

## Chapter 5. Conclusion

### A BRIEF REVIEW OF MATRIX MODEL APPLICATIONS

Transition matrix models have proven to be an enormously versatile application of population biology theory to the study of ecological dynamics. They have been used primarily to describe and forecast the population processes of individual species, including animals and plants. Some notable applications illustrating the diversity of species and life histories the models have been applied to are plants, such as *Pedicularis furbishiae* (Menges 1990), giant kelp (Burgman and Gerard 1990), clams (Nakoaka 1997), red cockaded woodpeckers (Maguire et al. 1995), salmon (Ratner et al. 1997), and possums (Ferson and Burgman 1995), including both stage- and age-classified population structures, and even density dependence (Jensen 1995, Ginzburg et al. 1990).

But ecologists have recently taken these structured models beyond description of species dynamics to a wide range of applications, such as theoretical (Chau 2000) and applied harvest scenarios for wildlife (Kokko and Lindstrom 1998), medicinal plants (Nantel et al. 1996), and economically useful palms (Olmsted and Alvarez-Buylla 1995); effects of disturbance on plant species (Giho and Seno 1997, Seno and Nakamijo 1999, Chapter 2); invasion dynamics of exotic species (Parker 2000) and impacts of biocontrol agents (Shea and Kelly 1998, McEvoy and Coombs 1999); metapopulation dynamics (e.g., Akçakaya and Raphael 1998); and description of host-pathogen (Yang et al. 1997) and predator-prey systems (Kittlein 1997). The scale of applications has ranged from the

dynamics of individual plant parts, such as demography of buds on birch trees (Maillette 1982), to dynamics of moss communities on decaying wood (Kimmerer 1993), forest tree succession (Osho 1996, Lin and Buongiorno 1997, Kolbe et al. 1999, Logofet 2000), and vegetation dynamics in general (Balzter 2000). Recent novel uses of matrix models in conservation biology have included developing recovery (Aplet et al. 1994) and reintroduction (Guerrant and Pavlik 1998) strategies for rare plants and animals (Heppell et al. 1996) and inclusion of genetic factors such as inbreeding depression (Oostermeijer 2000, Menges and Dolan 1998). Elasticity analysis, a type of sensitivity analysis possible with matrix models, has been of great value in population management and studies of life history evolution (e.g., Heppell et al. 2000).

## **GOALS AND CONCLUSIONS OF THIS DISSERTATION**

The addition of stochasticity to matrix models makes possible the assessment of probabilistic events, such as extinction, and this has made transition matrices one of the most important tools available for population viability analysis. Even so, many unanswered questions about the application of matrix models to field-collected demographic data have remained. For example, do different methods of including stochasticity in matrix models affect estimates of extinction probability and stochastic population growth rate? Do different methods of constraining stage-specific survival to  $\leq 100\%$ , a seemingly trivial but surprisingly important problem, affect these results? Does the inclusion of correlation among vital rates, such as recruitment, stasis, and

growth, affect estimates of population viability? If so, what aspects of correlation structure are important? And finally, if these methods yield divergent estimates of population viability, do they at least result in similar rankings of populations or treatments?

In this dissertation, I have attempted to demonstrate the usefulness of the matrix model technique and answer these questions through a case study and comparative analyses of stochastic methods. These analyses have emphasized the use of empirical observations at every step, so that the results will have the greatest utility to those interested in applied population and ecological models. I have also intentionally avoided extensive use of mathematical notation in hopes that the material presented will be as accessible as possible to ecologists with little formal mathematical training, but who desire to organize their field observations into a synthetic ecological model.

Use of a stochastic modeling approach showed that the effect of fire on the population viability of *Lomatium bradshawii* was clearly positive, and this effect was consistent across two study sites, two response variables, and through two different stochastic methods (Chapter 2). Increasing fire frequency reduced extinction risk and increased stochastic population growth rate, both measures of population viability, at both Rose Prairie and Fisher Butte. Precise estimates of these response variables differed slightly in some cases, but their relative ranking among fire treatments remained the same.

These conclusions set the stage for in-depth evaluations of the effects of stochastic techniques on estimates of population viability. Using field observations from

27 populations of five species, *Astragalus tyghensis*, *Cimicifuga elata*, *Haplopappus radiatus*, *L. bradshawii*, and *L. cookii*, collected over a period of five to ten years, I performed a series of comparisons of methods used to incorporate stochasticity into stage-based models for population viability analysis. Different methods of incorporating stochasticity (i.e., matrix selection vs. various statistical distributions for varying transition elements) and constraining stage-specific survival to #100% (resample vs. rescaling procedures) yielded substantially divergent estimates of stochastic growth rate, and there was a significant interaction between these methods (Chapter 3). Most of the variation in growth rate estimates was explained by bias in mean transition element values (weighted by their elasticities), such that methods that caused a reduction in average transition rates also reduced estimates of stochastic growth rate. There was no effect of study species on these results, suggesting that the conclusions are widely applicable, at least among perennial plants and possibly across a variety of organisms.

Incorporating correlation among transition elements caused a significant reduction in estimated stochastic growth rate in only two of five species examined (Chapter 4), and the maximum mean reduction (*L. bradshawii*) was only 3%. There was no interaction with stochastic method in this effect. Much of the variation in average response to correlation structure among species was due the relative balance between positive and negative associations among the vital rates. For example, as the number and strength of negative correlations increased, they tended to overwhelm the effects of positive correlations. Positive correlations are known to increase stochasticity and therefore reduce stochastic growth (Tuljapurkar 1982, Orzack 1997), so the presence of

so many negative correlations buffer populations from the stochastic effects of positive correlations. Therefore, it may be possible for population modelers to assess the importance of correlation structure in their target species prior to making the substantial effort to include it by evaluating the relative strength and number of positive and negative associations among their observed matrix elements.

In Chapter 2, no correlation structure was modeled in the element selection technique, despite the fact that I later learned correlation may be important in that species. Even so, the relative results of the matrix and element selection methods for estimating extinction probability and stochastic growth rate were qualitatively similar, an important point stressed in each of the chapters of this dissertation.

One question that may be worth pursuing with regard to correlation structure is, do species with different relative amounts of positive and negative correlations differ in their success or vulnerability to stochastic environments? For example, do invasive species have correlation structures with a higher rate of negative associations among vital rates that could buffer them against stochasticity or even give them an advantage over non-invasive species? Similarly, do rare species have more positive correlations among vital rates than their common congeners, and could this help explain their rarity? Could environmental stochasticity interact with the correlation structure of a species to determine its relative success over different portions of its range? To what extent do the correlation structures of species influence the composition of plant communities in habitats of differing degrees of environmental stochasticity? These and questions related to the evolution of correlation among vital processes may deserve further attention.

Perhaps the most important and consistent result of this dissertation is that, although alternative techniques may lead to very strong differences in estimates of population viability (differing by up to 18%), conclusions about the relative ranking of populations or treatments are robust to differences in stochastic methods (Chapters 2, 3 and 4). I observed very high correlations between most stochastic methods and their estimates of stochastic population growth rate. This adds considerable strength to the argument that viability analysis should be used as a comparative tool (as in Chapter 2) rather than a means of assessing the health of individual populations (Beisinger and Westphal 1998, Menges 2000). Quantitative estimates of extinction probability, for example, may be subject to wide margins of error (Ludwig 1999, Fieberg and Ellner 2000), but the qualitative ordering of populations in terms of viability estimates may not.

## **CONSIDERATIONS FOR STOCHASTIC MATRIX MODELERS**

In the future, practitioners of population viability analysis that use transition matrix models should consider the issues raised by this dissertation. In general, if sufficient data are available to implement a stochastic analysis with matrix selection, this technique may be preferred. It has the advantage of requiring no survival constraint correction, no assumptions about the distribution of the matrix elements (aside from the weighting of each matrix, which is generally assumed to be equal), and it includes correlation structure implicitly, as long as each matrix represents observed data from a single population in a single year.

If element selection is necessary, and it may be if there are areas of missing data or observations of various vital processes are pooled from a variety of sources or studies, then more assumptions will be required. For example, survivals will have to be constrained to #100% (unless the model is age-based), and I recommend the rescaling procedure described in Chapter 3. Other techniques may either cause substantial bias (such as resampling, Chapter 3) or be excessively cumbersome (as in Gross et al. 1998). Because available data are typically insufficient to test for a fit to a statistical distribution, one must be assumed. If a survival constraint method with low bias is used, the beta and truncated gamma distributions may be good choices of parametric distributions, as might the bootstrap (or observed/discontinuous), because results using these distributions are generally in close agreement with each other and with matrix selection. Finally, including correlations among vital rates may be desirable, but this will depend on the study system. Fortunately, new tools are now available for modeling correlation structure, and modelers can evaluate the likely importance of correlations for their data set simply by counting the number of positive and negative correlations and applying the linear regression model presented in Chapter 4. Careful consideration of these issues and selection of appropriate modeling techniques will improve the quality of population models and their results. Despite these warnings and words of advice, even if the quantitative predictions of stochastic matrix models differ substantially due to differing model assumptions, the qualitative results are very robust to differences in model implementation. Population models are most useful as comparative tools rather than predictors of future conditions.