Part Four

Experiences in Population Modeling and Population Viability Analysis 89

THE CONCEPT AND USE OF ELASTICITY IN POPULATION VIABILITY ANALYSIS

In this exercise, you will learn how to:

1. describe and apply the concept of elasticity in evaluating the output of a population viability analysis model.
2. identify varying levels of elasticity in different model variables, and interpret the meaning of different levels in applications for population management and further research.
3. assess interactions of demographic and environmental variation on elasticity in individual variables and transition probabilities.

BACKGROUND AND RATIONALE

As you have seen in exercise 12, plants, such as the western prairie fringed orchid, typically have distinct life stages and complex life cycles that require the matrix analyses associated with a stage-based population model. Some statistics that can be generated from such matrix analyses can be very informative in determining which variables in the model have the greatest effect on population growth rate and persistence. One such statistic is that of *elasticity*. *Elasticity analysis* is a type of sensitivity analysis that measures the effect of a variable on model outcomes (Burgman et al. 1993). The greater a variable's elasticity, the more a change in the value of the variable will change the value of λ, the population's rate of growth compared to other variables (de Kroon et al. 1986).

Recall the annual plant we discussed in assignment 12.A. During dry periods, seed germination might be very low. Plants that do emerge usually survive but produce a low number of seeds. An elasticity analysis would allow you to explore which transition had the greatest effect on the population growth rate of the annual plant: seed viability, seed germination, or seed production. Which transition do you think would have the highest elasticity in this situation? During a wet year, germination rates would be high, but seedling survival would be low due to increased competition. Therefore, the variable with the highest elasticity value might be different in a wet year than in a dry one. Such information would be helpful in designing potential approaches for enhancing the population of the plant.

Recall from our earlier discussion that good modelers always identify all possible assumptions. Elasticity shows us that, just as assumptions can be identified, they also can be ranked. The basis of this ranking resides in the fact that the sum of all elasticity values for elements in the matrix is equal to one. Thus, this property of elasticity values allows a conservation biologist to compare and rank the elasticities of different matrix elements and determine if any individual variables have disproportionately large effects on λ (Silvertown et al. 1996). Such a comparative evaluation can be useful in choosing among potential management strategies for threatened populations because our comparisons can identify which matrix element to change to provide the quickest route to population recovery (Beissinger and Westphal 1998).

Many programs used to perform population viability analyses can be used to calculate the elasticity of each matrix element. Thus, it is normally not necessary for a conservation biologist to calculate these separately. However, it is very important to understand what these elasticity values mean and how they can be used to gain insight beneficial to the population's management and persistence. To begin to gain these skills, in this exercise, you make some predictions about which transition probabilities will have the highest elasticities (that is, changes in these transitions or stages cause the largest change in λ), and why. Then you measure actual elasticities of different transition probabilities and compare them with your predictions. From this comparison, you formulate hypotheses and design experiments or management strategies that might test your explanation for varying elasticities among transition variables.

MAKING PROJECTIONS

Before making random guesses about which variable is likely to have the greatest effect on model outcomes, take a moment to think through what each variable represents in the model and the theoretical basis for why different variables may have different elasticities, and why the elasticity of the same variable might change under different conditions. Let's work through one example conceptually.

Recall that, in the western prairie fringed orchid, one life stage transition is from a seed in a state of dormancy to a seed that germinates and produces a seedling. Before you run the model, write down your answers to these questions:

1. Would small changes in rates of seed germination have proportionately large or proportionately small effects on the growth rate of the orchid population? Why?

2. Would this germination rate be environmentally sensitive? Why or why not?

Now run the model following the directions for exercise 12, but choose exercise 13 on the spreadsheet from your workbook website at www.mhhe.com/conservation As before, click on the "PVA excel file" link to reach the EXCEL workbook and click on "Enable Macros" when prompted.

Assignment 13.A: Elasticity Analysis of Model Transitions

1. Examine the model projections you produced for average conditions in exercise 12. Which transition variable has the highest elasticity?

   How does the model result compare to your *a priori* prediction?

2. Now examine your model projections for wet conditions. Which transition has the highest elasticity value?

3. Finally, examine output for the dry model. Which transition has the highest elasticity value?

Assessing Results

Recall that λ estimated for the average model was 0.97, which indicated that the population growth rate was projected to decline by 3% per year, and λ estimated for the wet model was 1.21, which indicated that the population was projected to increase by 21% per year. Is the variable with the highest elasticity value the same for both models? This is an important point to remember (Menges 2000). For the average model, with a declining growth rate, the elasticity analyses indicate that changes in the level of seed viability (proportion of seeds that remain viable in the soil) have the greatest effect on λ. For the wet model, with an increasing growth rate, the elasticity analyses indicate that changes in seed production and germination rates have the greatest effect on λ. Why do you think this difference exists?

We now use elasticity analyses to explore two questions. First, what if none of the seeds produced in a given year remain viable? And, second, what effect would increasing the seed production have on population growth rate and number of flowering orchids?

Assignment 13.B: Analyzing the Effect of zero Seed Viability

For populations with projected growth rates of < 1.0, elasticity analyses reveal that changes in seed viability have the greatest effect on population growth rates. Recall from exercise 12 that we have no data on how long seeds remain viable in the soil, but have assumed that 50% of the seeds produced in a given year are viable the following growing season. Therefore, our initial models used a seed-to-seed transition rate of 0.5. In this assignment, we assume that none of the seeds produced in a given year remain viable in the soil the following year. That is, that the seed-to-seed transition probability is zero.

Select the exercise 13 worksheet. Run a deterministic projection following the instructions in exercise 12 (see p. 98), except at step 4f, select the average matrix with seed viability reduced to zero (exercise 13, first matrix [b14:f18]).

1. What transition or stage has the highest elasticity value?

2. What is the value of λ at year 22, and what does this indicate?

3. What is the expected population size of flowering plants at year 22?

These results demonstrate that the population, in the absence of a viable seedbank, can be expected to decline by 17% per year. By year 22, the population is expected to consist of only three flowering individuals. The elasticity analyses indicate that changes in the number of seeds produced/plant and changes in the germination rates of seeds would have the greatest effect on population growth rates.

4. How might the number of seeds produced/plant be increased?

5. How might germination rates be increased?

Assignment 13.C: Analyzing the Effect of zero Seed Viability with Increased Seed Production

We again assume that seeds of the western prairie fringed orchid do not remain viable in the soil. This time, however, we increase the number of viable fruits/plant from 1.2 to 2.25.

1. Select the exercise 13 worksheet. In the second matrix, the number of viable seeds/plant has been changed to reflect an increase in the number of fruits/plant to 2.25, but still assumes an average of 21,618 seeds/fruit, of which 53% are viable. Therefore, the number of seeds produced/plant = 21,618(2.25)(.53) = 25,779.
2. Run a deterministic projection following the instructions in exercise 12 (see p. 98), except at step 4f, select the second matrix (b22:f26) (average matrix with seed viability reduced to zero, but with increased seed production).
3. Which transition or stage has the highest elasticity value?

4. What is the value of λ at year 22, and what does this indicate?

5. What is the expected population size of flowering plants at year 22?

6. What implications do these results have for population persistence in the absence of seeds remaining viable in the soil, even with increased seed production?

Assignment 13.D: Analyzing the Effect of zero Seed Viability Using the Wet Conditions Model

We again assume that seeds of the western prairie fringed orchid do not remain viable in the soil. But this time, we will run the wet condition model.

1. Select the exercise 13 worksheet. In the third matrix, seed viability remains at zero, but the transition probabilities reflect wet conditions.
2. Run a deterministic projection following the instructions in exercise 12 (see p. 98), except at step 4f, select the third matrix (b30:f34) (wet matrix with seed viability reduced to zero).
3. What transition or stage has the highest elasticity value?

4. What is the value of λ at year 22, and what does this indicate?

5. What is the expected population size of flowering plants at year 22?

6. What implications do these results have on population persistence in the absence of seeds remaining viable in the soil, even with increased seed production?

QUESTIONS AND ASSESSMENT

1. Which transition variable, when altered, had the greatest effect on λ? What biological mechanism or rationale can you suggest to explain the high sensitivity of λ to this variable? Describe an experiment you could perform to evaluate your hypothesis.

2. Assume that the hypothesis you have offered in question 1 is correct. What, if any, management strategy might you employ to increase the value of the variable with the highest elasticity? What environmental effects might lower the value of this variable, and what could be done to mitigate these effects?

3. Values of model outputs: Under what conditions does the model estimate a persistent population of > 50 flowering plants (consider all simulations under all conditions)? Under what conditions does the model predict sustained declines to populations of < 50 flowering plants?

4. Insights about demography and environment gained from the model (heuristic values):

   a. What insights did you gain about the biology of the orchid through using the model? How did the model provide these insights?

   b. Formulate a specific research hypothesis suggested by an outcome or outcomes of the model. Describe an experiment that would test your hypothesis.

5. Overall conclusions:

   a. Based on what you knew about biology before conducting this exercise in elasticity analysis, did the results make sense intuitively? Why or why not?

b. What is the difference between fecundity and recruitment? Based on what you have learned so far, are populations of the western prairie fringed orchid more limited by their fecundity or by their recruitment? What are the management and conservation implications of your answer for this species?

SYNTHESIS

Examination of elasticity values provides insights into which variables, when changed, result in the greatest change in population growth rates. These analyses are useful in: (1) understanding which variables have high elasticity values for populations projected to increase compared with those projected to decline; (2) testing basic assumptions about population persistence; (3) identifying variables on which to focus in developing management guidelines; and (4) identifying research needs.

In this exercise, we learned that variables with high elasticity values were different for the average model (with a projected declining population) than for the wet model (with a projected increasing population growth rate). In the case of the average model, changes in seed viability had the most profound effect on population growth rate. For wet conditions, seed production and germination rates had the greatest effect on projected population growth rates.

This exercise also allowed us to explore the implications of assuming that none of the seeds produced in a given year remained viable in the soil. Our deterministic projection for average conditions suggested that, in the absence of viable seeds in the soil, populations would decrease to only three flowering plants in 22 years. Even by nearly doubling the number of viable seeds produced/plant, the population was projected to continue to decline by a rate of 5% per year. The only way the population could increase under the assumption of zero seed viability was in wet conditions. This means that if wet conditions did not occur every year, the population would perish. This series of analyses helps us to realize that since wet conditions do not occur every year, some viable orchid seeds must be present in the soil for this population to persist through dry years.

The third way that we used the elasticity values was in identifying variables that, when increased, would result in the greatest change in the population growth rate. Because seed production was identified as having a high elasticity value, and increasing the number of viable seeds/plant increased the projected growth rate, we looked for ways to increase the number of viable seeds/plant. If the analyses showed high elasticity values for the vegetative to flowering transition, that would indicate that we should focus on protecting vegetative plants from damage so they would have a higher likelihood of returning as flowering plants the following year.

Finally, elasticity analyses might be most useful in identifying areas where more research is needed (Reed et al. 2002). This exercise demonstrated that those processes occurring belowground need further study. The variable with the greatest elasticity, seed viability, is the one variable for which we have no direct measurement. Thus, our analysis suggests that our most important research priority is to determine how long seeds remain viable in the soil. Only long-term research, conducted under field conditions, will provide this answer. Data collected *in situ* are difficult to obtain, but are far more likely to aid in the understanding of population viability of plants than knowledge of seed germination rates in laboratory settings (Doak et al. 2002). Regardless of the difficulty of obtaining these data, our preliminary modeling indicates that this is an essential question in understanding the persistence trajectories of the threatened western prairie fringed orchid.

LITERATURE CITED

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