

THE EFFECT OF STOCHASTIC TECHNIQUE ON ESTIMATES OF POPULATION VIABILITY FROM TRANSITION MATRIX MODELS

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Abstract. Population viability analysis is an important tool for conservation biologists, and matrix models that incorporate stochasticity are commonly used for this purpose. However, stochastic simulations may require assumptions about the distribution of matrix parameters, and modelers often select a statistical distribution that seems reasonable without sufficient data to test its fit. We used data from long-term (5–10 year) studies with 27 populations of five perennial plant species to compare seven methods of incorporating environmental stochasticity. We estimated stochastic population growth rate (a measure of viability) using a matrix-selection method, in which whole observed matrices were selected at random at each time step of the model. In addition, we drew matrix elements (transition probabilities) at random using various statistical distributions: beta, truncated-gamma, truncated-normal, triangular, uniform, or discontinuous/observed. Recruitment rates were held constant at their observed mean values. Two methods of constraining stage-specific survival to $\leq 100\%$ were also compared. Different methods of incorporating stochasticity and constraining matrix column sums interacted in their effects and resulted in different estimates of stochastic growth rate (differing by up to 16%). Modelers should be aware that when constraining stage-specific survival to 100%, different methods may introduce different levels of bias in transition element means, and when this happens, different distributions for generating random transition elements may result in different viability estimates. There was no species effect on the results and the growth rates derived from all methods were highly correlated with one another. We conclude that the absolute value of population viability estimates is sensitive to model assumptions, but the relative ranking of populations (and management treatments) is robust. Furthermore, these results are applicable to a range of perennial plants and possibly other life histories.

Key words: element selection; matrix selection; population viability; stochastic growth rate; survival constraint; transition matrix model.

INTRODUCTION

Population models are important tools for conservationists and represent applications of population biology theory. As key components of population viability analyses (PVA), they are widely applied to rare and endangered species. Conservationists and managers use population models to assess population health and trends, set priorities, and evaluate management options (Burgman et al. 1993). Different approaches to PVA, however, can lead to different conclusions, even with the same original data (Lindenmeyer et al. 1995, Mills et al. 1996, Pascual et al. 1997, Brook et al. 1999), and these differences can contribute to controversy and unstable priorities for management of imperiled species and the public lands on which they exist (Noon and McKelvey 1996). One common approach to PVA is to assemble field observations of survival and recruitment into a stage- or age-based transition matrix. Schemske

et al. (1994) suggested that matrix models could be widely effective in setting recovery objectives and evaluating management proposals for endangered plants. Partly because of its flexibility, the technique has been widely applied to rare and common species with diverse life histories. Even among matrix models, however, differences in implementation may produce divergent results.

Transition matrices can generate estimates of deterministic parameters such as population growth rate, sensitivities and elasticities, equilibrium population structure, and reproductive values. Often of greater interest to the conservationist are probabilistic measures of population health, such as extinction risk, time to extinction, and stochastic growth rate. These measures of population viability can be estimated when demographic and/or environmental stochasticity are incorporated into the model (Menges 2000, Caswell 2001). Inclusion of environmental stochasticity into matrix models has generally been accomplished through one of two mechanisms: matrix or element selection. For both methods of modeling environmental stochasticity, repeated estimates of annual recruitment, growth, and

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survival must be available or temporal variability must be somehow assumed.

Matrix selection involves selecting whole observed matrices at random at each time step of a simulation, while element selection requires drawing each component of the matrix at random from some statistical distribution. The two methods, however, do not always give the same results (Greenlee and Kaye 1997, Kaye et al. 2001). In addition, for implementation of the element-selection method, too few data are usually available for a formal assessment of goodness of fit. A statistical distribution is often assumed and the distribution is fit to the data at hand. In some cases, even if a reliable test of fit is possible, the statistically best distribution may be rejected on the basis of biological or theoretical reasons, or because of modeling convenience. Unfortunately, different statistical distributions of such input variables may change assessments of population viability (Nakoaka 1997), and information on actual temporal variation in demographic parameters is sparse (Menges 1992). The overall implications of which stochastic method is chosen remain unclear, although a recent comparison with simulated data suggests little impact of stochastic method (Fieberg and Ellner 2001).

Another issue that must be addressed when stochastic stage-based models are implemented with the element-selection method is that overall survival per stage should be limited to $\leq 100\%$. When individual transitions (elements) are selected at random, the cumulative survival (the sum of all transitions in a matrix column) for a given stage can (but should not) exceed 100%. It is important to constrain survival so that it is never $> 100\%$ or the model will create individuals from nothing (Caswell 2001:431) and produce an overly optimistic estimate of population viability. One exception to this rule is for populations in which new individuals may be produced through clonal increase, such as in some plants that are capable of vegetative reproduction (e.g., Bierzychudek 1982). Some authors of PVAs using stochastic matrix models have either ignored this issue or not mentioned it in their papers, and those that acknowledge the problem have used a variety of techniques to resolve it (e.g., Menges 1992, Gross et al. 1998, Kaye et al. 2001). To date, no simulated or empirical comparisons of survival constraint methods have been conducted. This problem does not exist for age-based models, since only one transition (survival to the next age) is selected at random for each age class, nor for matrix selection methods, because survival never exceeds 100% in an observed matrix.

No comparisons of different methods of limiting survival to 100% are available, only a few papers compare techniques of incorporating stochasticity, and those that do explore the results from a single species or simulated data (Greenlee and Kaye 1997, Nakoaka 1997, Fieberg and Ellner 2001, Kaye et al. 2001). In this paper, we compare seven methods of stochastic

matrix simulation (matrix selection and six statistical distributions of element selection) and two methods of constraining survival to $\leq 100\%$. We evaluate the results with a measure of population viability (stochastic growth rate) derived from field-collected data on multiple species and several populations, with stochasticity observed over several years for each. In our models, transition rates were allowed to vary while recruitment was held constant. Our primary objectives are to: (1) test for an effect of stochastic method on population viability estimate, (2) test for an effect of survival constraint method, (3) investigate why different methods yield divergent results, and (4) measure the correlation between estimates.

METHODS

Study species and data sets

Data from five plant species were included in this analysis: *Astragalus tyghensis* Peck (Fabaceae), *Cimicifuga elata* Nutt. (Ranunculaceae), *Haplopappus radiatus* Nutt. (Cronq.) (Asteraceae), *Lomatium bradshawii* Rose (Math. & Const.) (Apiaceae), and *L. cookii* Kagan (Apiaceae). All of these taxa are herbaceous perennials and rare or endangered in the western United States (Oregon Natural Heritage Program 2001). Data were collected from multiple populations of each species over a period of five to ten years (Table 1); the number of observed transition matrices for each population was one less than the number of years of observation, except for *L. bradshawii* because one year of sampling was skipped resulting in only seven matrices from nine years of observation. In total, multi-year data from 27 populations were used. We included species from a variety of habitats and ecoregions in Oregon. In all cases, individual plants were followed through time as mapped and/or tagged individuals, and recruitment of seedlings (first-year plants) was monitored annually. Stage-specific fecundity was estimated based on per-capita seed production in year t and seedling recruitment in year $t + 1$ (as in Kaye et al. 2001; "anonymous reproduction" of Caswell [2001:173–174]), or, if only one reproductive stage was recognized, based on seedlings observed in year $t + 1$ per reproductive plant in year t . No seed-bank stage was included in our models because biological evidence from studies of these species suggests that their seeds may not persist in the soil or have delayed germination. For example, no viable seeds more than one year old have been detected in field studies of *Lomatium* species (Thompson 1985), including *L. bradshawii* (Kaye et al. 2001), or *H. radiatus* (T. Kaye, unpublished data). Seeds of *C. elata* stored under dry, room-temperature conditions do not remain viable for greater than one year, and field-sown seeds of *A. tyghensis* emerge in the following spring only (T. Kaye, unpublished data). Information on each species, including field sampling

TABLE 1. Study species included in this analysis, number of populations and years observed, number of observed matrices and stage categories, habitat, and ecoregion.

Species	No. populations	No. years of observation (span)	No. observed matrices	No. stages	Habitat	Ecoregion†
<i>Astragalus tyghensis</i>	5	10 (1991–2000)	9	5 (seedling plus small, medium, large, and very large size classes)	arid range-land	Columbia Basin
<i>Cimicifuga elata</i>	3	5 (1992–1996), or 6 (1992–1997)	4–5	5 (seedling, small and large vegetative, reproductive, dormant)	mesic forest	Western Cascade Range
<i>Haplopappus radiatus</i>	10	10 (1991–2000)	9	4 (seedling, small and large vegetative, reproductive)	arid range-land	Blue Mountains/Owyhee Upland
<i>Lomatium bradshawii</i>	7	9 (1988–1994, 1996–1997)	7	5 (seedling, small and large vegetative, small and large reproductive)	wetland prairie	Willamette Valley
<i>L. cookii</i>	2	6 (1994–1999)	5	6 (seedling; small and large vegetative; small, medium and large reproductive)	serpentine wetland	Klamath Mountains

Note: All species are herbaceous perennial plants.

† Based on map in Oregon Natural Heritage Program (2001).

techniques, individual matrix construction methods, and the annual matrices, is available in the Appendix.

Stochastic population growth rate

We focused on stochastic population growth rate (λ_s) as a measure of population viability for this analysis. Stochastic growth rate was chosen over the more conventional extinction probability because it is not tied to a particular time horizon. Most estimates of extinction probability are based on simulations for a particular period of time, such as 100 years, and this time period may be selected to resolve differences between populations or treatments (i.e., if all populations go extinct after 100-year projections, the time window may be shortened until at least some populations have a chance of persisting). However, this variability in time span makes it difficult to compare results across studies (Menges 2000), and we found it difficult to identify a single time horizon appropriate to all 27 data sets included in this study. Any one period of simulation resulted in several populations with extinction probabilities of either 0 or 1. This resulted in an inability to resolve differences in these populations, and created many constant values inappropriate for evaluation with analysis of variance (ANOVA). Unlike the deterministic growth rate (λ), λ_s incorporates environmental variability and does not assume a stable (equilibrium) population structure (Tuljapurkar 1990). Further, as stochasticity increases, λ_s declines, and is always less than the mean growth rate (which estimates λ ; Caswell 2001). Populations with $\lambda_s > 1.0$ are projected to grow, while those with $\lambda_s < 1.0$ are projected to decline, making λ_s a convenient measure of population viability in stochastic environments. Therefore, in this paper we use λ_s as an index of relative population viability and do not consider extinction probability further.

To calculate λ_s , we followed the numerical simulation method outlined in Caswell (2001:396). When the log of population growth is averaged over a very large number of time steps, it converges to a fixed value determined by vital rates and environmental processes (Tuljapurkar 1990, Caswell 2001). For each type of simulation, we ran the models described below for 10 000 time steps (discarding the first 500 to omit transient effects) to calculate the stochastic growth rate. All stochastic modeling described in this paper was implemented in MATLAB 5 (Mathworks 1998).

Modeling environmental stochasticity

Environmental stochasticity was modeled in two main ways: through matrix selection and element selection. To incorporate stochasticity via matrix selection, the observed matrices were selected at random with equal probabilities. That is, they were assumed to be independently and identically distributed (i.i.d.). At each time step of a simulation, one matrix was selected at random and postmultiplied by the vector of individual abundances (e.g., Bierzychudek 1982, Lennartsson 2000). The initial stage distribution was the average observed distribution for each population. The use of a different initial distribution could alter the short-term dynamics of our models, but the long-term impacts, which are emphasized by our long-run estimates of λ_s after omission of the first 500 time steps, are unlikely to be much affected. In element selection, a statistical distribution was first fit to the observed data for each transition matrix element, then random values were drawn from the distribution to create a new matrix at each time step. This matrix was then postmultiplied by the abundance vector to iterate the model, as above.

We used six different statistical distributions to compare the effect of input distribution shape on λ_s . Each of these distributions has been used in prior stochastic

TABLE 2. Examples of stochastic models, their use of statistical distributions for varying transition elements, and methods of constraining survivals to 100%.

Distribution	Survival constraint	Species or study	Citation
Beta	transitions contingent on survival	<i>Hudsonia montana</i>	Gross et al. (1998)
Beta	none required	Desert tortoise	Doak et al. (1994)
Normal	none	comparative study	Guerrant (1996)
Truncated normal	none required	<i>Totoaba macdonaldi</i>	Cisneros-Mata et al. (1997)
Truncated normal	resampled	various, comparative	Menges (1992)
Truncated normal	if survival >100%, rescaled to 100%	<i>Lomatium bradshawii</i>	Kaye et al. (2001)
Truncated normal and log-normal	none required	<i>Yoldia notabilis</i>	Nakoaka (1997)
Truncated lognormal	not indicated (none?)	giant kelp	Burgman and Gerard (1990)
Lognormal (truncated for survivals)	none required	Northern Spotted Owl	Akçakaya and Raphael (1998)
Gamma	none required	Chinook salmon	Ratner et al. (1997)
Uniform	not indicated (none?)	<i>Pediocactus paradinei</i>	Frye (1998)
Uniform	not indicated (none?)	<i>Astragalus cremnophylax</i>	Maschinski et al. (1997)
Uniform	not indicated (none?)	<i>Euphorbia clivicola</i>	Pfab and Witkowski (2000)
Observed/discontinuous	none required	Red-cockaded Woodpecker	Maguire et al. (1995)

modeling studies (Table 2) or has been recommended for examination. They included the beta, truncated normal, truncated gamma, triangular, uniform, and observed/discontinuous (see Fig. 1 for examples of the shapes of these distributions as fit to observed transition values). Transition probabilities must be bounded by 0 and 1. Therefore, the fitted distributions must also be constrained to prevent transition probabilities <0 or >1 from being selected at random, a modeling error that, in the absence of clonal spread, is biologically unreasonable. Therefore, the beta distribution is a good candidate, since it is bounded by 0 and 1 by definition. The beta is also very flexible, capable of fitting to an extremely wide variety of distribution shapes (Evans et al. 2000). The normal distribution, on the other hand, must be truncated to 0 and 1, and in our implementation this was accomplished by omitting values outside <0 and >1 and resampling until an appropriate value was obtained. The gamma distribution is bounded by 0 on the left tail, but was truncated to 1 on the right by omitting values >1 and resampling. The triangular distribution may be appropriate when only minimum and maximum values are known (Caswell 2001), although a most likely value must be specified. We fit this model to our observed data by finding the minimum and maximum values, and using the mean as the most likely value (although the median or another most likely value might be appropriate in some cases). For the uniform distribution (also known as the rectangular distribution), we determined only the minimum and maximum values from our data sets. Finally, the observed/discontinuous distribution was defined here as the set of observed values for each transition, and these were drawn at random with equal probability (i.i.d.). Selecting from observed values may also be referred to as a bootstrap technique.

The method of matching moments was used to fit the beta and gamma distributions to our data because the observed values contained zeros and ones in some cases. An alternative would have been to use maximum-likelihood estimation techniques, but this would have forced us to drop observed values equal to 0 or 1. However, dropping values would necessitate dropping whole matrices if we were to compare element selection with matrix selection methods, and we wanted to emphasize the empirical basis of our data sets while maximizing the available sample sizes. Frey and Burmaster (1999) have shown that, for the beta distribution at least, although the method of matching moments produces less efficient statistical parameter estimates than maximum-likelihood methods, matching moment estimates are less sensitive to extreme values. Therefore, we used matching moment estimators because they appear to be adequately robust and because they tolerated the occasional zeros and ones among our observed values. For all our simulations, stochasticity was applied only to the transition elements; recruitment parameters were held constant at their observed mean values.

Constraining survival

We examined two methods of constraining overall survival to $\leq 100\%$. In the first method, if the sum of transition probabilities for a given stage exceeded 100%, the entire set for that stage was resampled until it did not exceed 100% (a method employed by Menges 1992). We refer to this trial-and-error method as resampling. Our second method, which we call rescaling, was to temporarily include mortality in our observed fates, draw a set of transition probabilities (including mortality) for each stage, rescale all probabilities to sum to 100%, then omit the mortality values in the final

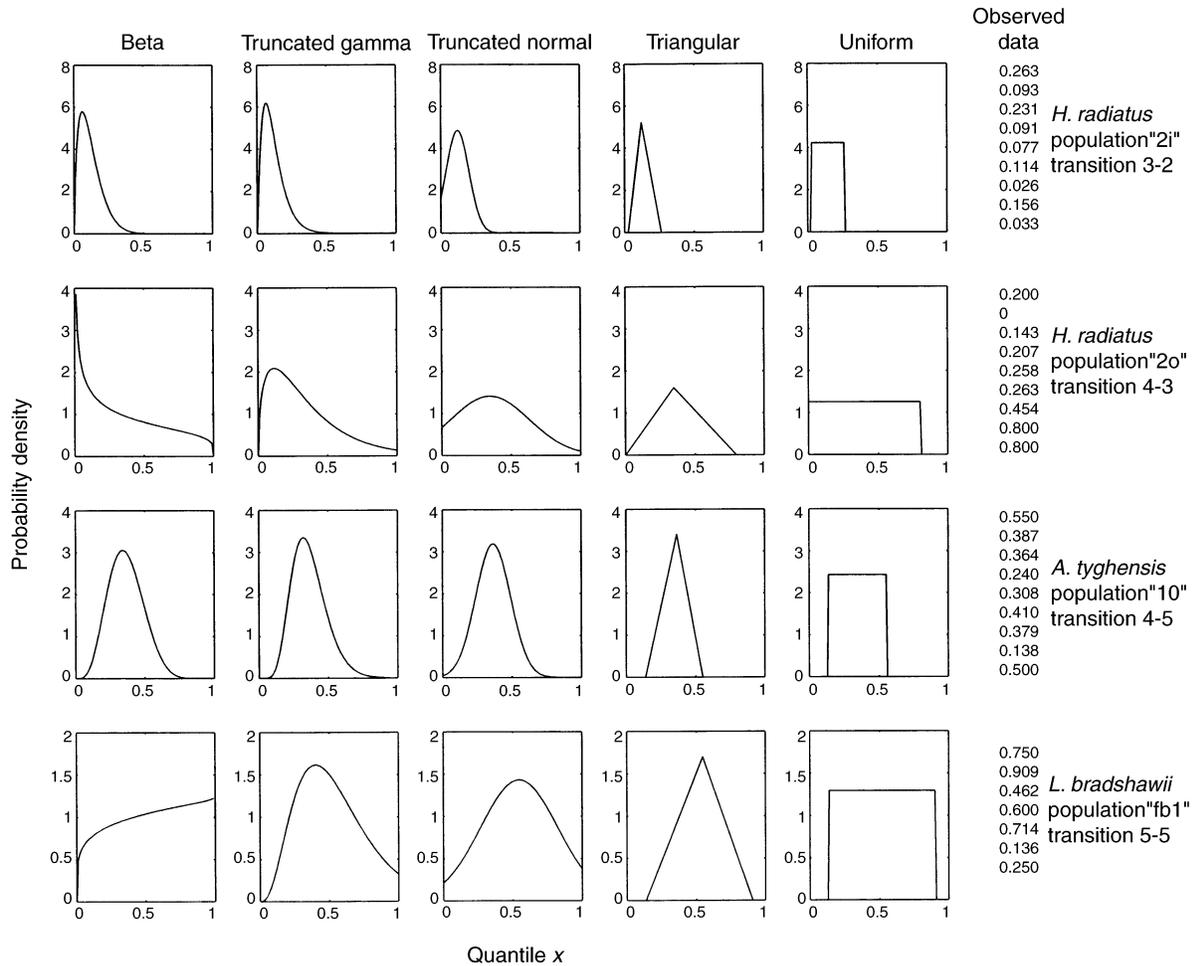


FIG. 1. Probability densities of some statistical distributions fit to examples of observed values of transition rates recorded over several years of observation. Each column illustrates a different distribution (beta, truncated gamma, truncated normal, triangular, and uniform), and each row represents the fit of these distributions to the data listed at the right, which are selections from among the data sets used in this paper. These data represent the observed values for a particular transition, as indicated in the notes at the far right. Note that the truncated normal distribution is truncated at both tails, and the truncated gamma is truncated only on the right; note also that the degree of truncation differs substantially among observed data sets.

matrix. In this process, rescaling was applied at every time step to every stage, forcing the sum of all fates (including mortality) to equal 100% (which they always do in the real world). We believe this method has not been employed previously.

Analysis

Testing for effects of input distributions, survival constraint, and study species.—We tested for effects of input distribution, survival constraint method, species, and interactions among these factors using SAS PROC MIXED (SAS Institute 1990). Use of raw estimates of λ_s as a response variable posed a difficulty because survival constraint methods were applied only to the element selection procedures, not the matrix selection procedure, making our design unbalanced. Therefore, we chose a response variable that compared the relative response of each element-selection pro-

cedure to matrix-selection estimates of λ_s . Specifically, for each population, we calculated the proportional difference in λ_s between the matrix-selection procedure and the procedures using various element-selection distributions and survival-constraint methods (i.e., $[\lambda_s \text{ element} - \lambda_s \text{ matrix}] / \lambda_s \text{ matrix}$). This step was appropriate given that we are interested in the relative effects of these methods more than their actual estimates of mean stochastic growth rate. We considered this response variable to be structured in a split-plot design, with species as the whole plot and individual populations as replicates. Species was included as a fixed effect to test for differences among taxa in their PVA sensitivity to model assumptions, and for interactions with the other factors.

Detecting bias in mean and variability.—To explore the fit of each simulation technique to the observed data, we compared the mean and variability of each

TABLE 3. Split-plot ANOVA for the effects of species, statistical distribution of input variables, and survival constraint method on the proportional change in λ_s relative to the matrix selection procedure (NDF and DDF are numerator and denominator degrees of freedom).

Source	NDF	DDF	Type III <i>F</i>	<i>P</i>
Whole plot effects				
Species	4	22	0.4	0.8044
Subplot effects				
Survival constraint method	1	242	686.17	0.0001
Stochastic method	5	242	53.79	0.0001
Interactions				
Stochastic method \times constraint method	5	242	24.91	0.0001
Species \times constraint method	4	242	0.94	0.4434
Species \times stochastic method	20	242	1.12	0.3326
Species \times stochastic method \times constraint method	20	242	0.46	0.9788

transition element from the observed data sets with results from each of the element-selection and survival-constraint techniques. First, we used each of the element-selection methods to generate 1000 random matrices from each population using each of the survival-constraint methods. Second, we calculated the mean and standard deviation (SD) for each transition element (excluding recruitment) from these simulated data sets. Third, we calculated the relative difference in mean and SD between those estimated from the observed values and those calculated from the simulated matrices. We defined bias broadly to include the combined differences between observed and simulated means and SDs due to survival constraint method and distribution shape. We then tested for correlations between mean estimates of relative bias and mean relative differences in λ_s , using multiple regression, to determine how much of the simulation technique effects were due to these biases.

This process was repeated using estimates of mean relative bias weighted by the elasticity of each element, so that bias in elements of relatively low importance to growth rate were down-weighted and those with high influence were weighted more strongly. Although stochastic elasticities may be estimated as measures of the importance of individual transitions on λ_s (Tuljapurkar 1990, Caswell 2001:402–408), we used elasticities calculated from mean observed matrices because they are easier to calculate and they are excellent predictors of stochastic elasticities, even though the deterministic and stochastic growth rates may be quite different (Caswell 2001, Caswell and Kaye 2001).

Correlation among techniques.—Even if the various techniques for incorporating stochasticity result in different estimates of λ_s , we would like to know if they yield similar relative results. That is, if one population has a higher λ_s than another as measured by one stochastic method, is it also higher as measured by a different method? To measure their degree of association, we tested for correlations between estimates of λ_s from each method of including temporal variability using

the Pearson product-moment (r), and this procedure was repeated for each method of constraining survival. The total sample size for these correlations was 27, which was the total number of populations sampled across all five species.

RESULTS

Effects of input distributions, survival constraint, and study species

Model procedures had substantial effects on estimates of stochastic population growth rates. The choice of input distributions and survival-constraint methods both had significant effects on mean proportional differences in λ_s relative to the matrix selection method (Table 3), but there was a significant two-way interaction between these factors ($P \leq 0.0001$). That is, the resampling method of constraining stage-specific survival to $\leq 100\%$ yielded mean estimates of λ_s consistently lower than the rescaling procedure, but the magnitude of this reduction differed among stochastic element selection methods (Fig. 2). Study species did not affect these results ($P = 0.804$), and there were no two- or three-way interactions with taxon ($P \geq 0.333$). Estimates of λ_s ranged from 0.658 to 1.173, making the results applicable to a wide range of population behavior.

When the resampling survival-constraint method was applied, most element-selection distributions yielded estimates of λ_s equal to or lower than estimates derived by matrix selection. The beta distribution yielded the lowest relative estimate of λ_s (14% lower than the matrix shuffle method), while the truncated gamma and observed/discontinuous distributions were only slightly (but significantly) closer to the matrix shuffle estimates (Fig. 2). Both the truncated normal and uniform distributions produced mean λ_s estimates indistinguishable from matrix selection. The mean estimate from the triangular distribution was intermediate between these two groups of procedures. In contrast, under the resampling procedure, most λ_s estimates were

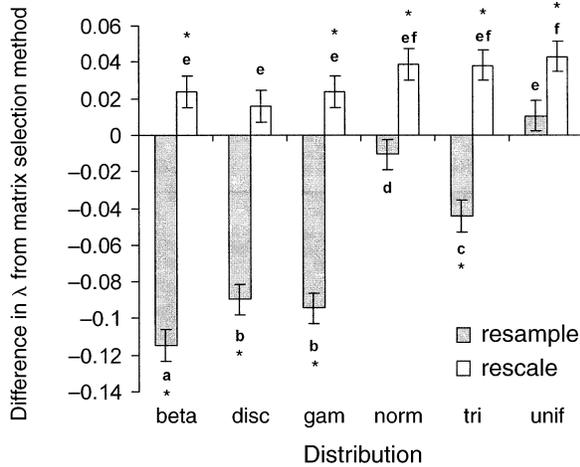


FIG. 2. Mean proportional difference (± 1 SE) in stochastic population growth rate (λ_s) between matrix selection and the element selection procedures. Six statistical distributions were used for the element selection method: beta, observed/discontinuous (disc), truncated gamma (gam), truncated normal (norm), triangular (tri), and uniform (unif). Two survival constraint methods, resample and rescale, were also compared. Bars with the same letter did not differ at the 0.05 level (Fisher's protected LSD). Asterisks (*) indicate a significant difference at $P < 0.05$ between the stochastic growth rate calculated via matrix selection and each element selection method.

higher than those from matrix selection. Estimates from the uniform distribution were highest ($\sim 4\%$ higher than estimates from matrix selection) and those from the beta, truncated gamma, and observed/discontinuous were lowest (Fig. 2). Those from the truncated normal and triangular distributions were intermediate. Estimates from the observed/discontinuous distribution did not differ significantly from the matrix selection method (Fig. 2).

Evaluation of bias in mean and variability

Unweighted mean and SD.—Bias was detected in the unweighted mean and SD of several element selection methods and both survival constraint techniques. Compared to the observed values, mean transition element values were reduced by 12–15% by the beta, truncated gamma, and observed discontinuous distributions when the resample constraint method was used. When the rescale technique was employed, however, these distributions had no detectable bias on transition means (Fig. 3, top left). In contrast, the truncated normal, triangular, and uniform distributions consistently increased the mean over the observed values by 6–31%, regardless of survival-constraint method. Standard deviations were also altered by the different methods. In all cases, SDs were depressed relative to the observed values. Values derived from the beta, truncated gamma, and observed/discontinuous showed the least bias (6–21% lower than observed), while those from the triangular had the greatest reduction (64–83%), depend-

ing on the method of constraining survival (Fig. 3, middle left). There were no consistent differences in bias to the standard deviation caused by the two survival constraint procedures. Multiple linear regression indicated that bias in the mean had a significant effect on proportional difference in λ_s ($P = 0.0017$), while reductions in SD did not ($P = 0.6603$). Bias in the mean explained 60.7% of the variability in λ_s estimates (Fig. 3, bottom left).

Weighted mean and SD.—When bias in mean transition elements was weighted by elasticity, a somewhat different picture emerged. The resampling procedure generally resulted in varying degrees of negative bias, depending on the statistical distribution used to incorporate stochasticity. For example, the beta, truncated gamma, and observed/discontinuous distributions resulted in reductions in the weighted means of 12–16% (similar to the unweighted case), but the truncated normal and triangular biased the weighted mean downward by 3% and 6%, respectively (Fig. 3, top right). The uniform distribution had no effect on the weighted means. The rescaling procedure resulted in no detectable bias on the weighted mean transition rates for all stochastic methods except the uniform, which increased the mean by about 2% (Fig. 3, top right). Overall, weighted SD biases differed little from the non-weighted cases (Fig. 3, middle right).

As in the unweighted case, multiple regression indicated a significant linear correlation between differences in λ_s and bias in the weighted mean ($P < 0.0001$), but not SD ($P = 0.1038$). Bias in the weighted mean explained 98.3% of the variability in proportional differences in lambda between element selection techniques and matrix selection (Fig. 3, bottom right). The slope of this relationship was indistinguishable from 1 (95% CI, 0.93–1.1), and the intercept was close to, but slightly higher than, 0 (95% CI, 0.018–0.031). Thus, variation in λ_s estimates derived through element selection relative to matrix selection were due almost entirely to biases in the weighted mean transition rates.

Correlation among techniques

Most methods of incorporating stochasticity into matrix models produced estimates of λ_s that were highly correlated with each other. For both methods of survival constraint, resampling and rescaling, the lowest correlation was between estimates via the beta and observed/discontinuous distributions ($r = 0.862$ and 0.849 , respectively) and the highest was between the truncated gamma and uniform ($r = 0.991$ and 0.992 , respectively; Table 4). Regardless of which survival-constraint technique was used, at least 16 of the 21 possible correlations had $r \geq 0.9$.

DISCUSSION

Effects of stochastic methods and survival constraints

Different methods of incorporating stochasticity into matrix models resulted in substantial variation in es-

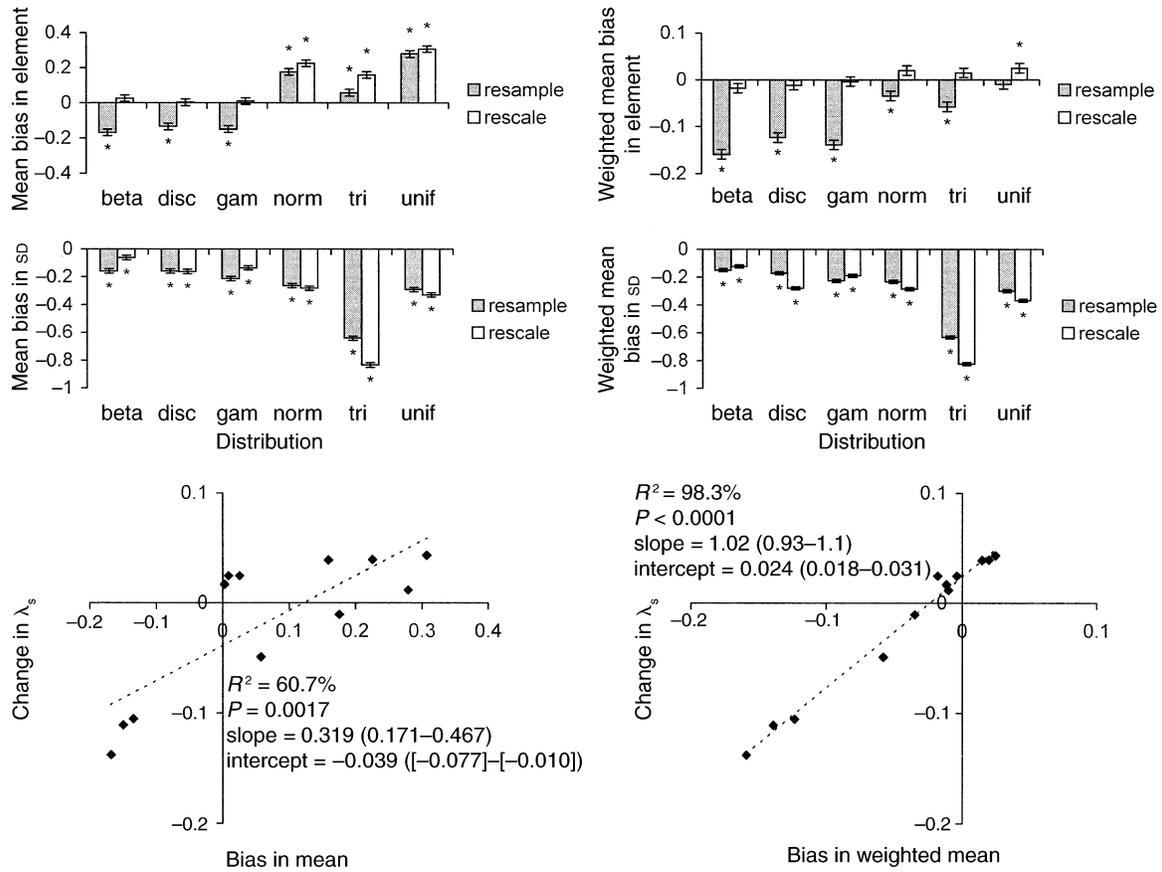


FIG. 3. Evaluation of relative bias in transition means (top panels) and standard deviations (middle panels) relative to observed values for each combination of element-selection distribution and survival-constraint method. The correlation between change in λ_s and bias in element means is shown (bottom panels) along with the linear models. Mean bias in standard deviation was omitted from the linear models because it was not significant in the multiple regressions ($P = 0.10-0.66$). Left panels use unweighted means, and right panels use means weighted by elasticities. Asterisks indicate significant difference from zero at $P < 0.05$. Distribution abbreviations as in Fig. 2.

timates of population viability. The species from which the observed data were collected, however, had no effect, and estimates of λ_s spanned a wide range, suggesting that these results may be broadly applicable, at least among herbaceous perennial plants from the ecoregions represented here (Table 1). In element selection, the distribution shape for sampling transition

probabilities had significant effects on estimates of λ_s , but the magnitude and direction of this effect depended on which method was used to constrain stage-specific survival to $\leq 100\%$ (Fig. 2). For example, when resampling was used to constrain survivals, the beta, observed/discontinuous, truncated gamma, and triangular distributions resulted in λ_s estimates significantly lower

TABLE 4. Pearson correlation coefficients (r) for each of seven methods of incorporating environmental variability to calculate stochastic population growth rate (λ_s).

Stochastic method	Matrix selection	Observed/discontinuous	Uniform	Truncated normal	Truncated gamma	Triangular	Beta
Matrix selection	...	0.869	0.928	0.877	0.926	0.915	0.905
Observed/discontinuous	0.916	...	0.877	0.970	0.913	0.977	0.862
Uniform	0.976	0.893	...	0.920	0.991	0.930	0.986
Truncated normal	0.955	0.975	0.945	...	0.943	0.959	0.895
Truncated gamma	0.962	0.900	0.992	0.954	...	0.949	0.988
Triangular	0.951	0.989	0.942	0.991	0.948	...	0.908
Beta	0.947	0.849	0.984	0.906	0.973	0.903	...

Note: Correlations with λ_s calculated using the resample survival constraint method are above the diagonal, while those derived via the rescale method are below ($P \leq 0.0001$ in each case).

than those derived from matrix selection. But when survivals were constrained through rescaling, all distributions, except the observed/discontinuous, produced similar results and exceeded matrix selection estimates of λ_s . Overall, combining the resampling method with the beta distribution resulted in the lowest mean estimates of λ_s (13.8% below the mean matrix selection estimates), while rescaling with the uniform distribution produced the highest (4.3% greater than matrix selection estimates). Despite variation in estimates of λ_s , the different stochastic methods produced highly correlated results ($r = 0.849\text{--}0.992$, Table 4), suggesting that although their quantitative estimates of population viability may have differed, their relative ranking of populations did not.

Concerns that choice of a stochastic method might influence the results of risk-assessment models are not new (Bukowski et al. 1995, Nakoaka 1996, Hamed and Bedient 1997, Menges 2000, Caswell 2001). Past comparisons of matrix and element selection procedures have found both large and small differences in estimates of population viability. For example, a comparison from *H. radiatus* found that element selection from a truncated normal distribution resulted in much lower estimates of extinction risk than matrix selection (Greenlee and Kaye 1997). Kaye et al. (2001) found estimates of λ_s derived for *L. bradshawii* from element selection (truncated normal distribution) to be indistinguishable from, or moderately higher than, estimates from matrix selection. Extinction probability estimates were either identical or slightly lower than from matrix selection. These patterns are consistent with those reported here, which should be expected because both examples used earlier portions of the same data sets used in this analysis. Even so, Greenlee and Kaye (1997) incorporated only four years of data and Kaye et al. (2001) used six, and both studies used a different approach to survival constraint than those conducted here. Although stochastic growth rate has been recommended as a measure of population viability suitable for comparisons across studies (Menges 2000), differences among stochastic methods make many comparisons dangerous. This problem can be avoided, however, if the same methods are used among studies (which seldom may be the case; see Table 2), or if the estimates of stochastic growth rate are first adjusted by the cumulative bias of the specific survival constraint methods and probability distributions. In general, comparisons across viability studies should strive to standardize as many model assumptions as possible, a practice that may find much agreement among techniques (Brook et al. 2000a, b).

Among element-selection methods, skewness has been identified as an important aspect of a distribution with potential effects on estimates of population growth rate (Slade and Levinson 1984), and the selection of a statistical distribution can, in theory, substantially affect the results of a risk assessment (Bukowski 1995).

The effects of different distributions have been much more thoroughly reviewed for randomly varying recruitment (Tallie et al. 1995) than for transition probabilities. Nakoaka (1997), for example, estimated λ_s for two populations of a marine clam by allowing recruitment to vary according to both lognormal and truncated normal distributions (one-tailed truncation was necessary because recruitment must be bounded by zero on the left). Relative to the truncated normal, the lognormal decreased λ_s at one site but increased it at the second. In our analyses, recruitment was held invariant at the mean observed values and stochasticity was applied only to the transition probabilities. If we had allowed recruitment to vary as well, estimates of λ_s may have been lower, our results may have differed, and there may have been an interaction between choice of recruitment and transition distributions. Since both types of vital rates are often varied in stochastic matrix models, this area deserves further research.

Resampling to constrain survival to $\leq 100\%$ always reduced λ_s relative to rescaling by introducing negative bias into weighted mean vital rates (Fig. 3, upper right panel). The rescaling method, on the other hand, did not introduce measurable bias (except for the uniform distribution, which was slightly positively biased). Although researchers have used various techniques to constrain stage-specific survivals to $\leq 100\%$, or ignored the problem (Table 2), we found the choice of survival constraint technique to have a strong effect on our results. Results from the rescaling technique were fairly consistent among element selection distributions, with the only significant differences being between the uniform distribution vs. the beta, discontinuous/observed, and truncated gamma (which were indistinguishable from each other, Fig. 2). Relative to estimates from matrix selection, λ_s estimates were higher by only 1.7% (discontinuous/observed) to 4.3% (uniform). Other methods used by previous authors of stage-based stochastic matrix models include a different form of rescaling used when survivals sum to $> 100\%$ (without regard to mortality, e.g., Kaye et al. [2001]) and making transitions contingent on underlying vital processes (e.g., Gross et al. 1998).

One reason for the similarity in results among the element selection methods compared here with rescaling (in the relative absence of bias) may be that some of their important differences are in their tails—their chance of extreme events—and these tails were either bounded to fall between zero and one, or were truncated to do so. In an examination of the tail behavior of the lognormal, Weibull, gamma, and inverse Gaussian distributions in Monte Carlo simulations, Haas (1997) found that, even at relatively high standard deviations, the important differences among them were in the extreme (upper) tails. Since the distributions with long tails included in our implementations (i.e., normal and gamma) were truncated, these differences were, at least in part, reduced. For example, the triangular and trun-

cated normal distributions have identical peak values, but substantial portions of both tails of the normal may be cut off (Fig. 1), thus increasing the similarity of the two distributions. Haas (1997) further showed that identifying the correct distribution from small data sets may be difficult or impossible (our samples numbered only four to nine, depending on the species), but the differences will be primarily in the tails. Again, if the tails are truncated, these differences may be partly mitigated.

Although truncation may help explain some of the similarities among the element-selection methods evaluated here, it is not necessarily a recommended practice. Especially in cases where only one tail is truncated, omitting chance events in this way from a distribution will change the mean and reduce variance, as illustrated here by negative bias in SD estimates (Fig. 3). Truncation of transition probabilities drawn from a normal distribution, especially those near 1, lowered the mean and increased extinction probability in viability models of the fish, *Totoaba macdonaldi* (Cisneros-Mata et al. 1997). In the case of Nakoaka's (1997) marine clam, truncation of the lower tail in the normal distribution was required to generate random numbers for modeling variation in recruitment. This one-tailed truncation increased the mean by ~25% and decreased the variance by 35% at one site (as discussed in Caswell 2001:412), destroying the fit of the distribution to the data. It may be that in many of our cases with observed data, substantial portions of the normal and gamma probability density functions were within the range 0–1, which would explain why truncating them produced little or no effect on the weighted mean and only "typical" reductions (Fig. 3) in standard deviation. Of course, the effect of truncation will be stronger as the mean approaches 0 or 1 (depending on the distribution), because a larger proportion of the probability density function will be truncated. For example, if a gamma distribution is fitted to a group of observed transition probabilities close to 1, the upper tail will extend substantially past 1, and truncation will remove a significant portion of the probability density function. If this is a concern, a clever procedure (Burgman and Gerard 1990) that will reduce its effect is to transform the observed probabilities (p) to $q = 1 - p$, fit the distribution, draw a random sample, then back transform the value to $1 - q$, thus avoiding most truncations.

Selecting a distribution that does not require truncation may be preferred. The endpoints of the uniform and triangular distribution were defined by the observed data, so they never fell beyond 0–1 in our samples. However, their shapes are simplistic and they did not capture variance well, resulting in relatively low SDs (28–83% below observed values). Even so, they may be appropriate in cases where few data are available. For example, the triangular distribution may be an efficient substitute for the beta in some cases (McCrimmon and Ryavec 1964). The beta distribution,

in contrast, is bounded by 0 and 1 and has a flexible shape within those bounds, traits that make it useful for modeling transition probabilities. It is perhaps the first distribution that should be explored when developing a stochastic matrix model with element selection. The observed/discontinuous distribution did not allow transition elements to vary outside the observed limits, and it did not allow selection of values other than those observed. Depending on the model, this may or may not be a desirable trait. When combined with the rescale survival-constraint method, it produced results indistinguishable from those derived with the beta distribution or matrix selection. Other distributions that have received little attention but that stochastic matrix modelers should explore include the S distribution, which is based on differential equations and is well suited to probabilities (Voit and Schwake 2000), and the beta binomial, which is appropriate for distributions based on probabilities derived from counts (Griffiths 1973, Tamura and Young 1987, Kahn and Raftery 1996). The beta binomial may be especially useful and appropriate for stochastic matrix models because it can separate demographic variability from estimates of environmental stochasticity (Kendall 1998).

Matrix vs. element selection

Both approaches for incorporating stochasticity, element selection and matrix selection, have advantages and disadvantages as modeling techniques. For example, because element selection can sample from parametric distributions of transition probabilities, the possible trajectories that a population size can follow are limited only by the distribution shape. In contrast, matrix selection limits the number of pathways a population can follow in a stochastic simulation because, at each time step, one of a finite number of matrices must be selected. Through parametric element selection, a greater number of possible paths can be explored, especially those that occur with lower frequency (the tails in a distribution). These rare events may be important for assessing chance events like extinction (Burgman et al. 1993). Element selection may also accommodate missing data more efficiently than matrix selection by fitting a distribution to the vital rates for which data are available. In matrix selection, individual missing vital rates must be estimated or replaced with pooled data from the other individual matrices. However, matrix selection, unlike element selection in most stage-structured models, is free of the problem of constraining stage-specific survivals to $\leq 100\%$. Finally, element selection may be a better choice when stochasticity must be applied to individual vital rates through a functional relationship with an environmental factor, such as precipitation (e.g., Gross et al. 1998).

One weakness of standard element selection methods is that transition probabilities may not be explicitly correlated with one another, even though a "good" year for one vital rate, such as survival of reproductive

plants, is often a good year for another, such as fecundity. Therefore, a matrix could be constructed from random elements that has a mixture of “good” and “bad” vital rates—a condition that may not occur in nature. Matrix selection is not usually faced with this problem, since all of the elements in an individual matrix usually come from the same year and represent observed vital rates. Correlation among vital rates is believed to be widespread (Horvitz and Schemske 1995, Oostermeijer et al. 1996, Horvitz et al. 1997, Gross et al. 1998, Caswell 2000, 2001, Menges 2000) and may tend to reduce population viability (Ferson and Burgman 1995, Cisneros-Mata et al. 1997, Pfab and Witkowski 2000, Fieberg and Ellner 2001). In the current study, differences in estimates of λ_s were largely explained ($r^2 = 98.4\%$) by degree of bias in mean transition rates (after weighting with elasticities), and the slope of the regression line for this linear correlation did not differ from 1.0 (Fig. 3). The intercept of this line was slightly higher (2.4%) than expected, however, and this may be due, in part, to increases in λ_s (relative to matrix selection) through omission of correlation structure during element selection. Unfortunately, tools for multivariate random number generation are not widely available (Caswell 2001) for distributions other than the normal, but recent advances in statistical methods (e.g., Ferson and Burgman 1995, Haas 1999, Fieberg and Ellner 2001, Kaye 2001; P. Fackler, *unpublished manuscript*) may make their application more accessible for stochastic matrix models.

Conclusion

For many observed data sets, it may be difficult to test the fit of a particular distribution, partly because of limited samples (Karian and Dudewicz 2000:90–96). Sorribas et al. (2000) demonstrated that even with 160 random samples from known distributions, a best-fit screening algorithm failed to identify the source distribution in a majority of cases. Despite this uncertainty, most stochastic modelers select a distribution that seems reasonable, fit it to their available data, and execute the model. We have shown that distribution choice for transition probabilities may or may not have a strong influence on stage-structured matrix model outcomes, depending on what method of constraining overall stage-specific survival to 100% is used. Further, this conclusion is consistent across a variety of perennial plant species. Although distribution shapes can cause differences in viability estimates, their effects interacted with the two different survival constraint methods we employed and were largely explained by the degree of bias induced by these methods.

Little previous attention has been given to the survival constraint problem, which applies only to stage-structured models in which individuals can make more than one transition, but choice of this procedure can be at least as important as element selection technique (Fig. 2), and ecological modelers need to be aware that

how they treat this issue could have substantial impacts on their results and should take steps to control bias in their simulations. If a method of constraining survival is employed that results in a negative bias, modelers can expect relatively low estimates of λ_s and substantial differences in model results among various statistical distributions used for parametric element-selection models. However, when this bias is eliminated, estimates of λ_s from different element-selection methods tend to converge. To avoid bias in influential transitions, we recommend the use of either an element selection procedure combined with the rescaling technique described here, or matrix selection. Note, however, that this recommendation applies to organisms with complex life histories that result in multiple possible transitions from any given stage. Survival constraints are not necessary in age-based models or other life histories in which individuals have only one possible survival pathway. Results from this study and others (Fieberg and Ellner 2001) suggest that in the absence of the survival constraint problem, or if bias is not induced in its correction, different statistical distributions used in element selection often yield very similar results in PVA.

Element-selection methods are often necessary, especially when the number of complete matrices is insufficient for matrix selection, if element means or variances must be estimated from the literature or another study, and when a specific correlation between elements and environmental variables is desired. Our rescaling procedure for constraining survival to 100% reduces bias and leads to estimates of λ_s from element selection methods that are similar to those from matrix selection (although slightly higher in some cases, possibly due to the lack of correlation among elements in our technique).

The wide range of population-viability estimates possible from a single data set analyzed by slightly different methods is cause for concern; one technique might indicate a robust population while another could project a rapid decline (Fig. 2). We agree with Beissinger and Westphal (1998), Menges (2000), and Fieberg and Ellner (2001) that the strength of viability analysis rests in its use as a comparative tool rather than a means of assessing the health of individual populations. Life-table response experiments (e.g., Caswell 1989, 2001), in which vital rates of a population form the response variable in an experimental design, are a powerful tool for comparing populations exposed to different treatments. Especially in the face of uncertainty due to measurement error, which can create very wide confidence intervals on estimates of extinction probability (Ludwig 1999, Fieberg and Ellner 2000), the use of viability analyses to assess the relative vigor of a group of populations or the impact of a habitat alteration should be emphasized over quantitative estimates of viability. Fortunately, the relative ranking of plant populations examined here appears to

be fairly robust to differences in stochastic methods (i.e., the results of different techniques are highly correlated). It may also be sound practice to compare several PVA methods when developing management recommendations for endangered species (e.g., Pascual et al. 1997, Fisher et al. 2000).

Although stochastic growth rate has been identified as a measure of population viability suitable for comparisons across studies (Menges 2000), differences among stochastic methods make such comparisons dangerous. This problem can be avoided, however, if the same methods are used among studies (which is seldom the case, see Table 2), or if the estimates of stochastic growth rate are first adjusted by the cumulative bias of the specific survival constraint methods and probability distributions.

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APPENDIX

Field sampling techniques, matrix construction notes, and original transition matrices for five perennial plant species are available in ESA's Electronic Data Archive: *Ecological Archives* E084-038-A1.