EXERCISE 14

USING STOCHASTIC MODELS TO INCORPORATE SPATIAL AND TEMPORAL VARIABILITY

In this exercise, you will learn how to:

1. describe differences between deterministic and stochastic population models.
2. describe the structure and organization of a stage-based, stochastic population viability analysis model.
3. execute ("run") a stage-based, stochastic population viability analysis model, and correctly interpret its output.
4. make an assessment of population viability and uncertainty of population estimation using a stage-based, stochastic population viability analysis model.
5. add effects of environmental stochasticity to a stage-based, stochastic population viability analysis model.

BACKGROUND AND RATIONALE

To this point, our analysis of population processes and viability in the western prairie fringed orchid has used only *deterministic* models. In this exercise, we conduct a similar analysis, using a *stochastic* model instead. This distinction is of great importance to population biology in general and to conservation biology in particular. In deterministic models, transition probabilities are held constant throughout the projected time period, and populations are allowed to increase without bound (Beissinger and Westphal 1998). Deterministic models are mathematically convenient, but biologically unrealistic. As population biologist Robert Lacy has noted, "With the exception of aging, almost all events in the life of an organism are stochastic" (Lacy 1993).

By their very nature, natural events are stochastic. That is, they change randomly over time. For example, refer back for a moment to Assignment 12.C, Calculating Population Data, and look at the table in which you calculated the transition probabilities for a vegetative plant to become a flowering plant. Note that this probability changes from year to year—that is, the rate of transition from vegetative plants to flowering plants is a stochastic event. Stochastic models are those that allow model elements to vary randomly through time, like this vegetative-to-flowering plant transition rate in the orchid. Precisely for that reason, stochastic models, if properly constructed, may more accurately represent demographic events of most species. In general, because stochastic models allow natural events to fluctuate randomly (as they actually do), they can reduce the number and need of rigid, and often unrealistic, model assumptions. For example, in this population, the stochastic model need not assume that "average" conditions occur every year, or that rates of transition from vegetative to flowering plants always occur at "average" rates. Further, stochastic events are especially important in small populations because deviations from "average" values of demographic or environmental conditions can move small populations below critical numerical thresholds, from which they may not recover.

To incorporate the array of variation in nature that can influence population growth, stochastic models contain many elements that deterministic models do not. For example, stochastic models incorporate the variability inherent in annual rates of reproduction and death (demographic stochasticity) as well as climatic changes, such as wet and dry years (environmental stochasticity), which in turn influence demographic rates. Further, stochastic models often incorporate the concept that habitats have a *carrying capacity;* that is, there is a limit to the number of individuals that the habitat can support. A "population ceiling" may be invoked in the model to designate an upper numerical limit beyond which the population cannot grow (Burgman et al. 1993). Stochastic models may also incorporate probabilities for uncommon environmental events (catastrophes) that have disproportionately severe effects on population size.

Before going further, answer these questions:

1. Conceptually, how would you model environmental stochasticity? How would you model demographic stochasticity? In each case, what variables would you allow to fluctuate randomly?

2. Would you model catastrophic events as special cases of environmental stochasticity, or would you model them as a separate category of events? In either case, which variables would you allow to fluctuate?

DEMOGRAPHIC AND ENVIRONMENTAL STOCHASTICITY IN THE WESTERN PRAIRIE FRINGED ORCHID

In exercises 12 and 13, which use deterministic models, we have employed average, fixed values for model variables. But every average that is derived from many, varying observations of the same variable also has a *standard deviation*, or an average ("standard") difference between the value of each observation and the value of the mean. The program we have been using can incorporate these standard deviations in the analyses.

In this exercise, we use the standard deviations associated with the transition matrices introduced in exercise 12 to explore how the incorporation of variation influences projected population levels for the western prairie fringed orchid. Specifically, we incorporate standard deviations associated with aboveground demographic transitions of the western prairie fringed orchid, allowing us to place confidence intervals around our population projections. In addition, we impose a ceiling on the maximum population of flowering orchids, and use 1,000 iterations of the model so that an average percentage of population projections of less than 50 individuals can be calculated. Assuming that populations of fewer than 50 individuals have a low probability of persisting, this estimate will provide us with a measure of the probability of "quasi-extinction." Finally, to make the model even more realistic, we also project population growth rate and persistence under varying probabilities of average, wet, and dry conditions.

Assignment 14.A: Running a Stage-Based, Stochastic Population Viability Analysis Model

1. Open the EXCEL workbook that you have used previously in exercises 12 and 13. As before click on "Enable Macros" when prompted.
2. Switch to the exercise 14 worksheet.
3. Click on the Tools pull-down menu, and choose "Macro."
4. Select "Macros," then "PVAStage," then "Run."
5. PVA Stage will ask for:
   a. *Length of time sequence*: Type "22."
   b. *Stage names*: Either highlight column A, rows 4 through 8, or type "a4:a8."
   c. *Stage parameter for lambda calculations*: Select "flowering plants."
   d. *Initial values*: Either highlight column B, rows 4 through 8, or type "b4:b8."
   e. *Ceiling values*: Either highlight column D, rows 4 through 8, or type "d4:d8." In this model, our specified ceiling of 8,000 plants is based on observations in a wet year when more than 5,000 orchids were counted.
   f. *Specification of first Lefkovitch matrix*: Highlight the average matrix (b14:f18)
   g. *Specification of the next matrix*: Select "Cancel."
   h. *Specify element standard deviations?* Select "Yes."
   Now scroll down and select the standard deviation matrix for the average conditions (b38:f42).
   i. *Specify number of random iterations of matrix elements:* Type "1000," or select "Cancel."
   j. *Specify a random number seed for matrix elements*: Select "13579." Specifying this seed will standardize the results, but you can also specify another seed, or use the computer system clock.
   k. *Monitor minimum threshold*: Select "Yes."
   l. *Specify minimum threshold for flowering plants*: Type "50."

We will arbitrarily select 50 flowering plants as a quasi-extinction level.

6. The program now provides a summary of the model specifications. Make sure it says:
   Sequence length is 22
   Stage names from Exercise 14!A4:A8
   Initial stage parameter values from Exercise 14!B4:B8
   Stage ceiling values from Exercise 14!D4:D8
   Lefkovitch matrices from Exercise 14!B14:F18
   Lefkovitch SD matrices from Exercise 14!B38:F42
   1000 random iteration(s) of matrix elements, with element seed = 13579
   Minimum threshold of 50 will be monitored for flowering plants.
7. The program now asks if you want to begin computations. Select "Yes."
8. On the next screen query ("extended results") select "flowering plants."
9. Finally, complete the execution of the model by instructing it to plot selected population parameters (select "Yes" to query "plot population parameters?", and then select "Flowering plants.")

Stop and Reflect

1. What is the terminal value of λ under average conditions?

   a. What is the projected population of flowering orchids at the end of this 22-year simulation?

   b. What percentage of the iterations at the end of 22 years fell below a minimum of 50 flowering plants?

   c. What do these values suggest about population persistence under average conditions?

2. Scroll to the bottom of the first worksheet of the output. Look up the 2.5 and 97.5 percentiles at step 22 under the "Projection summary for Flowering plants." These are the 95% confidence intervals on the projected population of flowering plants in year 22. What are the values associated with these percentiles?

3. What is the benefit of having confidence interval estimates associated with the population estimates?

ADDING ENVIRONMENTAL STOCHASTICITY

In this model, we incorporate the occurrence of three climate scenarios, based on their historic probabilities. U.S. Geological Survey data on water table levels between 1976 and 1997 indicated that average conditions occur at a frequency of 0.333, wet conditions at a frequency of 0.381, and dry conditions at a frequency of 0.286 (Hof et al. 1999). We will incorporate these probabilities into the model. That is, we will have the model randomly select one of the three matrices (average, wet, or dry) based on the probabilities of 0.333 for average, 0.381 for wet, and 0.286 for dry. Unlike the previous model, this model does not incorporate the standard deviations on demographic data.

Assignment 14.B: **Running the Model with three Climate Scenarios**

1. Open the EXCEL workbook, and click on "Enable Macros" when prompted.
2. Switch to the Exercise 14 worksheet.

3. Select the Tools pull-down menu and choose "Macro."
4. Select "Macros," then "PVAStage," then "Run."
5. PVA Stage will ask for:
   a. *Length of time sequence*: Type "22."
   b. *Stage names*: Either highlight column A, rows 4 through 8, or type "a4:a8."
   c. *Stage parameter for lambda calculations*: Select "Flowering plants."
   d. *Initial values*: Either highlight column B, rows 4 through 8, or type "b4:b8."
   e. *Ceiling values*: either highlight column D, rows 4 through 8, or type in "d4:d8."
   f. *Specification of first Lefkovitch matrix*: Highlight the average matrix, or type "b14:f18."
   g. *Next matrix*: Highlight the wet matrix, or type "b21:f25."
   h. *Next matrix:* Highlight the dry matrix, or type "b28:f32."
   i. *Next matrix*. Select "Cancel."
   j. *How the Lefkovich matrix should be selected*: Select "Random."
   k. *Selection Probability for matrix* 1: Enter "0.333."
   l. *Selection Probability for matrix 2*: Enter "0.381."
   m. *Selection Probability for matrix 3*: Enter "0.286."
   n. *Specify number of random sequences*: Type "1000" or enter "Cancel" for default value of 1000.
   o. *Specify random number generator seed for matrix selection*: Select "97531."
   p. *Do you wish to specify element standard deviations*? Enter "No."
   q. *Monitor minimum threshold*: Enter "Yes."
   r. *Minimum threshold for flowering plants*: Type "50."
6. The program will then provide a summary of the model specifications: Make sure it says:
   Sequence length is 22
   Stage names from Exercise 14!A4:A8
   Initial stage parameter values from Exercise 14!B4:B8
   Stage ceiling values from Exercise 14!D4:D8
   Lefkovitch matrices from Exercise 14!B14:F18, B21:F25, B28:F32
   Random selection of matrices with selection probabilities = {0.333, 0.381, 0.286}, 1000 random sequence(s), with selection seed = 97531
   Minimum threshold of 50 will be monitored for flowering plants.
7. *Begin computations*? Enter "Yes."
8. *Extended results*: Select "Flowering plants."
9. *Plot selected population parameters*? Select "yes."
10. Select "Flowering plants."

QUESTIONS AND ASSESSMENT

1. What is the terminal value of λ at the end of the model projection (year 22) (see cell I36)?
   a. What is the projected population of flowering orchids at the end of each of these 22-year simulations?
   b. What percentage of the iterations at year 22 was below the threshold of 50 flowering plants?
2. Scroll to the bottom of the first worksheet of the output. Look up the 2.5 and 97.5 percentiles at step 22 under the "Projection summary for flowering plants." These are the ninety-fifth confidence intervals on the projected population of flowering plants in year 22. What are the lower and upper limits of this confidence interval?
3. This model incorporated three climate scenarios that were randomly selected based on their historic probability. The results therefore provide some estimate of the affect of environmental stochasticity.
   a. Does this model also incorporate some demographic stochasticity?
   b. In what way is demographic stochasticity included?

4. Compare the outcomes of this model with the outcomes of the deterministic model you used in Exercise 12.
   a. What are the most important differences between the two model outputs?
   b. What are the most important differences in predictions that could be derived from each model?
5. Why would a researcher or manager choose one kind of model (deterministic or stochastic) over the other? Explain, as specifically as you are able, the most important differences in management and conservation implications of using deterministic versus stochastic models.

SYNTHESIS

The increased realism of stochastic models comes through the addition of uncertainty about the outcome of individual events in a population's life history. At first glance, such uncertainty may appear to be a "cost" of switching from a deterministic to a stochastic approach. No longer can the model provide a single, definitive answer or outcome. However, most conservation biologists would view such a change as a benefit because this uncertainty is itself part of the realism of population biology and part of the context in which conservation biologists must make management decisions. Population management, especially of threatened and endangered species, is in large part the management of uncertainty and risk.

The randomness, or stochasticity, that generates such uncertainty arises from multiple factors, often working interactively and synergistically. Our previous questions have been designed to guide your reflections on how such interactions may occur between demographic and environmental stochasticity, producing effects that neither would produce alone. Restoration of small populations to viable levels requires conservation biologists to successfully integrate multiple, interactive effects of many factors into their management planning process.

LITERATURE CITED

Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62:821–841.

Burgman, M. A., S. Ferson, and H. R. Akcakaya. 1993. *Risk assessment in conservation biology.* London: Chapman and Hall.

Hof, J., C. H. Sieg, and M. Bevers. 1999. Spatial and temporal optimization in habitat placement for a threatened plant: The case of the western prairie fringed orchid. *Ecological Modelling* 115:61–75.

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