	RTM, stochastic sensitivity analysis (numerically)	No	NA	No	
Morone saxatilis (striped bass); Cohen *et al.* (1983)	Age (15)	13 (survival of eggs to yearlings)	Estimate μ	RTM	No	NA	No	

Table 1 continued

Species (references)	Type of matrix (number of classes)	Number of sets of transition estimates	Purpose of the model	Methods used	Autocorrelation included (Y/N)	Distribution/correlation (if PMM used)	Covariates	Comments
Panax quinquefolium (American Ginseng) and *Allium* (wild leek); Nantel *et al.* (1996)	Ginseng size (6) Wild leek Size (7)	4 (from multiple populations of ginseng) 4 (wild leek)	Estimate μ,P_{ext}, and "minimum viable population size" under various harvesting strategies. Determine optimal harvest strategy	RTM	No (ginseng) Yes (wild leek)	NA	No	Used spatial variance to represent temporal variance
Ascophyllum nodosum (brown alga); Aberg (1992a,b)	Size (5)	3 (at two different sites)	Estimate μ, P_{ext} sensitivity analysis. Determine the effect of ice severity and its frequency on vital rates and μ	RTM, stochastic elasticity analysis (numerically)	No	NA	Type of year (no ice, moderate damage due to ice, and large damage due to ice)	Used 30 years of data to determine frequency of each type of year (no ice, moderate ice, large ice).
Haplopappus radiatus (herbaceous perennial plant); Greenlee & Kaye (1997)	Size (4)	3 (at each of 4 different sites)	Estimate μ, compare RTM and PMM estimators.	RTM, PMM	No	Truncated Normal	No	
Andropogon breviffolius (savanna grass); Canales *et al.* (1994)	Age (6)	6 monthly (1 burn plot, 1 control plot)	Estimate μ, sensitivity analysis, estimate optimal burn frequency.	RTM, periodic matrix model; LTRE sensitivity analysis	Yes	NA	Fire (burn year, non-burn year)	
Andropogon semiberbis (savanna grass; Silva *et al.* (1991)	Size (4)	2 (one burn, one non-burn)	Determine burn frequency needed to ensure $\mu > 0$, sensitivity analysis.	RTM, LTRE sensitivity analysis	Yes	NA	Fire (burn year, non-burn year)	

Table 1 continued.

Species (references)	Type of matrix (number of classes)	Number of sets of transition estimates	Purpose of the model	Methods used	Autocorrelation included (Y/N)	Distribution/correlation (if PMM used)	Covariates	Comments
Hudsonia montana (shrub); Gross *et al.* (1988)	Size (5)	4 (plots divided into 3 treatment groups: control burn, and competitors hand clipped)	Determine burn frequency that maximizes μ; sensitivity analysis; examine effectiveness of trampling reduction vs. controlled burns	PMM and periodic matrix model; deterministic elasticity analysis using mean matrix	No	Beta (survival rates); Normal (fecundity rates); rates correlated	Fire (burn year, year after burn, 2 years after burn, and non-burn year)	
Cervus elephas (red deer); Benton *et al.* (1995)	Age (19)	21 (survivorship & reproduction)	Estimate μ, sensitivity analysis comparing stochastic and deterministic measures. Compare RTM amd SFA estimates of μ.	RTM, SFA, stochastic snd deterministic sensitivity analysis	No, but test for autocorrelation	NA	No	
Carex bigelowii (sedge); Carlsson & Callaghan (1991)	Size/stage and age (26)	3 (used 2 sets of transition estimates from "non-flowering" and one estimate of rates during "flowering years")	Estimate μ, sensitivity analysis	RTM, deterministic elasticity analysis (for each type of year – flowering and non-flowering)	Indirectly (through restrictions on the number of consecutive draws of each type of matrix)	NA	Flowering year and non-flowering year	
Rostrhamus sociabilis (Snail Kite; hawk); Beissinger (1995)	Stage (3)	Mean and variances determined from other literature sources	Estimate P_{ext}, determine effect of low water levels on population viability	RTM (choice of environmental states), PMM within each state	Indirectly through periodic matrix formulation	Normal (survival rates)	Drought year, Year after drought, high water level	
5 savanna species (1 subshrub, two shrubs, and two trees); Hoffman (1999)	Size (4,6,5,5,5)	3-5 (non-burn year, year of burn, year after burn – 3 years after burn) after pooling data over space and time	Sensitivity analysis, determine fire frequency that will allow persistence of the population	RTM, periodic matrix, LTRE sensitivity analysis	No	NA	Fire (burn year, year after burn, non-burn year)	

Table 1 continued.

Species (references)	Type of matrix (number of classes)	Number of sets of transition estimates	Purpose of the model	Methods used	Autocorrelation included (Y/N)	Distribution/correlation (if PMM used)	Covariates	Comments
		and different burn intensities						
Calidris pusilla; Hitchcock and Gratto-Trevor (1997)	Age (3)	6 (survival)	Sensitivity analysis, determine which rates were responsible for population decline	Combination of RTM (juvenile survival, # of hatched eggs per nest, number of immigrants) and PMM (adult survival, # of eggs per nest in second set of simulations)	No	Beta (adult survival), uniform (number of eggs hatched per nest)	No	
Carduus nuans (thistle); Shea & Kelly (1998)	Size (4)	3 (one site) 1 (second site)	Estimate μ; sensitivity analysis to determine which rates to target for population control	RTM, deterministic elasticity analysis	No	NA	No	
Totoaba macdonaldi; Cisneros-Mata *et al.* (1997)	Stage (4)	Unclear. Provide mean values	Sensitivity analysis to determine how variability and correlation among vital rates affects μ and P_{ext}. Compare SFA diffusion approximation estimate of P_{ext} with estimate calculated using PMM.	SFA, PMM	No	Truncated normal, correlation included	No	Survival estimates from age structure data (1955–1990) and catch-per-unit-effort data. Fecundity rates determined so $\lambda = 1$.
Picoides borealis (red-cockaded woodpecker); Maguire *et al.* (1995)	Age (5)	4 (juvenile survival) 1 (adult survival)	Estimate P_{ext}, sensitivity analysis	RTM using RAMAS/stage (version 1.3) deterministic elasticity analysis	No	NA	No	Juvenile survival calculated using life table methods; included demographic stochasticity
Asarum canadense	Size (5) and Stage (5)	5 at 4 locations	Estimate μ, P_{ext}, minimum viable	RTM, deterministic	No	NA	No, but modeled "early successional"	Included demographic

Table 1 continued.

Species (references)	Type of matrix (number of classes)	Number of sets of transition estimates	Purpose of the model	Methods used	Autocorrelation included (Y/N)	Distribution/correlation (if PMM used)	Covariates	Comments
estimates (clonal woodland herb); Damman & Cain (1998)	for both clones and ramets	giving 10 transitions in two different types of habitat	population size, sensitivity analysis.	elasticity anlaysis (on plot by year basis)			and "late successional" habitats separately	stochasticity
Silene regia (prairie perennial); Menges & Dolan (1998)	Size (6)	2–12 (at 16 populations)	Estimate μ, P_{ext}, sensitivity analysis.	RTM (using POPPROJ), deterministic elasticity analysis	No	NA	Recruitment Y/N (two sets of matrices – with and without recruitment – for each set of transition estimates).	
Vireo latimeri (passerine songbird); Woodworth (1999)	Age (2)	Parameter means and standard errors drawn from multiple literature sources	Examine the effect of predation and parasitism on P_{ext}	PMM, deterministic sensitivity & elasticity analysis	No	Uniform distribution for all rates (using RAMAS/stage); no correlation	No	
Centrocercus urophasianus (Sage Grouse); Johnson & Braun (1999)	Stage (3)	23	Sensitivity Analysis, estimate μ under various management scenarios	PMM using @Risk software package; deterministic sensitivity & elasticity analysis	No	Normal distribution for all rates, no correlation	No	

Few long-term data sets have been collected from which one can infer typical distribution shape, strength of correlation (between rates within years) or the degree of autocorrelation. In the following section, we present a simulation study comparing the RTM, PMM and SFA approaches to estimating the stochastic growth rate μ under a range of environments and with different amounts of available data. The estimated probability of extinction is extremely sensitive to the estimate of μ in density-independent models (Fieberg & Ellner 2000), as well as models with density dependence incorporated by imposing a ceiling on population density (see Middleton *et al.* 1995; Figures 3 and 4). The results of this study are therefore informative with respect to extinction risk: better estimates of μ imply better estimates of extinction risk. Although extinction risk is the more relevant parameter in most applications, it has serious disadvantages as a summary statistic for comparing methods. First, the relationship between μ and extinction risk is highly dependent on the time horizon (Fieberg & Ellner 2000) and is strongly nonlinear in μ, so the results of a study using extinction risk would not necessarily be meaningful for other values of these parameters. Second, the sampling variability of $\hat{\mu}$ is characterized well by the mean and variance (as evidenced by our simulation study below), whereas the estimated extinction risk often has a U-shaped distribution with clusters near 0 and 1 (Fieberg and Ellner 2000).

Simulation study I: RTM versus PMM versus SFA

We consider the following stage-structured matrix model with three stage classes (juveniles, subadults and adults):

$$\begin{pmatrix} n_j(t+1) \\ n_{sa}(t+1) \\ n_a(t+1) \end{pmatrix} \begin{pmatrix} 0 & 0 & f_a \\ s_j & 0 & 0 \\ 0 & s_{sa} & s_a \end{pmatrix} \begin{pmatrix} n_j(t) \\ n_{sa}(t) \\ n_a(t) \end{pmatrix}$$

where, $n_j(t)$, $n_{sa}(t)$ and $n_a(t)$ represent the number of juveniles, subadults and adults respectively at time t; f_a represents the fecundity rate of adults; s_j, s_{sa} and s_a represent survival rates of juveniles, subadults and adults respectively. This model was used by Ferson and Burgman (1995) to examine the effect of correlation among vital rates on short-term extinction risk. We assume that all four vital rates are density independent with constant means and variance over time (no autocorrelation) given by:

$$\mu = \begin{pmatrix} E(f_a) \\ E(s_j) \\ E(s_{sa}) \\ E(s_a) \end{pmatrix} = \begin{pmatrix} 0.99 \\ 0.50 \\ 0.63 \\ 0.72 \end{pmatrix} \quad \sigma = \begin{pmatrix} \mathrm{SD}(f_a) \\ \mathrm{SD}(s_j) \\ \mathrm{SD}(s_{sa}) \\ \mathrm{SD}(s_a) \end{pmatrix} = \begin{pmatrix} 0.12 \\ 0.083 \\ 0.11 \\ 0.12 \end{pmatrix}.$$

The above standard deviations agree with those reported in Ferson and Burgman (1995); the means were reduced by a factor of 0.9 in order to give μ near 0. We examine three distributional assumptions, three different correlation structures and varying assumptions regarding the amount of data available to parameterize the model (Table 2). For each combination of distributional assumption × correlation structure × sampling frequency (N = number of sampled transition matrices), we use the following approach: Given the true joint probability distribution function of $(f_a, s_j, s_{sa}, s_a) = G(x_1, x_2, x_3, x_4)$.

1 Calculate the true growth rate of the population by projecting for 900,000 iterations (after 1000 iterations to remove transient dynamics) by randomly drawing survival and fecundity rates from $G(x_1, x_2, x_3, x_4)$, resulting in a random transition matrix each year. In order to compare true growth rates for different probability distributions, it was desired that the true growth rates be estimated with very little error. Nine hundred thousand iterations were sufficient to estimate the true growth rate to 4 significant digits in our examples.

2 Sample $N+1$ sets of transition rates from $G(x_1, x_2, x_3, x_4)$, giving N sampled transition matrices. Estimate μ via RTM, PMM and Tuljapurkar's approximation:

(a) RTM: project the population for 10,000 iterations (after 1000 initial iterations to remove transient dynamics) by randomly choosing among the N sampled transition matrices for each iteration.

(b) PMM: parameterize a multivariate normal distribution using the estimated sample mean vector and covariance matrix of vital rates. Project the population for 10,000 iterations (after 1000 iterations to remove transient dynamics) by randomly drawing survival and

Table 2 Simulation to examine effect of correlation structure, distribution, sampling frequency.

Distribution*	Correlation†	No. of sampled matrices
All rates multivariate normal	0, 0.5, 0.99	1, 2, 3, 4, 5, 10
Survival rates ~ beta; Fecundity rate ~ gamma	0, 0.5, 0.99	1, 2, 3, 4, 5, 10
All rates ~ uniform	0, 0.5, 0.99	2, 10

*We used a "folded" or "reflected" multivariate normal distribution. Rates falling out of biologically feasible ranges (survival rates <0 or >1, fecundity rates <0) were set to values just inside the biologically feasible range (see Appendix A).

†All rates assumed to be equally correlated. Correlations are approximate when using uniform and beta/gamma distributions (see Appendix A).

fecundity rates from the parameterized normal distribution each iteration. (Note: we consider cases in which the true distribution of vital rates is non-normal. However, we simulate a researcher who does know the true distribution of vital rates and therefore chooses to use a PMM approach with a multivariate normal distribution).

(c) SFA: estimate the sample mean vector and covariance matrix of the vital rates and form the mean matrix, with entries corresponding to the sample means of each parameter in the matrix model, and then estimate μ using Equation (2) above.

3. Repeat step 2 for 10,000 randomly sampled sets of transition rates giving 10,000 estimates of μ via each method.
4. Estimate the sampling distribution of $\hat{\mu}$ (for each method) using a kernel density estimator (Simonoff 1996).

Table 2 lists the different cases considered in this simulation study. All simulations were conducted using MATLAB Version 5.3. Software written by Dr. Christian C. Beardah, The Nottingham Trent University, was used to perform kernel density estimation (software available at http ://euler.ntu.ac.uk/maths.html).

Results of simulation study I

True growth rates for each scenario are listed in Table 3. As expected, the true growth rate decreases as the correlation among vital rates increases. Furthermore, the sampling distribution of $\hat{\mu}$ becomes wider as the correlation among rates increases (Fig. 1a), indicating that estimates of μ are more variable when vital rates are positively correlated.

The choice of distribution had very little effect on the stochastic growth rate (Table 3). Furthermore, the sampling distribution of $\hat{\mu}$ was relatively unaffected by the distribution of vital rates (Fig. 1b). The means, variances,and covariances of vital rates used to simulate population projections were only approximate (Appendix A). Slight differences in the correlation structure may be in part responsible for the slight differences in the observed growth rates in Table 3. Plotting the marginal distributions of each rate (normal versus beta versus uniform and normal versus gamma versus uniform) indicates that the marginal distributions are fairly similar for the means and variances used in this simulation study (Fig. 2). In each case, the distributions were symmetric (or nearly symmetric). Therefore, it is not surprising that the choice of distribution had very little impact on the stochastic growth rate.

We found that all three methods (RTM, PMM and SFA) resulted in very similar estimates of μ. Figure 1c shows the results for the case where all rates are independent and distributed as a multivariate normal. Similar results were obtained for the other distributions and correlation structures considered. We know of only one other study comparing estimation methods (Greenlee & Kaye 1997). They found that the RTM approach ($N = 4$ sampled matrices) resulted in a higher extinction risk than the PMM approach (using a truncated normal distribution with all rates varying independently). Greenlee and Kaye conjecture that the PMM approach gave optimistic results since all rates were assumed to vary independently, whereas the RTM method accounts for correlation among vital rates. In contrast to their study, we estimated and included correlation in the PMM approach – possibly allowing a fairer comparison of these two methods. Truncation of fecundity rates in Greenlee and Kaye's (1997) analysis may also explain the discrepancy between the RTM and PMM methods. The variance of seedling reproduction was quite large in comparison with the mean for all four study sites in their analysis, resulting in a high probability of truncation (setting negative values to 0). Truncation of negative values substantially increases the resulting mean of the distribution and could also explain the optimistic predictions using the PMM approach in their study.

For each of the different estimation methods we considered, the sampling distributions converged on the true value of μ as the sample size increased, regardless of

Table 3 True stochastic growth rates determined from 900,000 iterations of the model.

	Correlation		
Distribution*	0	0.5	0.99
All rates ~ multivariate normal	0.0134	0.00885	0.00437
All rates ~ uniform	0.0136	0.00910	0.00444
Survival rates ~ beta; Fecundity rate ~ gamma	0.0134	0.00922	0.00435

*We used a "folded" or "reflected" multivariate normal distribution. Rates falling out of biologically feasible ranges (survival rates < 0 or > 1, fecundity rates < 0) were set to values just inside the biologically feasible range (see Appendix A).

†All rates assumed to be equally correlated. Correlations are approximate when using uniform and beta/gamma distributions (see Appendix A).

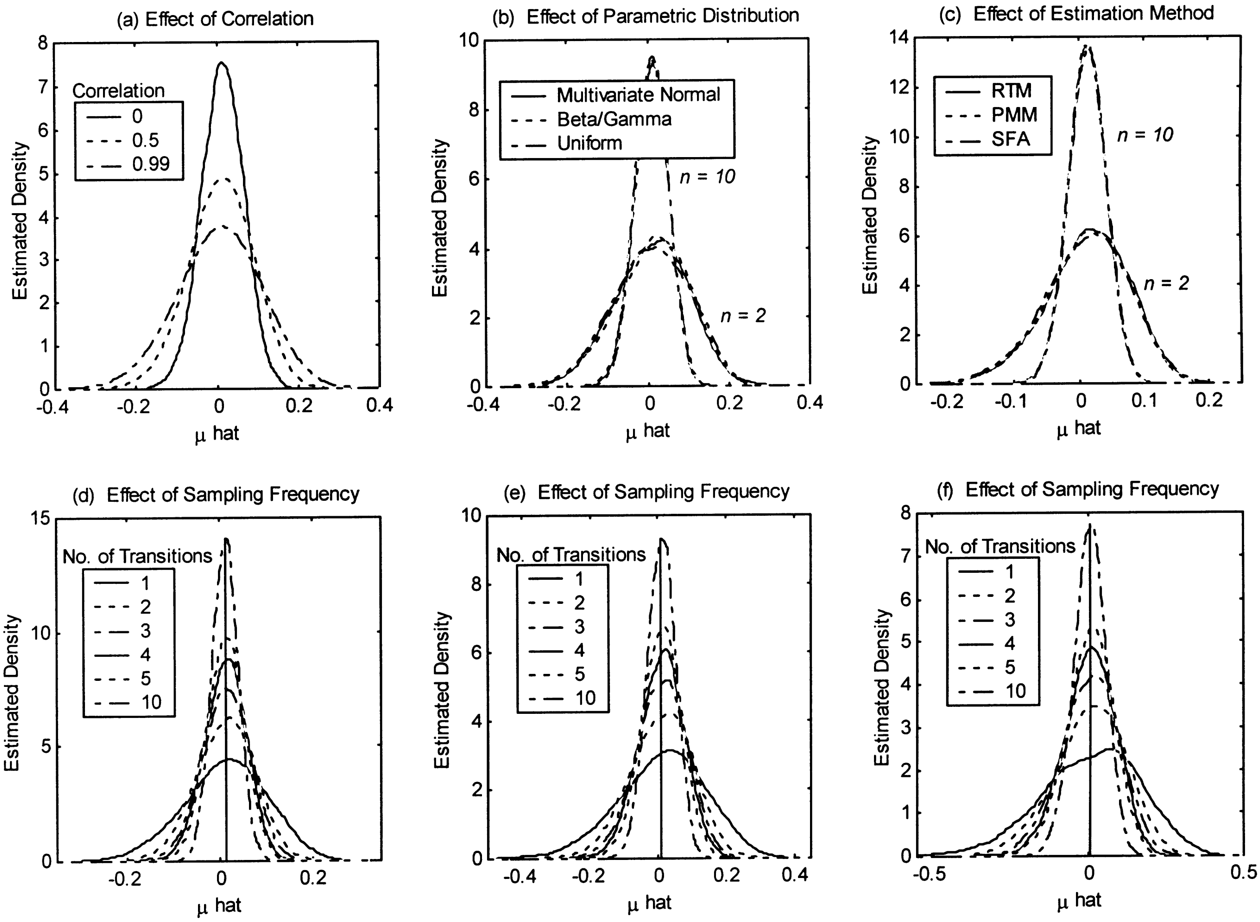


Figure 1 Sampling distributions of $\hat{\mu}$ (a) effect of correlation structure (all rates multivariate normal, method = RTM, $N = 3$ transition matrices); (b) effect of distribution (correlation = 0.5, $N = 2$, 10, method = RTM); (c) effect of estimation method (all rates multivariate normal, correlation = 0, $N = 2$, 10); (d–f) effect of sampling frequency (all rates multivariate normal, method = RTM, $N = 1$, 2, 3, 4, 5, 10; correlation among all rates = 0 (d), 0.5 (e), 0.99 (f)). The true values of μ are indicated by solid vertical lines in plots (d–f). RTM, random transition matrix method (matrices chosen at random to simulate population projections); PMM, parametric matrix method (matrices are chosen from a parametric distribution each iteration); SFA, small fluctuations approximation (growth rate estimated using Tuljapurkar's (1990) approximation).

the underlying distribution governing fluctuations in vital rates (Fig. 1d–f). The estimators are unbiased or nearly so for $N = 10$, although there may be a slight bias for small N (Fig. 1d–f). More importantly, the sampling distributions are quite broad even with 10 sets of transition rates, indicating that estimates of μ are highly variable and should be interpreted with caution. It seems, somewhat subjectively, that gains in precision are substantial up to $N = 4$ matrices (5 years of data), and then "diminishing returns" on sampling effort set in (Fig. 1d–f). It should be noted that the results included in this paper may not hold true for other matrices of different size and density. A larger simulation study is needed before our conclusions can be generalized. Nonetheless, our analyses can be used to offer useful suggestions regarding analytical methods.

RECOMMENDATIONS FOR ESTIMATING μ AND P_{EXT}

Ease of computation

Tuljapurkar's approximation requires only minimal computational effort and therefore is useful for providing a quick estimate of a population's viability. However, this approximation may break down when rates are subjected to a higher degree of variation and/or catastrophic events (Benton & Grant 1996). The RTM approach also offers a simple method for estimating μ and extinction probabilities. Furthermore, this approach may be reasonable for modeling the effect of discrete events (e.g. "catastrophes" due to flooding, fire, hurricanes, etc.) that occur infrequently but affect multiple transition rates

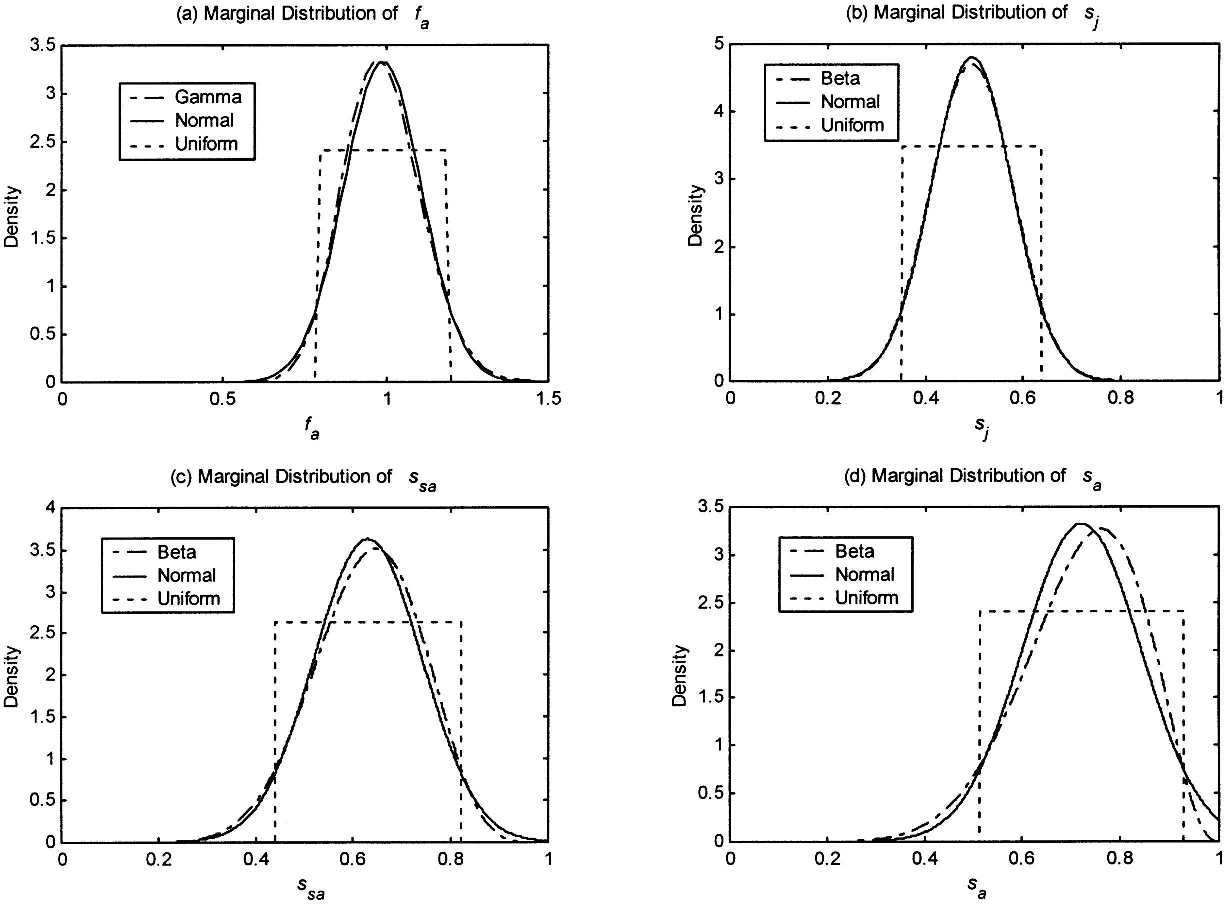


Figure 2 Marginal distributions of f_0, s_j, s_{sa}, s_a for the model considered in *Simulation Study I.*

simultaneously and by substantial amounts (Morris *et al.* 1999). The PMM method requires the most effort since one must choose an appropriate distribution and correlation structure.

Ability to incorporate assumptions regarding correlation

In order for means, variances and correlations to be estimable (statistically), a minimum of $p + 1$ sets of transition estimates are required, where p is the number of model parameters (non-zero elements in the matrix). Attempting to simultaneously estimate means and variances/covariances using less data will result in an estimated covariance matrix that is not necessarily positive definite. While one can continue to use the resulting covariance matrix, it should be noted that positive definiteness is a property of all covariance matrices and therefore obtaining a realistic estimate is problematic. A possible advantage of the RTM approach is that correlation need not be directly estimated; the approach automatically incorporates correlation structure through the process of drawing entire sets of transition rates estimated during the same year.

Assumptions about correlation have strong effects on sampling variance and therefore on the standard error that would be estimated for $\hat{\mu}$ (Fig. 1a). The estimated standard error can in turn have large effects on the estimated extinction risk and the associated confidence interval (Ludwig 1996). Consequently, when the goal of modeling is to estimate extinction risk, it is important for the model analysis to include a sensitivity analysis with respect to estimated correlation parameters, not just means and variances. We strongly recommend using the PMM and SFA methods when conducting PVAs since these methods have the flexibility to examine a variety of correlation structures. Cisneros-Mata *et al.* (1997) provide a useful example of this type of analysis using the SFA method.

Choice of parametric distribution

Using the PMM method requires that one specify a parametric distribution and estimate parameters associated with this distribution. Ecological data sets are typically sparse, providing little information regarding the variability of transition rates over time. In most cases, distributions are chosen based on convenience. The most frequently used distributions include the multivariate normal, beta, gamma, uniform and lognormal distributions. Of these distributions, only the multivariate normal distribution allows one to build correlation into the model in a simple manner. However, a normal distribution can result in values that are not biologically feasible (ex. negative survival or fecundity rates). In some cases, a truncated normal distribution is used (including some commercial programs, e.g. RAMAS). However, truncation will result in a different mean and variance than originally intended and may result in a bimodal distribution if rates are highly variable. For this reason, the beta distribution is frequently used to model survival rates since random draws are constrained to lie in the interval between 0 and 1. Similarly, gamma and lognormal distributions are convenient for modeling fecundity rates since the support of these distributions includes all positive numbers. Finally, uniform distributions are frequently used to model environmental fluctuations in vital rates when data are not available to directly estimate their means and variances. A uniform distribution can be completely defined by specifying an interval of plausible values – a task that is often attempted based on biological considerations when data are incomplete.

While our study suggests that the choice of distribution may not be important, the choice of distribution will likely have a greater impact when alternate distributions differ in their third and fourth moments (Slade & Levenson 1984). The shape of the distribution of fecundity rates is likely to be more influential than that for survival rates since survival rates are constrained to the interval (0,1) (Slade & Levenson 1984). Nakaoka (1996) found signficant differences in estimated growth rates depending on whether a normal or lognormal distribution was used to model yearly variation in recruitment. Our analyses suggest a useful approach to assessing the importance of the assumed distribution when formulating a matrix model. A plot of several proposed densities or an examination of third and fourth moments (skewness and kurtosis respectively) of the data offers a simple way to evaluate the likelihood that results will be sensitive to the assumed distribution. Our results suggest that the choice of distribution will not significantly alter results when alternate densities are similar. In fact the PMM approach using a multivariate normal distribution performed quite well even when the true distribution governing vital rates was a mixture of beta and gamma distributions (Fig. 3).

To further test the notion that proposed densities describing vital rate fluctuations will be similar, we examined fecundity rates reported in Brook *et al.* (2000b) for four species representing a range of taxa (Fig. 4). The means and variances for the four species varied considerably. However, in three of the four cases the probability densities most commonly used to model fecundity rates (gamma, lognormal, uniform and normal distributions) are fairly symmetric and do not differ significantly. Discrepancies among alternate densities are largest for the sage brush lizard (Fig. 4d). However, even in this case gamma and lognormal distributions are similar to each other, as are the uniform and normal distributions. Therefore, we expect that in most cases alternate parametric distributions will be similar, and therefore the choice of distribution may not have a large impact on model predictions.

Data requirements

Two types of sampling frequency must be considered when evaluating the quality of a demographic data set. First, one must sample enough individuals to ensure that each set of transitions is estimated accurately. Our simulation study ignores this type of sampling variability, assuming that all rates are measured without error. Uncertainty in predictive ability due to sampling a small number of individuals can be estimated by resampling techniques (McPeek & Kalisz 1993). These techniques, while useful, have rarely been used (but see Bierzychudek 1999). Secondly, one must consider the sampling intensity needed to characterize environmental variability. Specifically, how many transition rates should be sampled in order to characterize the environment and its affect on

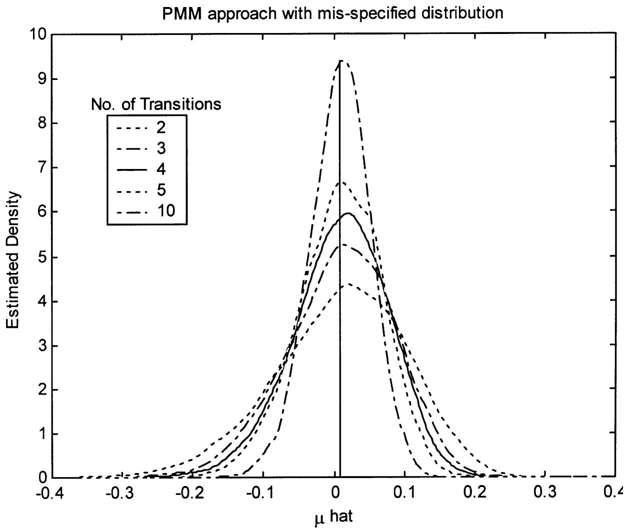


Figure 3 Sampling distribution of $\hat{\mu}$ using PMM approach with a multivariate normal distribution (true survival rates ∼beta; true fecundity rates ∼gamma, correlation among all rates = 0.5); the true μ is given by the solid vertical line.

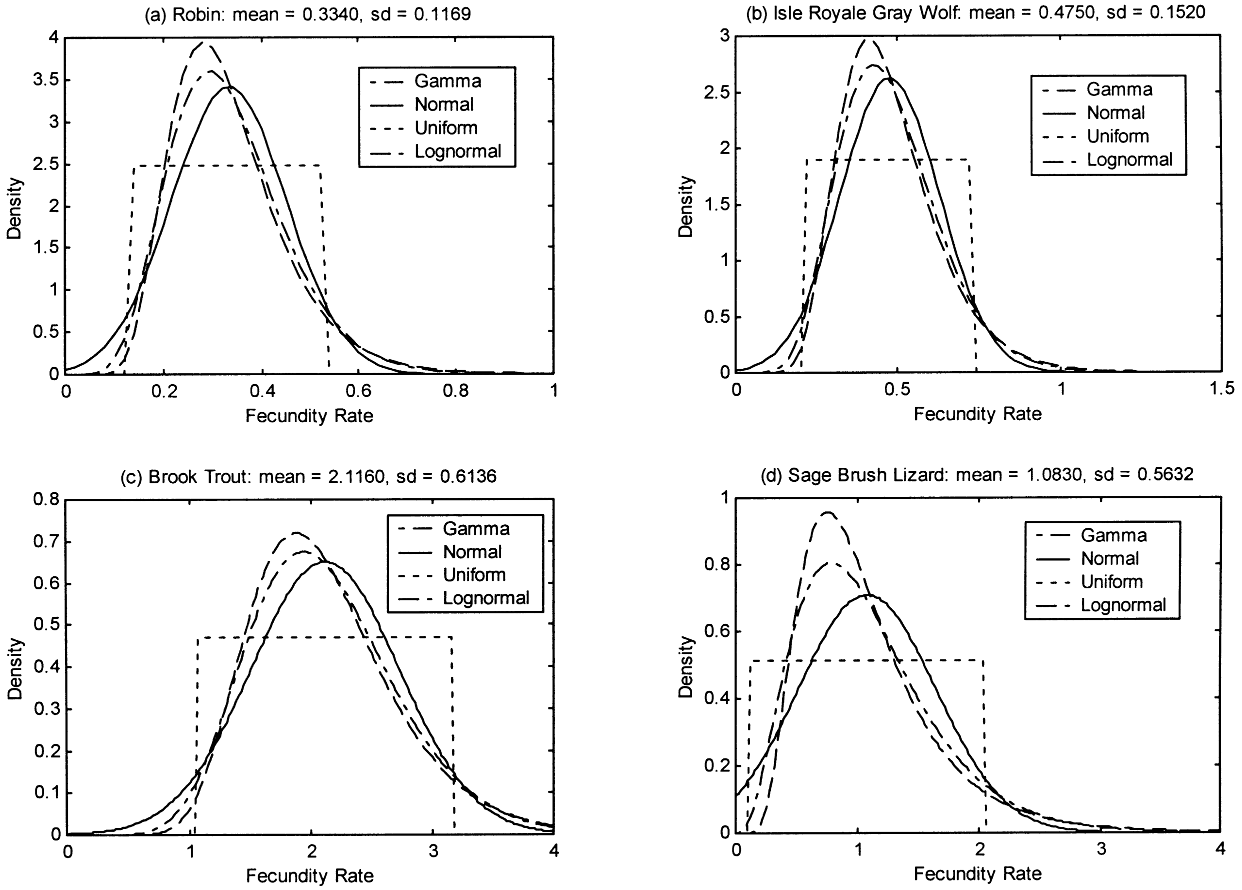


Figure 4 Alternate probability densities parametenzed using means and variances reported in Brook *et al.* (2000b).

vital rates? Data sets including a small number of transition estimates are not likely to provide an adequate description of the environment (Bierzychudek 1999). The consequences of not sampling an adequate number of transitions have not been fully explored. Furthermore, there are no straightforward methods for incorporating this uncertainty (arising from limited sampling of environmental states) into demographic analyses.

Our results suggest that estimates of μ are likely to be fairly imprecise even if one has collected data for 11 years, yielding 10 estimated transition matrices. Fieberg and Ellner (2000) have shown that extinction probability estimates using stochastic matrix models are likely to be unreliable for forecast intervals greater than 1/5 to 1/10 of the sample size of the data set used to predict extinction. Many PVAs attempt to estimate extinction risk over time intervals of 100 to 200 years (Beissinger & Westphal 1998, p. 825) with less than 10 years of data (Table 1). Therefore, the sampling intensity has severe ramifications regarding the conclusions that can be drawn from these models. We suggest below that modeling with environmental covariates may help overcome these data requirements.

SENSITIVITY ANALYSES

The goal of a sensitivity analysis is to determine which vital rates have the largest influence on the growth rate of the population or on its probability of extinction. An appropriate sensitivity analysis can therefore provide useful information regarding which stages of the life history are most important to target via management actions (Crowder *et al.* 1994). Methods for performing sensitivity analyses have been developed for periodic (Caswell & Trevisan 1994) and stochastic environments (Tuljapurkar 1990; Caswell 1996; Grant & Benton 2000) as well as for density-dependent populations (Grant & Benton 2000). Life Table Response Experiments (LTRE), originally developed to analyze experimental data, offer another alternative for conducting a sensitivity analysis (Caswell 1989; Ehrlen & van Groenendael 1998; Mills *et al.* 1999; Grant 1998). All of these methods require one to estimate how the population growth rate will change following a small perturbation in each matrix element, $\left(\frac{\partial\mu}{\partial a_{ij}}\right)$. Alternatively, simulation methods can be used to conduct a "global sensitivity analysis" to examine the effect of varying multiple rates simultaneously and by large amounts (Saltelli *et al.* 1999). Several other new developments in the field of sensitivity analysis may prove useful to conservation (see Benton & Grant 1999 for a useful review and "Special feature-elasticity analysis in population Biology", *Ecology* 81(3): 605–708, for recent developments).

Analytical approaches to sensitivity analysis have typically focused on quantifying the relationship between μ and vital rates. However, in most cases interest lies in examining how the probability of extinction changes under various management scenarios that may affect vital rates. Plots of the cumulative distribution function of the conditional time to extinction (Dennis *et al.* 1991; Morris *et al.* 1999) under different management scenarios can be a useful method of performing a sensitivity analysis of extinction to changes in vital rates. Alternatively, McCarthy *et al.* (1994) have developed a method of performing a global sensitivity analysis using the probability of extinction as the response variable.

MODELING WITH COVARIATES

Collection of demographic data can be difficult and time consuming. Annual transition matrices are obtained at a rate of one per year per population. Therefore most data sets contain a small number of vital rate estimates. On the other hand, many environmental variables (temperature, annual precipitation, atmospheric pollutants, etc...) are easily measured and have been collected across large spatial and time scales. Spatial replicates may provide a means to tie transition rates to environmental conditions, using natural variation over space or via experiments in which environmental conditions are artificially manipulated, thereby increasing sample size. As such, methods that incorporate environmental covariates have the potential to overcome typical time constraints regarding data collection. Runge and Moen (1998) have developed a modeling strategy that allows correlation (and autocorrelation) among vital rates via their common link to an assumed, although not necessarily identified and measured, environmental variable. However, reliable estimation of model parameters, in most cases, will require information regarding the environmental process controlling the variability in vital rates. Therefore, the first step will be to discover available environmental variables that can be shown to have an effect on vital rates.

Connections between environmental variables and population processes may be difficult to elucidate. Swanson (1998) found only two studies indicating significant cross-correlation between the rate of population increase and local precipitation (out of 175 vertebrate and 88 precipitation data sets), despite significant autocorrelation in 17.8% of mammalian time series, 61.5% of avian time series, and 97.7% of precipitation time series. Comprehensive studies providing a link between vital rates and important environmental variables will be necessary before the methodology proposed by Runge and Moen (1998) can be effectively utilized. Once important environmental variables have been identified, experiments in which these variables are manipulated should provide the information needed to model the relationship between demographic rates and the environment. Used in conjunction with information regarding the distribution of these environmental variables over time, models incorporating covariates may lead to more efficient estimates of population viability.

Many studies have modeled the effects of using discrete covariates (Table 1), most notably fire disturbance, in conjunction with a stochastic matrix model. Silva *et al.* (1991), Canales *et al.* (1994) and Gross *et al.* (1998) estimated transitions in burnt and unburnt plots and then used this information in conjunction with periodic (deterministic) and stochastic matrix models to determine the fire frequency required for population persistence for three fire-dependent plant species. Hoffman (1999) conducted similar analyses to determine fire return intervals required for the persistence of five woody plant species negatively affected by fire. Hoffman (1999), Silva *et al.* (1991) and Canales *et al.* (1994) also used LTRE measures to determine how fire disturbance affected demographic rates and in turn how these changes affected the population growth rate in each of the environments.

Aberg (1992a, b) utilized a stochastic matrix model to assess the importance of winter ice damage on populations of the seaweed *Ascophyllum nodosum* located at two different study sites. He estimated transition matrices under three environmental conditions (years with no ice, moderate ice damage, and large ice damage) and then varied the frequency of each type of environment according to observed frequencies at the two study sites. In addition to standard analyses (estimating μ and performing a sensitivity analysis), varying the probability of each environmental type allowed a method of examining the sensitivity of μ to the severity of the ice disturbance. Wethey (1985) conducted a similar analysis to examine the effect of sea ice on barnacle species. Beissinger (1995) assessed the impact of low water levels on the viability of the Snail Kite by incorporating three "environmental state" matrices corresponding to drought years, lag years (after a drought) and high water level years. Altering the frequency of droughts provided an estimate of the inter-drought interval necessary for population persistence.

These studies illustrate the usefulness of incorporating environmental variables into stochastic matrix models.

Sensitivity analyses allow one to examine the relative importance of demographic rates under different environments and simulations allow one to determine how the frequency of various environmental types affects the viability of populations. Careful attention to experimental design and model formulation is likely to be highly beneficial in such studies. For example, experiments at several treatment levels (e.g. different fire intensities) may be necessary to accurately characterize how environmental variables interact with demographic rates. Furthermore, it will be important to sample plots for several years after a treatment is applied if the effects of an environmental disturbance is distributed over multiple years. Finally, demographic rates will naturally vary within each type of environmental state due to other variables that are not included in the analysis. Sampling plots of each treatment type for multiple years will allow one to incorporate temporal variability in each type of environment. Of the studies examining the effect of environmental disturbance mentioned above, only Beissinger (1995), Gross *et al.* (1998) and Hoffman (1999) measured transition rates during the year after a disturbance, providing the means to incorporate the effect of environmental disturbance over a longer time frame. Similarly, only Wethey (1985), Beissinger (1995) and Gross *et al.* (1998) incorporated variability among demographic transitions within different environmental states.

We conducted a simulation study to examine the usefulness of incorporating environmental covariates in stochastic matrix models. In particular, we aim to determine the consequences of discretizing continuous environmental variables, such as rainfall, into "environmental states" and to assess the potential gain in the precision of estimates obtained using models that include covariates.

Simulation study II: true population dynamics

We based our simulation study on Beissinger's (1995) model for the Snail Kite. The simulation model considers three stage classes (fledglings, subadults and adults). Beissinger (1995) found that survival rates were considerably lower during drought years. Furthermore, nesting success, the proportion of birds nesting and the number of nesting attempts per year were affected by the previous year's water level as well as the current water level; clutch size was not found to vary with water level. Therefore, we assume that survival rates depend on the current (yearly) mean water level, $x(t)$, and that fecundity rates depend on both the current and the previous (yearly) mean water levels. Using a similar model structure to that of Runge and Moen (1998), survival rates for fledglings, subadults and adults, $S_i (i = 1,2,3)$ are determined by:

$$S_i(t, x) = (1 + \exp[-\alpha_{s_i} - \beta_{s_i}(t) + \sigma_{s_i}\varepsilon_{s_i}\}])^{-1};$$

$$i = 1, 2, 3. \qquad (3)$$

The above formulation assumes a logistic response of survival to water levels, taking values between 0 and 1. β_{s_i} controls the sensitivity of survival rates to water levels, and ε_{s_i} is a normal (0, 1) random variable, the source of unexplained variance in S_i.

Only subadults and adults breed. The proportion of Kites successfully nesting, $p_i(x,t)$, is determined by:

$$p_i(x, t) = (1 + \exp[-\alpha_{F_i} - \beta_{F_i}x(t) - \gamma_{F_i}$$

$$\{x(t-1) + \sigma_{F_i}\varepsilon_{F_i}\}])^{-1}; i = 2, 3. \qquad (4a)$$

Here again, we assume a logistic response of nest success to water levels, with γ_{F_i} and β_{F_i} controlling the sensitivity of vital rates to the current and previous year's water levels respectively; ε_{F_i} is a normal (0,1) random variable. The number of nesting attempts in year t, $b_i(x,t)$ is determined using:

$$b_i(x, t) = \begin{cases} 1 \text{ for } i = 2 \\ \max\{0, a + bx(t) + cx(t-1) + \varepsilon_{b_i}\} \text{ for } i = 3 \end{cases} \qquad (4b)$$

Again, b and c control the sensitivity of nesting attempts to water levels and ε_{b_i} is a uniform (0, 0.1) random variable; ε_{s_i}, ε_{F_i} and ε_{b_i} are assumed to be independent. Clutch size was assumed to be constant, two fledglings per year. Fecundity rates are given by the product of nesting success, proportion of Kites nesting, number of nesting attempts per year and clutch size:

$$F_i(x, t) = 2p_i(x, t)b_i(x, t) \qquad (5)$$

Parameter values used in the simulation study (Table 4) were chosen to match the mean rates reported for each environmental state (Beissinger 1995; Table 2). "True" Snail Kite population dynamics were simulated using amplitude-adjusted Fourier Transform surrogate data series (Theiler *et al.* 1992) generated from the water level data presented in Beissinger (1986, Fig. 3) and then randomly drawing survival and fecundity rates according to equations (3) and (5).

Effect of discretizing water levels

Following Beissinger (1995), we consider a matrix model that incorporates three environmental states: drought year, lag year and high water level years. Water levels less than 13.75 feet were considered drought years and lag years were defined as having water levels $\geqslant$ 13.75 feet with a drought the previous year. The "true" distribu-

Table 4 Parameter values used in simulation study II

Parameters	Value
α_{S1}, α_{S2}, α_{S3}	–16.99, –18.76, –18.76
β_{S1}, β_{S2}, β_{S3}	1.13, 1.48, 1.48
σ_{S1}, σ_{S2}, σ_{S3}	0.224, 0.224, 0.224
α_{F2}, α_{F3}	–29.45, –39.83
β_{F2}, β_{F3}	1.34, 2.43
γ_{F2}, γ_{F3}	0.44, 0.16
σ_{F2}, σ_{F3}	0.002, 0.002
a, b, c	–9.54, 0.47, 0.32

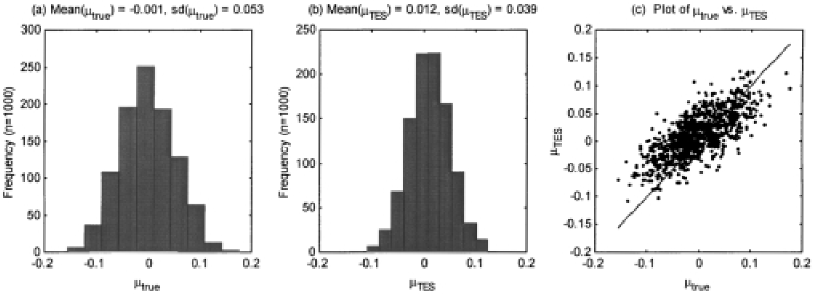
tions of $x(t)$, S_i and F_i (given by the surrogate water level data sets and equations (3) and (5)) were used to determine the distribution of S_i and F_i within each environmental state. This information was then used to construct a matrix model that differs from the "true" population model only in that the effect of water levels occurs through discrete environmental states rather than the continuous functions given by equations (3) and (4) (see Appendix B). We refer to this model as the "true environmental states model" (TES model). Comparison of this model with population dynamics obtained from direct simulation of equations (3) and (5) measures the effect of partitioning environmental variables into discrete states.

Values of the population's growth rate over the next 50 years are given in Fig. 5a (true population dynamics, μ_{true}) and Fig. 5b (TES model population dynamics, μ_{TES}) for 1000 surrogate water level data sets. Discretizing water levels into environmental states led in general to slightly higher (more optimistic) growth rates. The mean value of μ_{TES} (over the 1000 water level data sets) was 0.012 versus -0.001 for the mean of μ_{true}. Plotting μ_{TES} versus μ_{true} (Fig. 5c) indicates that the values for μ_{TES} were typically higher than μ_{true} for harsh environments and slightly lower in favourable environments. In the TES model, the water level in year $t-1$ only affects the current vital rates in deciding whether a water level year > 13.75 feet is a lag year or a high year. However, in the true model, the previous year's water level has the potential to affect vital rates more substantially (through the functions given in equation (4)), perhaps offering an explanation for the discrepancies between the μ_{true} and μ_{TES}. Values of μ_{true} were more variable than values of μ_{TES} across water level data sets [var(μ_{true}) = 0.053; var(μ_{TES}) = 0.039]. On the other hand, growth rates within a given water level data set were more variable for the TES model since the distribution of vital rates was less closely connected to water levels.

Using covariates to improve the precision of viability estimates

Next, we simulate two different experimental approaches leading to six transition estimates. In the first case, the researcher estimates survival and fecundity rates by following the population for seven consecutive years and then uses an RTM approach to estimate the population's growth rate over the next 50 years, μ_{RTM}. In the second case, the researcher decides to incorporate historical data regarding the distribution of water levels in conjunction with a 4-year experiment in which he measures vital rates in a treatment and a control plot. Between the first and second years of the study, the researcher keeps water levels at 13 feet to simulate a drought. The following 2 years, he/she keeps water levels at 14.5 feet to simulate a lag and high year respectively. The researcher also collects data from a control area for each of the three transition periods, giving a total of six transition matrices. In addition, we assume the researcher has available $t = 30$ or 50 years of historical water level data from which to estimate transition probabilities between environmental states. An "environmental states" model is then used to estimate the population's growth rate over the next 50 years, μ_{ES}. To determine the potential gain from incorporating water level data into a stochastic matrix model, we simulate the above research

Figure 5 Effect of discretizing water level data on Snail Kite growth rates for 1000 surrogate water level data sets: (a) distribution of true growth rates, μ_{true}; (b) distribution of growth rates from the TES model, μ_{TES}. The TES model reflects the true population dynamics model outlined in *Simulation Study II*, except that the effect of water level occurs through discrete environmental states (drought years, lag years and high water level years) rather than through the continuous functions given by equations (3) and (4) in the text; (c) plot of μ_{true} versus μ_{TES} for the 1000 water level data sets used to produce parts (a) and (b).



projects (Appendix B) for each of 1000 surrogate water level data sets (representing replicates of the experiments).

The resulting growth rate estimate using the RTM approach, μ_{RTM}, was slightly optimistic, while the environmental states model led to a slightly conservative estimate of μ [mean(μ_{ES}) = -0.04, mean(μ_{RTM}) = 0.008, mean(μ_{true}) = -0.001]. More importantly, incorporating water level data into the matrix model reduced the variance of growth rate across simulated data sets by nearly a factor of 4 (Fig. 6a, b). When several consecutive years of the same environmental type occur (either drought or high water level years), the RTM approach will give more extreme conclusions since rates will have been sampled from a narrow range of environments. This result is illustrated by plotting estimates of μ_{ES} versus μ_{RTM} (Fig. 6d) for the 1000 surrogate water level data sets. Estimates of μ obtained from the RTM model were overly pessimistic when the study years were worse than average and overly optimistic when the study years were better than average. Little gain in precision was observed when additional data regarding water levels was available (μ_{ES} with $t = 30$ versus $t = 50$; Fig. 6a and 6c), suggesting that sampling 30 years of water level data was sufficient to improve estimates of the population's growth rate.

CONCLUSIONS

When data are abundant, one *may* expect inefficient "seat of the pants" methods to give correct answers to questions of interest. However, limited data sets require efficient analyses and careful consideration of available methods. Most demographic data sets are relatively sparse, containing fewer than 10 sets of transition estimates (Table 1). Therefore, there is a real need to compare various methods of parameterizing and analyzing stochastic matrix models. We have given a few examples of the types of research that will be needed to guide fruitful applications of these models in the future.

Based on our review and simulation studies, we make the following recommendations:

1 Sensitivity analyses should be a standard component of PVAs. Extinction risk estimates from stochastic matrix models can be highly sensitive to the correlation structure among vital rates. Therefore, we suggest PMM or SFA approaches since they allow examination of a variety of correlation structures. The distribution used in the PMM approach is likely to be of lesser importance.

2 Estimates of population viability are likely to be highly variable. Therefore, we recommend that stochastic matrix models are best used to test alternative management scenarios using relative measures of viability. Estimates of viability should not be published or trusted without an estimate of their precision (e.g. confidence intervals). Dennis *et al.* (1991) and Ludwig (1999) provide methods of calculating confidence intervals for extinction parameters.

3 Matrix models that incorporate covariates may improve the precision of viability estimates. Furthermore, these models are often useful for framing population dynamics in terms of environmental variables that could be manipulated by wildlife and conservation managers. Therefore, the collection of data for PVAs should include efforts to identify environmental variables responsible for the variation in vital rates.

Clearly there is a need for further studies that examine the relative merit of alternative methods. The availability of carefully conducted and well-documented PVAs for a range of taxa means that such studies can be grounded in

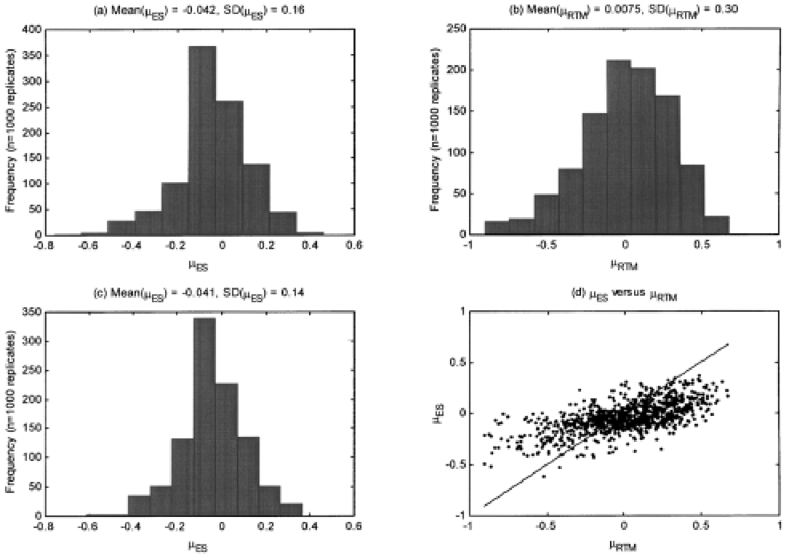


Figure 6 Estimated Snail Kite growth rates from $n = 1000$ surrogate water level data sets (experimental replicates) and samples of six sets of transition rates. The ES model uses t years of historic water level data to parameterize a matrix model with three discrete environmental states (drought years, lag years and high water level years; see *Simulation Study II*). The RTM model uses a random transition matrix approach, ignoring water level data. (a) ES model parametenzed using $t = 30$ years of historic water level data; (b) RTM model results; (c) ES model parameterized using $t = 50$ years of historic water level data; (d) Plot of μ_{ES} (with $t = 50$) versus μ_{RTM} for the 1000 surrogate water level data sets used to produce the plots in parts (b) and (c).

ecological reality. By simulating the process of collecting data (from the "imaginary world" where a selected PVA model is exactly true), analyzing the data in alternative ways, and comparing results with the "truth", competing approaches can be evaluated objectively.

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REFERENCES

Aberg, P. (1992a). A demographic study of two populations of the seaweed. *Ascophyllum nodosum. Ecology*, 73, 1473–1487.

Aberg, P. (1992b). Size-based demography of the seaweed *Ascophyllum nodosum* in stochastic environments. *Ecology*, 73, 1488–1501.

Akçakaya, H.R. (1997). *RAMAS Metapop: Viability Analysis for Stage-structured Metapopulations.* Applied Biomathematics, Setauket.

Bessinger, S.R. (1986). Demography, environmental uncertainty, and the evolution of mate disertion in the snail kite. *Ecology*, 67, 1445–1459.

Beissinger, S.R. (1995). Modeling extinction in periodic environments: Everglades water levels and Snail Kite population viability. *Ecologic. Applications*, 5, 618–631.

Beissinger, S.R. & Westphal, M.I. (1998). On the use of demographic models of population viability in endangered species management. *J. Wildlife Manag.*, 62, 821–841.

Benton, T.G. & Grant, A. (1996). How to keep fit in the real world: elasticity analyses and selection pressures on life histories in a variable environment. *Am. Naturalist*, 147, 115–139.

Benton, T.G. & Grant, A. (1999). Elasticity analysis as an important tool in evolutionary and population ecology. *Trends Ecol. Evol.*, 14, 467–471.

Benton, T.G., Grant, A. & Clutton-Brock, T.H. (1995). Does environmental stochasticity matter? Analysis of red deer life-histories in Rum. *Evolutionary Ecol.*, 9, 559–574.

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. *Ecology*, 9, 12781–287.

Boyce, M. (1992). Population viability analysis. *Ann. Rev. Ecol., Systematics*, 23, 481–506.

Brook, B.W., Cannon, J.R., Lacy, R.C., Mirande, C. & Frankham, R. (1999). A comparison of the population viability analysis packages GAPPS, INMAT, RAMAS and VORTEX for the Whooping Crane (*Grus americana*). *Animal Conservation*, 2, 23–31.

Brook, B.W., Burgman, M.A. & Frankham, R. (2000a). Differences and congruencies between PVA packages: the importance of sex ratio for predictions of extinction risk. *Conservation Ecol.*, 4(1), 6. [online] URL: http://www.consecol.org/vol4/iss1/art6.

Brook, B., O'Grady, J.J., Chapman, A.P., Burgman, M.A., Akçakaya, H.R. & Frankham, R. (2000b). Predictive accuracy of population viability analysis in conservation biology. *Nature*, 404, 385–387.

Canales, J., Trevisan, M.C., Siva, J.F. & Caswell, H. (1994). A demographic study of an actual grass (*Andropogon brevifolius* Schwarz) in burnt and unburnt savannas. *Acta Oecologica*, 15, 261–273.

Carlsson, B.A. & Callaghan, T.V. (1991). Simulation of fluctuating populations of *Carex bigelowii* tillers classified by type, age and size. *Oikos*, 60, 231–240.

Caswell, H. (1989). *Matrix Population Models.* Sinauer Publishers, Sunderland, MA.

Caswell, H. (1996). Second derivatives of population growth rate: calculation and applications. *Ecology*, 77, 870–879.

Caswell, H. & Trevisan, M.C. (1994). Sensitivity analysis of periodic matrix models. *Ecology*, 75, 1299–1303.

Cisneros-Mata, M.A., Botsford, L.W. & Quinn, J.F. (1997). Projecting viability of *Totoaba macdonaldi*, a population with unknown age-dependent variability. *Ecological Applications*, 7, 968–980.

Cohen, J.E., Christensen, S.W. & Goodyear, C.P. (1983). A stochastic age-structured population model of striped bass (*Morone saxatilis*) in the Potomac River. *Can. J. Fisheries Aquatic Sci.*, 4, 446–460.

Crowder, L.B., Crouse, D.T., Heppell, S.S. & Martin, T.H. (1994). Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. *Ecological Applications*, 4, 446–460.

Damman, H. & Cain, M. (1998). Population growth and viability analyses of the clonal woodland herb, *Asarum canadense. J. Ecol.*, 86, 13–26.

Dennis, B., Munholland, P.L. & Scott, M.J. (1991). Estimation of growth and extinction parameters for endangered species. *Ecological Monographs*, 61, 115–143.

Dixon, P., Friday, N., Ang, P., Heppell, S. & Kshatriya, M. (1997). Sensitivity analysis of structured population models for management and conservation. In: *Structured-population Models in Marine, Terrestrial, and Freshwater Systems* (eds S. Tuljapurkar and H. Caswell). Chapman and Hall, New York, pp. 471–513.

Doak, D., Kareiva, P. & Klepetka, B. (1994). Modeling population viability for the desert tortoise in the Western Mojave desert. *Ecological Applications*, 4, 446–460.

Easterling, M.R., Ellner, S.P. & Dixon, P. (2000). Size-specific sensitivity: applying a new structured population model. *Ecology*, 81, 694–708.

Ehrlen, J. & van Groenendael, J. (1998). Direct perturbation analysis for better conservation. *Conservation Biol.*, 12, 470–474.

Ferson, S. (1994). *RAMAS Stage: Generalized Stage-based Modeling for Population Dynamics.* Applied Biomathematics, Setauket.

Ferson, S. & Burgman, M. (1995). Correlations, dependency bounds and extinction risks. *Biological Conservation*, 73, 101–105.

Fieberg, J. & Ellner, S.P. (2000). When is it meaningful to estimate an extinction probability? *Ecology*, 81, 2040–2047.

Golubov, J., Del Carmen Manujano, M., Franco, M., MontaZa, C., Eguiarte, L.E. & Lopez-Portillo, J. (1999). Demography of the invasive woody perennial *Prosopis glandulosa* (honey mesquite). *J. Ecol.*, 87, 955–962.

Gotelli, N. (1991). Demographic models for *Leptogorgia virgulata*, a shallow-water gorgonian. *Ecology*, 72, 457–467.

Grant, A. (1998). Population consquences of chronic toxicity: incorporating density dependence into the analysis of life table response experiments. *Ecological Modelling*, 105, 325–335.

Grant, A. & Benton, T.G. (2000). Elasticity analysis for density-dependent populations in stochastic environments. *Ecology*, 81, 680–693.

Greenlee, J. & Kaye, T.N. (1997). Stochastic matrix projection: a comparison of the effect of element and matrix selection methods on quasi-extinction risk for *Haplopappus radiatus* (Asteraceae). In: *Conservation and Management of Native Plants and Fungi* (eds T.N. Kaye *et al.*). Native Plant Society, Oregon, pp. 66–71.

van Groenendael, J.M. & Slim, P. (1988). The contrasting dynamics of two populations of *Plantago Lanceolata* classified by age and size. *J. Ecol.*, 76, 585–599.

Groom, M.J. & Pascual, M.A. (1998). The analysis of population persistence: an outlook on the practice of viability analysis. In: *Conservation Biology* (eds P.L. Fielder and P.M. Kareiva). Chapman and Hall, New York, NY, pp. 4–27.

Gross, K., Lockwood, J.R., III, Frost, C.C. & Morris, W.F. (1998). Modeling controlled burning and trampling reduction for conservation of *Hudsonia montana*. *Conservation Biol.*, 12, 1291–1301.

Harris, R.B., Metzgar, L.H. & Bevins, C.D. (1986). *GAPPS: Generalized Animal Population Projection System.* Version 3.0. Montana Cooperative Wildlife Research Unit, Unviersity of Montana, Missoula, MT.

Heyde, C.C. & Cohen, J.E. (1985). Confidence intervals for demographic projections based on products of random matrices. *Theor. Popul. Biol.*, 27, 120–153.

Hitchcock, C.L. & Gratto-Trevor, C. (1997). Diagnosing a shorebird local population decline with a stage-structured population model. *Ecology*, 78, 522–534.

Hoffman, W.A. (1999). Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. *Ecology*, 80, 1354–1369.

Hortvitz, C.C. & Schemske, D.W. (1995). Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. *Ecological Monographs*, 65, 155–192.

Johnson, K.H. & Braun, C.E. (1999). Viability and conservation of an exploited sage grouse population. *Conservation Biol.*, 13, 77–84.

Lacy, R.C. (1993). VORTEX: a computer simulation model for population viability analysis. *Wildlife Research*, 20, 45–65.

Lande, R. & Orzack, S.H. (1988). Extinction dynamics of age-structured populations in a fluctuating environment. *Proc. Nat. Acad. Sciences, USA*, 85, 7418–7421.

Ludwig, D. (1996). Uncertainty and the assessment of extinction probabilities. *Ecological Applications*, 6, 1067–1076.

Ludwig, D. (1999). Is is meaningful to estimate an extinction probability? *Ecology*, 10, 298–310.

Maguire, L.A., Wilhere, G.F. & Dong, Q. (1995). Population viability analysis for red-cockaded woodpeckers in the Georgia Piedmont. *J. Wildlife Manag.*, 59, 533–542.

McCarthy, M.A., Franklin, D.C. & Burgman, M.A. (1994). The importance of demographic uncertainty: an example from the Helmeted Honeyeater *Lichenostomus melanops cassidix. Biological Conservation*, 67, 135–142.

McPeek, M.A. & Kalisz, S. (1993). Population samplings and bootstrapping in complex designs: demographic analysis. In: *Design and Analysis of Ecological Experiments* (eds S. Scheiner and J. Gurevitch). Chapman and Hall, New York, NY, pp. 232–252.

Menges, E. (1990). Population viability analysis for an endangered plant. *Conservation Biology*, 4, 41–62.

Menges, E. (2000). Population viability analyses in plants: challenges and opportunities. *Trends Evol. Ecol.*, 15, 51–56.

Menges, E.S. & Dolan, D.W. (1998). Demographic viability of populations of *Silene regia* in midwestern prairies: relationships with fire management, genetic variation, population size and isolation. *J. Ecol.*, 86, 63–78.

Middleton, D.A.J., Veitch, A.R. & Nisbet, R.M. (1995). The effect of an upper limit to population size on persistence time. *Theor. Popul. Biol.*, 48, 211–305.

Mills, L.S. & Smouse, P.E. (1994). Demographic consequences of inbreeding in remnant populations. *Am. Naturalist.*, 144, 412–431.

Mills, L.S., Hayes, S.G., Baldwin, C., Wisdom, M.J., Citta, J., Mattson, D.J. & Murphy, K. (1996). Factors leading to different viability predictions for a grizzly bear data set. *Conservation Biol.*, 10, 863–873.

Mills, L.S., Doak, D.F. & Widsom, M.J. (1999). Reliability of conservation actions based on elasticity analysis of matrix models. *Conservation Biol.*, 13, 815–829.

Moloney, K.A. (1986). A generalized algorithm for determining category size. *Oecologia*, 69, 176–180.

Morris, W., Doak, D., Groom, M., Kareiva, P., Fieberg, J., Gerber, L., Murphy, P. & Thompson, D. (1999). A Practical Handbook for Population Viability Analysis. *The Nature Conservancy*, 80 pp.

Nakaoka, M. (1996). Dynamics of age- and size-structured populations in fluctuating environments: applications of stochastic matrix models to natural populations. *Res. Popul. Ecol.*, 38, 141–152.

Nakaoka, M. (1997). Demography of the marine bivalve *Yoldia notabilis* in fluctuating environments: an analysis using a stochastic matrix model. *Oikos*, 79, 59–68.

Nantel, P., Gagnon, D. & Nault, A. (1996). Populations viability analysis of American Ginseng and wild leek harvested in stochastic environments. *Conservation Biol.*, 10, 608–621.

Noda, T. & Nakao, S. (1996). Dynamics of an entire population of the subtidal snail *Umbonium costattum*: the importance of annual recruitment fluctuation. *J. Animal Ecol.,* 65, 196–204.

Oostermeijer, J.G.B., Burgman, M.L., de Boer, E.R. & dens Nijs, H.C.M. (1996). Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. *J. Ecol.*, 54, 153–166.

Possingham, H.P. & Davies, I. (1995). ALEX: a model for the viability of spatially structured populations. *Biological Conservation*, 73, 143–150.

Reed, J.M., Murphy, D.D. & Brussard, P.F. (1998). Efficacy of population viability analysis. *Wildlife Society Bulletin*, 26, 244–251.

Runge, M.C. & Moen, A.N. (1998). A modified model for projecting age-structured populations in random environments. *Mathematical Biosciences*, 150, 21–41.

Saltelli, A., Tarantola, S. & Chan, K. (1999). A quantitative model-independent method for global sensitivity analysis of model output. *Technometrics*, 41, 39–56.

Shea, K. & Kelly, D. (1998). Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecological Applications*, 8, 824–832.

Silva, J.F., Raventos, J., Caswell, H. & Trevisan, M.C. (1991). Population responses to fire in a tropical savanna grass, *Andropogon semiberbis*: a matrix model approach. *J. Ecol.*, 79, 345–356.

Simonoff, J. (1996). *Smoothing Methods in Statistics.* Springer-Verlag, London.

Slade, H.A. & Levenson, H. (1984). The effect of skewed distributions of vital statistics on growth of age-structured populations. *Theor. Popul. Biol.*, 26, 361–366.

Swanson, B.J. (1998). Autocorrelated rates of change in animal populations and their relationship to precipitation. *Conservation Biol.*, 12, 801–808.

Theiler, J., Eubank, S., Longtin, A., Galdrikian, B. & Farmer, J.D. (1992). Testing for nonlinearity in time series data: the method of surrogate data. *Physica D*, 58, 77–94.

Tuljapurkar, S.D. (1982). Population dynamics in variable environments. III. Evolutionary dynamics on *r*-selection. *Theor. Popul. Biol.*, 21, 141–165.

Tuljapurkar, S.D. (1990). *Population Dynamics in Variable Environments. Lecture Notes in Biomathematics*, Vol. 85.

Tuljapurkar, S.D. & Orzack, S.H. (1980). Population dynamics in variable environments. I. Long-run growth rates and extinction. *Theor. Popul. Biol.*, 18, 314–342.

Vandermeer, J. (1979). Choosing category size in a stage projection matrix. *Oecologica*, 32, 199–225.

Wethey, D.S. (1985). Catastrophe, extinction, and species diversity: a rocky intertidal example. *Ecology*, 66, 445–456.

Wood, P.B. & Collopy, M.W. (1993). Effects of egg removal on bald eagle productivity in northern Florida. *J. Wildlife Manag.*, 57, 1–9.

Woodworth, B.L. (1999). Modeling population dynamics of a songbird exposed to parasitism and predation and evaluating management options. *Conservation Biol.*, 13, 66–76.

BIOSKETCH

John Fieberg is interested in the application of statistical and mathematical models to problems in conservation biology. He is particularly interested in the implications of parameter and system uncertainty on model performance.

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APPENDIX A: DRAWING CORRELATED VITAL RATES FOR SIMULATION

Multivariate normal random variables may lead to parameters that fall outside of the range of biologically feasible values (survival rates < 0 or >1, fecundity rates <0). In simulations involving the multivariate normal distribution, survival and fecundity rates <0 were set to $0 + 0.0001u$, and survival rates > 1 were set to $1 - 0.001u$, where u is a uniform random variable between 0 and 1.

Correlated beta and gamma random variables and correlated uniform random variables were simulated using the protocol outlined in Gross *et al.* (1998). First, multivariate normal random variables with the desired correlation structure were generated. These random variables were then individually transformed back to beta/gamma uniform random variables as follows:

$$\text{vital rate} = F\{G^1(x)\}$$

where G is the cumulative distribution of a standard normal random deviate and F is the cumulative distribution function of the desired distribution (beta, gamma or uniform). The method resulted in fair approximations to the desired correlation structure, although the correlations between s_a and (f_a, s_j and s_{sa}) were underestimated when all rates were drawn from uniform distributions (see below):

Resulting correlation structure (900,000 random draws)

Intended correlation: beta/gamma distribution All rates ~ uniform

$$\begin{array}{cccc}
 & (f_a\ s_j\ s_{sa}\ s_a) & & \\
\begin{pmatrix} f_a \\ s_j \\ s_{sa} \\ s_a \end{pmatrix} &
\begin{pmatrix} 1 & 0.5 & 0.5 & 0.5 \\ & 1 & 0.5 & 0.5 \\ & & 1 & 0.5 \\ & & & 1 \end{pmatrix} &
\begin{pmatrix} 1 & 0.499 & 0.498 & 0.493 \\ & 1 & 0.498 & 0.497 \\ & & 1 & 0.496 \\ & & & 1 \end{pmatrix} &
\begin{pmatrix} 1 & 0.482 & 0.483 & 0.482 \\ & 1 & 0.483 & 0.482 \\ & & 1 & 0.482 \\ & & & 1 \end{pmatrix} \\
 & \begin{pmatrix} 1 & 0.99 & 0.99 & 0.99 \\ & 1 & 0.99 & 0.99 \\ & & 1 & 0.99 \\ & & & 1 \end{pmatrix} &
\begin{pmatrix} 1 & 0.988 & 0.983 & 0.973 \\ & 1 & 0.988 & 0.982 \\ & & 1 & 0.988 \\ & & & 1 \end{pmatrix} &
\begin{pmatrix} 1 & 0.997 & 0.966 & 0.792 \\ & 1 & 0.999 & 0.798 \\ & & 1 & 0.798 \\ & & & 1 \end{pmatrix}
\end{array}$$

APPENDIX B: MODELING WITH COVARIATES

Comparing the TES model with true population dynamics

We estimated the true average growth rate of the population, μ_{true}, from 1000 50-year population projections for each of 1000 surrogate water level data sets; μ_{true} = the average growth rate over the 1000 model runs (within a given surrogate water level data set). To estimate growth rates from the TES model, μ_{TES}, we first created distributions of S_i and F_i from 1000 surrogate 50-year water level data sets by categorizing the rates simulated using equations (3) and (5) into drought years, lag years and high years. We then estimated μ_{TES} from 1000 50-year population projections for each of 1000 surrogate water level data sets by first determining the environmental state (according to the current and previous years' water levels in the surrogate water level data set) and then drawing vital rates from the distributions created in the previous step.

Simulating experimental replicates to test the precision of population estimates

The following protocol was used to simulate experimental replicates:

1 Sample vital rates using equations (3) and (5) at water levels $x(t) = 13$, 14.5, 14, giving one set of vital rate estimates in a drought, lag and high year, respectively.

2 Sample six sets of vital rates using equations (3) and (5) along with the last 6 years of water level data in the surrogate water level data set.

3 Classify the last three sets of vital rate estimates from (step 2) as a drought year, lag year or high water level year.

4 Sample the last t consecutive water levels in the surrogate water level data set. Use these data to estimate the frequency of each environmental state and the transition probabilities between each pair of environmental states.

5 Estimate the growth rate of the population from 1000 50-year population projections using the environmental states matrix model defined by the frequency of environmental states (step 4) and an RTM approach within each environmental state (using the matrices in steps 1 and 3).

6 Estimate the growth rate of the population using the RTM approach (with the six matrices in step 2) from 1000 50-year population projections; pick matrices with equal probability (i.e. ignoring water level).

7 Repeat steps 1–6 for each surrogate water level data set to obtain 1000 separate estimates of μ_{ES} and μ_{RTM} (for each value of t).