Chapter 4

Does Correlation among Vital Rates Matter? The Effect of Correlation Structure, Vital Rate Distribution, and Species On Estimates of Population Viability

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INTRODUCTION

Population viability analysis (PVA) is a central tool in conservation biology (Soulé 1987). The use of population models in this context represents an application of ecological theory to real world problems, often in an attempt to develop management practices that minimize the risk of extinction of protected species (Burgman et al. 1993). Transition matrix models are a widely used method for PVA (Menges 1990, 2000). The technique involves pooling information on many aspects of a species' life-cycle, including recruitment, survival, and growth, into a single structured model (Caswell 2001). The method has been promoted as a powerful tool for PVA and for understanding the basic life-history of species targeted for conservation, partly because of its flexibility in accommodating different species and the variety of useful demographic parameters it can estimate (Schemske et al. 1994). However, differences in implementation of PVA models can lead to alternative, even conflicting, conclusions, even when the same source data are used (Lindenmeyer et al. 1995, Mills et al. 1996, Pascual et al. 1997, Brook et al. 1999), and this is true for matrix models as well (Nakoaka 1996, Chapter 3).

Correlation among vital rates may affect the outcome of risk assessments in general (Bukowski et al. 1995) and stochastic matrix models in particular (Tuljapurkar 1982, Caswell 2001). Positive correlations are possible when different stages respond in similar ways to their environment. For example, if rainfall in a given year promotes growth of both small and large individuals to the next higher size class, these growth probabilities will likely be correlated over time. Positive correlations among vital rates have been shown to increase variability in estimates of average growth rate and extinction risk (Doak et al. 1994). There is ample evidence that demographic parameters are correlated across years and environments (Horvitz and Schemske 1995, Horvitz et al. 1997, Caswell 2000, Oostermeijer et al. 1996), and inclusion of this correlation structure in stochastic models may be necessary to avoid overly optimistic estimates of population viability (Nakoaka 1996). However, negative correlations among vital rates are also possible (Oostermeijer et al. 1996), and these tend to counteract the effects of positive correlations (Tuljapurkar 1982, Ferson and Burgman 1995, Orzack 1997). Therefore, the effect of correlation structure on population viability estimates may depend on the nature of the correlations among vital rates, which, in turn, may differ among species and environments.

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 concern 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 a 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, repeated estimates of annual recruitment, growth and survival must be available (e.g., Bierzychudeck 1982) or temporal variability must be somehow assumed (e.g., Menges 1992). Matrix selection involves shuffling 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. However, the two methods do not always give the same results (Greenlee and Kaye 1997, Kaye et al. 2001, see also Chapter 3). In addition, for implementation of the element selection method, too few data are usually available for a formal assessment of goodness of fit, so 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 temporal variation in demographic parameters is sparse (Menges 1992). The overall implications of which stochastic method is chosen remain unclear.

Few examples of incorporating correlation structure into stochastic matrix models are available, and these tend to emphasize positive correlations and single species. Comparisons of different methods of incorporating stochasticity are also infrequent, especially those that examine the effects of various statistical distributions for element selection (Chapter 3). One reason correlation structure is seldom included is that multivariate random number generators are not widely available (Caswell 2001) and implementation is generally complex. In this paper, we compare the effects of correlation among vital rates on population viability using five methods of stochastic matrix simulation (bootstrap, beta, truncated normal, truncated gamma, and uniform distributions). We evaluate the results with a measure of population viability (stochastic growth rate) derived from observed data for multiple species and several populations. Our primary objectives are to 1) assess the effects of correlations among vital rates on population viability estimates and determine if these effects differ among species and stochastic methods, 2) explore factors that influence the effects of these correlations, and 3) measure the correlation of viability estimates derived through different methods.

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 4.1); 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

Table 4.1. Study species included in this analysis, number of populations and years observed, number of observed matrices and stage categories, habitat, and ecoregion. All species are herbaceous perennial plants.

species	number of populations	years of observation	number of observed matrices	number of stages	habitat	ecoregion[^]
Astragalus tyghensis	5	10 (1991-2000)	9	5 (seedling plus small, medium, large and very large size classes)	arid rangeland	Columbia Basin
Cimicifuga elata	3	5-6 (1992-96)	4-5	5 (seedling, small and large vegetative, reproductive, dormant)	mesic forest	Western Cascade Range
Haplopappus radiatus	10	10 (1991-2000)	9	4 (seedling, small and large vegetative, reproductive)	arid rangeland	Blue Mountains/ Owyhee Upland
Lomatium bradshawii	7	9 (1988-94, 1996-97)	7	5 (seedling, small and large vegetative, small and large reproductive)	wetland prairie	Willamette Valley
L. cookii	2	6 (1994-99)	5	6 (seedling; small and large vegetative; small, medium and large reproductive)	serpentine wetland	Klamath Mountains

[^] Based on map in Oregon Natural Heritage Program (2001).

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* (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 (Kaye unpublished data). Information on each species, including field sampling 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 either resulted in several populations with extinction probabilities of 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 average growth rate (which estimates λ) (Caswell 2001). Populations with λ_s greater than 1.0 are projected to grow, while those with λ_s less than 1.0 are projected to decline, making λ_s a convenient measure of population viability in stochastic environments.

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 (Caswell 2001, Tuljapurkar 1990). For each type of simulation, we ran the models for 10,000 time steps (discarding the first 500 to omit transient effects) to calculate λ_s. All stochastic modeling described in this paper was implemented in MATLAB 5 (The Mathworks 1998).

Modeling environmental stochasticity

Environmental stochasticity was modeled by randomly selecting transition matrix elements from either observed values (a bootstrap approach) or parametric distributions fit to the observed values. We compared these approaches to evaluate the effect of distribution shape on the importance of correlation to estimates of λ_s. The observed values represented the temporal variability known for each population of each species. At each time step of a simulation, a matrix was constructed at random and post-multiplied by the vector of individual abundances to obtain a new vector of individual stage abundances. The initial stage distribution was the average observed distribution over all years of observation for each population. For the bootstrap method, stage specific recruitment (the top row of the transition matrices) was allowed to vary through time by randomly selecting from among the observed recruitment rates. For each of the parametric methods described below, recruitment varied according to a gamma distribution, which has been shown to work well for fecundities (Tallie et al. 1995). When individual transitions (elements) are selected at random, the cumulative survival (the sum of all transitions in a matrix column excluding recruitment) for a given stage can, but should not, exceed 100%. It is important to constrain stage-specific survival so that it is never greater than 100%, or the model will create individuals from nothing (Caswell 2001) and produce an overly optimistic estimate of population viability. We constrained survival with the rescaling method of Chapter 3, which rescales each transition rate (including mortality) so that the sum of all rates of a given stage always sums to 100% while minimizing bias to the element means.

Distributions of vital rates. We compared five methods of randomly varying transition elements. These were the bootstrap and four parametric distributions: beta, truncated gamma, truncated normal, and uniform. To incorporate stochasticity via the bootstrap, the observed values were assumed to be independently and identically distributed (iid) (the observed/discontinuous distribution of Chapter 3). For the parametric approaches, a statistical distribution was first fit to the observed data for each transition element, then random values were drawn from the distribution to create a new matrix at each time step. Each of these distributions has been used in previous stochastic modeling studies (Table 4.2). Because transition probabilities must be bounded by 0 and 1, the fitted distributions must also be constrained or transition probabilities less than zero or greater than 1 might be selected at random, a modeling error that is biologically unsound. 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. The gamma distribution is bounded by 0 on the left tail, but was truncated to 1 on the right in our simulations. For the uniform distribution (also known as the rectangular distribution), we determined only the minimum and maximum values from our data sets.

Table 4.2. Examples of stochastic models, their inclusion of correlation structure, and use of statistical distributions for varying transition elements.

correlation among vital rates	distribution	species or study	citation
none	normal	comparative study	Guerrant 1996
none	truncated lognormal	giant kelp	Burgman and Gerard 1990
none	truncated normal	various, comparative	Menges 1992
none	truncated normal	*Lomatium bradshawii*	Kaye et al. 2001
none	truncated normal and lognormal	*Yoldia notabilis*	Nakoaka 1997
none	gamma	Chinook salmon	Ratner et al. 1997.
none	uniform	*Pediocactus paradinei*	Frye 1998
none	uniform	*Astragalus cremnophylax*	Maschinski et al. 1997.
none	observed/ discontinuous	red-cockaded woodpecker	Maguire et al. 1995
perfect positive correlation	lognormal (truncated for survivals)	spotted owl	Akçakaya and Raphael 1998
perfect positive correlation	truncated normal	*Totoaba macdonaldi*	Cisneros-Mata et al. 1997.
perfect positive correlation	uniform	*Euphorbia clivicola*	Pfab and Witkowski 2000
as observed	beta	Desert tortoise	Doak et al. 1994
as observed	beta	*Hudsonia montana*	Gross et al. 1998
retained within whole matrices	bootstrap (matrix selection)	jack-in-the-pulpit	Bierzychudeck 1982
retained within whole matrices	bootstrap (matrix selection)	*Gentianella campestris*	Lennartsson 2000

The method of matching moments was used to fit the beta and gamma distributions to our data because observed values contained zeros and ones in for some transitions. 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 these values would necessitate dropping entire matrices if we were to compare element selection with bootstrapping of observed whole matrices, 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.

Correlation among vital rates. For all distributions except the bootstrap, we used the method of Fackler (1999) to generate dependent random variables (e.g., matrix elements such as recruitment, vegetative plant growth, stasis of reproductive individuals, etc.) with the marginal distributions we selected. The pairwise dependence of the variables was specified by an observed correlation matrix for each population. Even though our sample sizes were relatively low (4-9) for estimating correlations, they were typical (if not large) for demographic studies of rare species. The key to this technique is to specify the correlation matrix using a non-parametric correlation measure that is not sensitive to monotonic transformations of the variables (Fackler 1999). This method is equivalent to the normal copula (Fackler, personal communication), and appears to be similar to that proposed by Iman and Conover (1982) and reviewed in Haas (1999). It does not seem to have been implemented previously in the context of stochastic matrix models. Copulas are functions that describe the relationship between variables based on their joint dependencies and marginal distributions (the reader is referred to Genest and MacKay 1986 and Nelson 1999 for introductions to copulas). We used Spearman rank correlation coefficients (R_s) (which, for the joint normal distribution, are associated with the Pearson fractile correlations [C] by $C=2\times\sin[\pi/6\times R_s]$), because they are not sensitive to non-linear transformations of the variables, while Pearson product moment correlations are. This method involves generating a set of correlated normal variates, through use of the Cholesky decomposition of C, which are then transformed to have uniform marginals. The desired inverse probability transform is then applied to each variate individually, thus retaining the fractile correlation structure. One convenient feature of this approach is that individual variates may be transformed to different marginal distributions and still maintain the specified correlation structure, which accommodates our use of the gamma distribution for recruitment and the same or other distributions for transition probabilities. Use of the Cholesky function requires that the correlation matrix be positive semidefinite, which was not always the case in our data sets (possibly because some correlations could be derived from linear combinations of others). Therefore, we applied a ridge correction to the correlation matrices prior to their use by adding a value equal to the minimum eigenvalue of each matrix. In all cases, this value was extremely small (#10^{-16}), and resulted in no detectable corruption of the realized marginals or correlations.

Maintaining correlation structure for the bootstrap method was treated as a special case. Instead of selecting correlated variates using Fackler's (1999) method, we selected whole observed matrices from among the observed data sets. This technique of incorporating environmental stochasticity is also known as matrix selection (Chapters 2 and 3), and preserves the observed association of matrix elements (Greenlee and Kaye 1997, Menges 2000, Kaye et al. 2001).

Analysis

Tests for effects of correlation, input distributions, and study species. We tested for effects of correlation among vital rates, input distributions, species, and interactions among these factors using SAS proc mixed (SAS Institute, Inc. 1990). Use of raw estimates of λ_s as a response variable posed a difficulty because we were likely to detect species effects simply because some species may have had stronger or weaker population growth rates. Further, we were interested in the relative effects of these methods more than their actual estimates of mean λ_s. Therefore, we chose as a response variable the proportional change in λ_s when correlation among elements was included. We considered this response variable to be structured in a split plot design, with species as the whole plot.

Detecting bias in mean $\mathbf{R}_s$. Our procedure of constraining survival to #100% was applied to each column of a matrix independent of the other columns after random values were drawn. This procedure introduced the possibility of altering the correlation among the transition elements in unpredicted ways. To test for bias to the Spearman rank correlation coefficients, we compared the mean R_s of each transition element in the observed data sets with simulated results for each species. First, we used the distributions and correlation method described above to generate 1000 random matrices from each population. Second, we calculated the mean R_s for each of these sets. Third, we calculated the difference between the mean observed R_s and the simulated R_s as an estimate of bias. Mean estimates of bias for each species were then evaluated for significant difference from zero and from one another using ANOVA.

Explaining variation in effects of correlation. The magnitude and direction of correlations are both important aspects of the overall correlation structure among the vital rates in a transition matrix. In theory, as the correlation among elements increases, so to will its effect on population dynamics. This effect, however, will be controlled, at least in part, by the sign of the correlations, with positive and negative correlations cancelling each other out. From the observed correlation matrices for each of our study populations, we calculated 1) the mean absolute value of R_s ($|R_s|$), 2) the difference between the absolute value of the mean positive and negative R_ss (0_{posRs}&$|0_{negRs}|$), and 3) the ratio of the number of positive to negative correlations. The first is a measure of overall correlation strength, such that as the magnitude of correlations increase, average $|R_s|$

increases as well, regardless of correlation sign. The other two are indices of the balance between positive and negative correlations. For example, if the strength of positive correlations is exactly matched by negative correlations, their difference will be zero. But if negative correlations are stronger than the positives, the difference will be less than zero (and vice versa). Similarly, if negative R_s outnumber positive R_s, their ratio will be less than one (and vice versa). We performed a stepwise multiple regression with mean proportional change in λ_s due to correlation for each species as the dependent variable, and mean $|R_s|$, difference between mean positive and negative R_s, and ratio of positive to negative R_s as the potential explanatory variables.

Correlation between techniques. Even if combining dependencies among transition elements with the various techniques for incorporating stochasticity results in different estimates of λ_s, we would like to know if the various methods yield relatively similar results. That is, if one population has a higher estimated λ_s than another as measured by one stochastic method in combination with correlation among vital rates, is it also higher as measured by a different method? Does this relationship change if correlation structured is omitted? To measure their degree of association, we correlated estimates of λ_s from each method of including temporal variability using the Pearson product moment (R), and this procedure was repeated for estimates with and without correlation among vital rates.

RESULTS

Effects of correlation, input distributions, and study species

The effect of including correlation among vital rates on estimates of λ_s differed between study species (*P*=0.0101) but not among the various statistical distributions and methods used to incorporate stochasticity (*P*=0.1209), and there was no interaction between these terms (*P*=0.1147) in a split-plot ANOVA (Table 4.3). The significant effect of species in this model can be interpreted as an interaction between species and correlation effects on estimated λ_s. Estimates of λ_s were significantly lower when correlation was included than when it was omitted from the stochastic models for two of the five species examined here (Figure 4.1, note asterisks). Including observed correlation among transition elements reduced estimates of λ_s by 1.7% on average for *A. tyghensis* and 3.0% for *L. bradshawii*, but there was no detectable effect in three other species. The magnitude of this effect was greatest in *L. bradshawii* and least in *C. elata* and *H. radiatus*, and intermediate in *A. tyghensis* and *L. cookii*.

Bias in R_s

A small, but significant, positive bias was detected among the correlation coefficients in our simulated matrices relative to the observed R_s. The strength of this bias differed among species, ranging from an average of 0.012 in *H. radiatus* to 0.047 in *C. elata*, and was significantly different from zero (*P*#0.0001) in each case (Figure 4.2).

Table 4.3. Split-plot ANOVA for the effects of statistical distribution of input variables and species on the proportional change in λ_s when correlations among vital rates are included (NDF and DDF are numerator and denominator degrees of freedom).

source	NDF	DDF	Type III *F*	*P*
whole plot				
species	4	22	4.3	0.0101
subplot				
distribution	4	88	1.88	0.1209
interaction				
species×distribution	16	88	1.51	0.1147

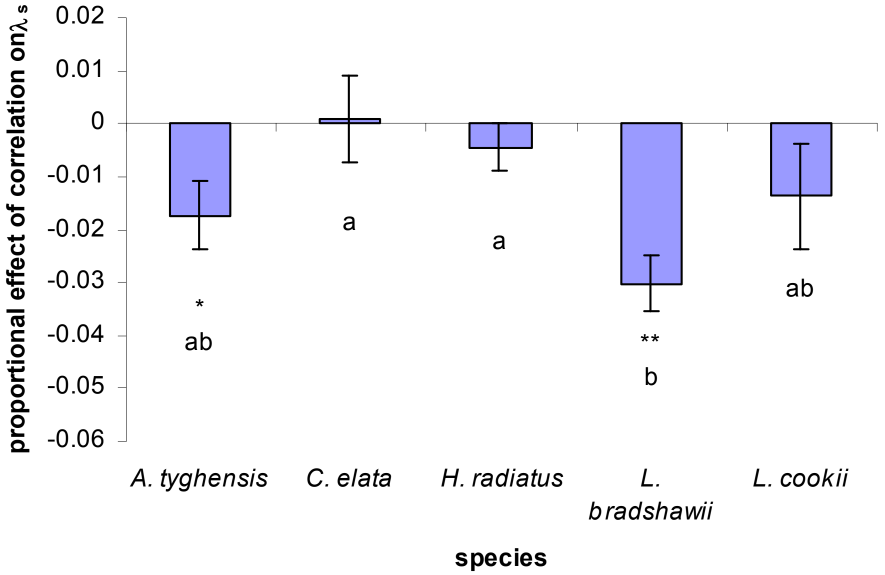

Figure 4.1. Mean (±1 SE) proportional effect of correlation on stochastic growth rate (λ_s) for five plant species. Bars with the same letter do not differ at the 0.05 level of probability (Fisher's protected LSD) and asterisks indicate significant difference from zero (*0.05>P\$0.01, **P#0.0001).

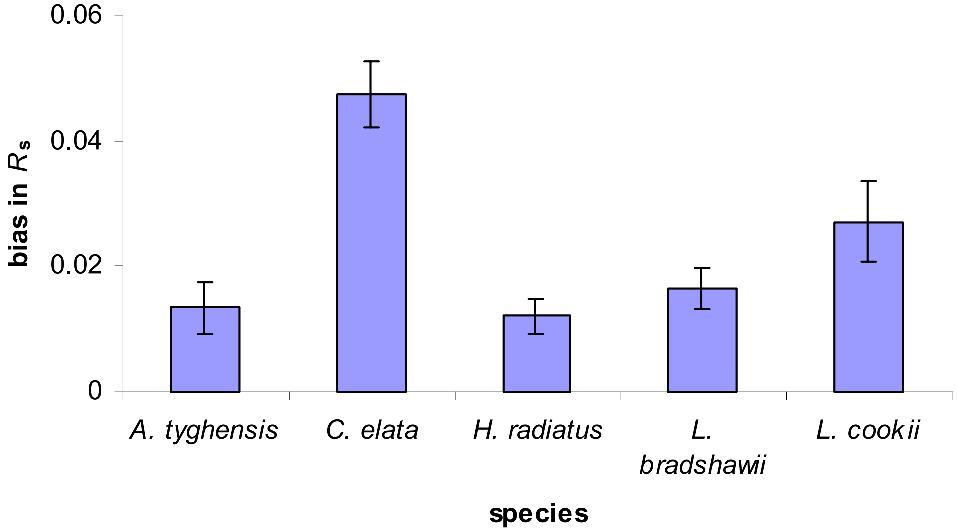

Figure 4.2. Mean (±1 SE) bias in Spearman rank correlation coefficients (R_s) for each of five plant species examined. Bias was defined here as the average difference between mean observed and simulated R_s.

Effects of correlation strength and sign on stochastic growth rate

The average absolute value of R_s ranged from 0.35 in *H. radiatus* to 0.51 in *L. cookii* (Figure 4.3, top), while the average difference between mean positive and negative R_s was closest to zero in *L. bradshawii* (0.001) and most negative in *H. radiatus* (-0.044) (Figure 4.3, center). Negative R_s outnumbered positive R_s by a ratio of 0.930 in *L. bradshawii* to 0.858 in *H. radiatus* (Figure 4.3, bottom). In stepwise multiple regression with proportional effect of correlation on λ_s as the dependent variable, the only factor in the final model was the ratio of the number of positive to negative R_s (Figure 4.4). The final model explained 95.6% of the variability in correlation effect (P=0.0026), and took the form:

$$\text{proportional effect of correlation on } \lambda_s = 0.392 \times [\text{no. positive:negative } R_s] - 0.335$$

In separate regressions, the proportional effect of vital rate correlations on λ_s was also associated with the difference between mean positive and negative R_s at (R=0.84, P=0.075), but the linear association of this factor with the ratio of positive to negative R_s (R=0.89, P=0.044) prevented it from entering the stepwise regression model. There was no significant association between effect of correlation on λ_s and mean $|R_s|$ either alone (R=0.22, P=0.73), or as part of a larger regression model.

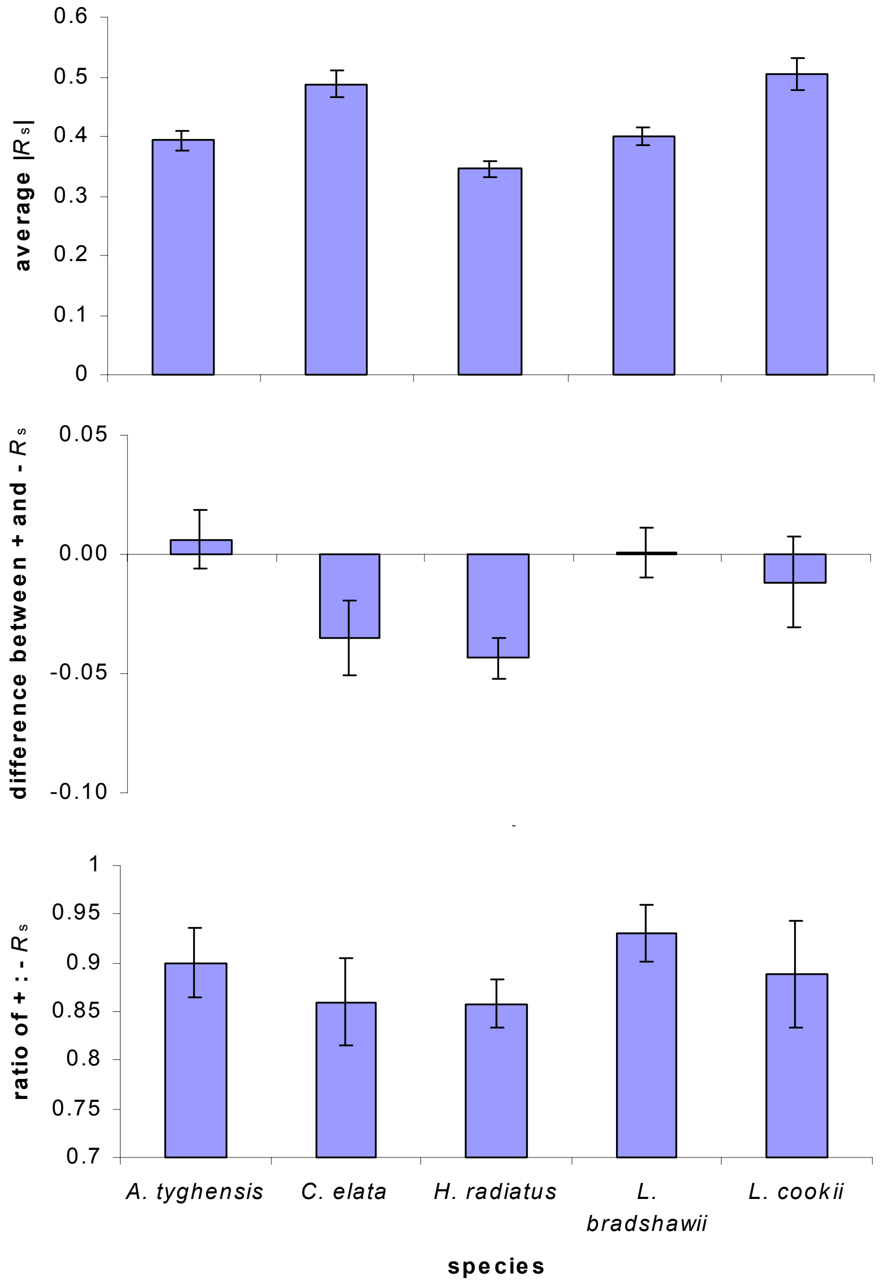

Figure 4.3. Mean (±1 SE) absolute value of observed correlation coefficients (|R_s|, top), difference between mean positive and negative R_s values (middle) and ratio of number of positive to negative R_s (bottom) for each of five species included in this study. For the ratios, when negative correlations outnumber positives, the value is less than 1.

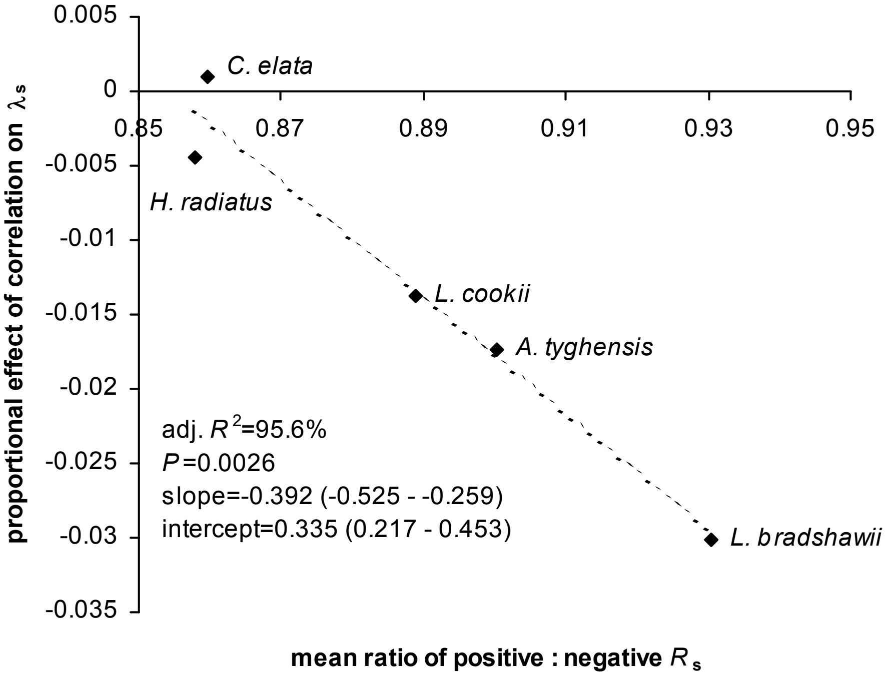

Figure 4.4. Mean ratio of positive to negative R_s values vs. proportional effect of including correlation structure on estimates of stochastic growth rate (λ_s). Ratios less than 1.0 indicate that negative correlations outnumber positive values. The fitted linear regression line (dashed) and model parameters are also shown.

Correlation among techniques

Most estimates of λ_s were highly and significantly correlated. When correlation among vital rates was included in the models, the various statistical distributions yielded estimates of λ_s that were correlated between R=0.847 (uniform vs. beta) and R=0.993 (bootstrap vs. truncated gamma) (Table 4.4, above diagonal, all P#0.0001). When correlation among elements was excluded (Table 4.4, below diagonal), association among estimates of λ_s from the various techniques ranged from R= 0.843 to R=0.980 (P#0.0001), except for correlations involving the bootstrap method, which were much lower (R=0.579 to 0.703, P#0.0016). Within each statistical distribution, estimates of λ_s derived with and without correlation structure were also highly correlated (R=0.973-0.988) (Table 4.4, diagonal).

DISCUSSION

Correlations among vital rates

Including correlation among vital rates in stochastic matrix models significantly reduced estimates of population viability in two plant species, but no effect was detected in three others examined here. Adding correlation to the models resulted in an average 1.7% decline in estimated λ_s in *A. tyghensis* and a 3% reduction in *L. bradshawii* (Figure 4.1). Effects of correlation were not significant in *C. elata*, *L. cookii*, or *H. radiatus*. Our modeling correlation structure resulted in very little bias to the correlations (Figure 4.2). Although published comparisons of stochastic models

Table 4.4. Pearson correlation coefficients (*R*) for estimates of stochastic population growth rate (λ_s) derived from five methods of incorporating environmental stochasticity. Correlations with λ_s calculated by including correlation structure are above the diagonal (*P*#0.0001), while those estimated without correlation structure are below (*P*#0.0016). Values on the diagonal (in bold) are correlations between λ_s estimates with and without correlation structure (*P*#0.0001 in all cases).

Stochastic method	bootstrap	uniform	truncated normal	truncated gamma	beta
bootstrap	**0.973**	0.884	0.991	0.993	0.975
uniform	0.579	**0.985**	0.920	0.874	0.847
truncated normal	0.626	0.974	**0.986**	0.990	0.964
truncated gamma	0.703	0.884	0.944	**0.988**	0.978
beta	0.638	0.843	0.904	0.980	**0.980**

with and without cross-correlations among transition elements are few, their conclusions are in general agreement with ours. For example, population simulations with *Totoaba macdonaldi* using both a diffusion approximation approach and Monte Carlo methods found that inclusion of correlations among vital rates tended to increase extinction risk (Cisneros-Mata et al. 1997). In that study, the authors assumed perfect positive correlations in their comparisons. For most species in natural stochastic environments, however, correlations among matrix elements may include many negative values and are rarely, if ever, perfect, as in herbaceous plants such as *Calathea ovandensis* of Mexican rainforests (Horvitz and Schemske 1995) and *Gentiana pneumonanthe* of Scandinavian heathlands (Oostermeijer et al. 1996). Doak et al. (1994) found that adding observed correlations (which included both positive and negative values) to their desert tortoise model increased variability in mean growth rate and population size estimates after 25-50 years. Presumably this increase in variability would translate into a reduction in estimates of population viability, although they did not test this explicitly.

Our analysis suggests that the effect of correlations among vital rates on stochastic matrix model outcomes depends on the nature and type of correlations present, and this differs among species. The average ratio of the number of positive to negative correlations among vital rates was an excellent predictor (adj. R^2=95.6%) of the proportional change in stochastic growth rate among species due to inclusion of these correlations (Figure 4.4). This measure of correlation structure is simple to calculate and represents the relative distribution of positive and negative correlations across all vital processes. There was an indication that the relative strength of positive vs. negative correlations ($0_{\mathrm{pos}Rs}\&|0_{\mathrm{neg}Rs}|$) was also important in explaining this variation, but its function was weaker (adj. R^2=60.1%, P=0.075) and it was not included in the regression model after a stepwise procedure. We were surprised that the average strength of correlations was not a significant factor in explaining variation among species in mean λ_s, because stronger correlations should, in theory, result in a greater effect (Tuljapurkar 1982). It may be that inclusion of a greater number of species could elucidate these relationships by encompassing life histories with a greater range in absolute and relative correlation strengths. Even so, it is clear that the relative mix of positive and negative correlations among model parameters is an important aspect of correlation structure. Ferson and Burgman (1995), using various hypothetical correlation structures in a stochastic model for Leadbeater's possum, found that estimates of extinction probability increased or decreased depending on whether correlations were positive, negative, or mixed, and whether dependencies were linear or non-linear. The simplistic assumption of complete positive correlation used in some models (e.g., Table 4.2) may yield overly pessimistic estimates of population viability. We suggest that if inclusion of correlation structure is desired, empirically derived correlations should be incorporated over hypothetical structures.

Correlation structure is clearly a complex factor in population models (Tuljapurkar 1982), and its effect on model results will differ among species and life histories (Orzack 1993, 1997). Although omitting correlation structure, as many authors of population viability models have done (e.g., Table 4.2), may appear to be a hazardous assumption, it may have little effect on results of PVAs in some species due to the balancing effect of positive and negative correlations. Even in our most extreme case, *L. bradshawii*, in which the average 3% decline was statistically significant, its biological significance was less obvious, and conservationists will have to decide for themselves what magnitude of effect on viability is important. Within a given technique for incorporating environmental stochasticity, estimates of λ_s derived with and without cross-correlation among elements were strongly correlated (*R*$0.973), suggesting that for purposes of assessing the relative differences among populations or management actions, inclusion of correlation structure may be of little significance.

Input distributions

The effects of correlation structure did not depend on which method we used to incorporate stochasticity into the transition matrix models (Table 4.3). Including correlation structure had the same effect on estimates of λ_s for each species regardless of whether stochasticity was driven by a bootstrap method, or parametric distributions such as the beta, truncated gamma, truncated normal, or uniform. Some authors (e.g., Menges 2000) have noted that the bootstrap method of shuffling whole observed matrices (matrix selection) could exaggerate correlations among vital rates, but we found no evidence that stochastic method altered the effects of correlation.

Even though stochastic method did not alter the effects of correlation structure, different input distributions can have significant effects on estimates of population viability. For example, we found (in Chapter 3) significant differences in estimates of λ_s among bootstrap, beta, truncated gamma, truncated normal, uniform and triangular distributions of transition rates for incorporating stochasticity. In the present study, we found a close association (*R*=0.847-0.993) in estimates of λ_s among various input distributions when correlation among vital rates was included. However, in the absence of correlation structure, associations between the bootstrap method and each parametric method were weaker (*R*=0.579-0.703). These correlations are lower than those observed in Chapter 3 (*R*=0.849-0.990) with the same data sets and similar modeling procedures. The primary difference between methods in these two studies was that, in the current case, we allowed recruitment to vary (via the bootstrap or gamma distribution) while it was held constant in the previous study. Apparently, stochasticity in recruitment can have a substantial effect on estimates of λ_s, possibly interacting with the choice of distribution shape used to model transition probabilities. Nakoaka (1997), for example, found that lognormal and truncated normal distributions for varying recruitment in clam population models yielded estimates of λ_s that differed significantly. Our results suggest that if correlation is included among all vital rates, and transitions and recruitment vary stochastically, then estimates of population viability may differ among stochastic methods but their relative rankings will not.

This is relevant because conservationists have expressed concern that viability analyses yield results so sensitive to model parameters that any conclusions are uncertain, if not misleading. We agree with Beissinger and Westphal (1998) and Menges (2000) that the strength of viability analysis lies in its use as comparative tool rather than a means of precisely assessing the health of individual populations. 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 analysis 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 populations appears to be fairly robust to differences in stochastic methods, especially when correlation structure is included.

Conclusion

Temporal correlation among vital rates in our stochastic matrix models altered estimates of population viability, but this effect differed among species and was generally weak. The magnitude of change in estimated λ_s for each species examined here was largely explained by the ratio of positive to negative cross-correlations of transition matrix elements; as the relative number of negative correlations decreased, the impact of correlation structure increased. When deciding whether or not to include such correlation structure in viability models, conservationists may want to examine the correlations in their species as a means of assessing their anticipated effect, and we have provided a tentative linear regression model for doing so. Examples of stochastic matrix approaches that incorporate correlations are few, but we hope our illustration of a straightforward method based on rank correlations will encourage others to include this aspect of stochastic population dynamics in future models where correlation is deemed important. Our implementation, which was based on an approach described by Fackler (1999), is only one of a variety of methods that may be useful for this purpose, and the extent to which correlation technique affects model results deserves further attention. The use of copulas in functions for generating multivariate random numbers may be particularly fruitful (Haas 1999, Frees and Valdez 1998), especially because of their ability to accommodate non-linear dependencies (Embrechts et al. 1999 and in press) and a mixture of statistical distributions for different vital rates.

We found no interaction between inclusion of correlation structure and various distribution shapes for incorporating stochasticity. Stochastic method may, however, have significant effects on estimates of λ_s, which can lead to differing conclusions regarding the health of a given population. When correlation structure is maintained in stochastic models, the estimates of λ_s are generally highly correlated, suggesting that PVA should stress comparisons between populations over quantitative estimates of population health. Incorporating stochasticity into matrix models through bootstrapping whole observed matrices (matrix selection) may be preferable in many cases because the method appears to be relatively conservative and does not bias transition elements (Chapter 3). In addition, it does not bias correlation structure and its results do not appear to differ substantially from other methods of including correlation.

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