

Part Four

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CREATING A STAGE-BASED DETERMINISTIC PVA MODEL— THE WESTERN PRAIRIE FRINGED ORCHID

In this exercise, you will learn how to:

1. describe the structure and organization of a stage-based, deterministic population model.
2. construct a stage-based deterministic population model and its transition matrices.
3. estimate the value of transition probabilities and other model variables from field data.
4. execute (“run”) a stage-based, deterministic population viability analysis model and correctly interpret the model’s output.
5. alter a stage-based, deterministic population viability analysis model to account for variation in environmental conditions.

BACKGROUND AND RATIONALE

Contemporary efforts to conserve populations and species often employ *population viability analysis* (PVA), a specific application of population modeling that estimates the effects of environmental and demographic processes on population growth rates. These models can also be used to estimate probabilities that a population will fall below a certain level. This information is helpful in understanding the threat of a species’ extinction from environmental and demographic factors.

Like all models, PVA-based models force the modeler to clearly identify assumptions about the population and its processes. A good modeler always states all the assumptions that he or she can specifically identify. Such identification not only helps to clarify our thinking about populations, but also may help us to identify those areas in which research is most needed. Models also enable us to identify the boundaries of system fluctuation. In PVA models, this means the model permits us to determine expected ranges of population highs and lows over time, and thus to know if a given population level exists within these expected boundaries. It is precisely by bounding the system that a

modeler is able to evaluate risk. In the case of populations, such evaluation of risk is an important dimension in determining management strategies to prevent extinction.

PVA-based models are data demanding and require a thorough understanding of the life stages of the species of interest, as well as careful ecological modeling. Such models have value in their ability to predict patterns of population change over time, as well as in estimating the probability of population persistence under specified conditions. In addition, PVA-based models are useful in exploring potential causes of population decline and potential routes to recovery, estimating the relative strength of different threats to population persistence, and discovering the importance of neglected aspects of population demography. Model building or model analysis guides the investigator toward insights about the system, reveals previously unsuspected interactions, or illustrates unsuspected dimensions of a population’s demography or environment. Collectively, these are referred to as *heuristic* benefits of modeling, and may be at least as important as the model’s final results or predictions. Such heuristic benefits of model building and analysis help to (1) develop and evaluate hypotheses regarding causes of population increase or decline, and (2) evaluate the relative effectiveness of various management options (Beissinger and Westphal 1998).

Models are especially appropriate and prudent when managing small populations common to threatened and endangered species because direct experimental manipulation would have low statistical power (insufficient numbers of individuals and groups) and unacceptable risk (high probability of losing some individuals from an already small population in experimental treatments). However, PVA models cannot replace field studies and experiments needed to test hypotheses generated by modeling efforts.

Population models may be classed generally as *deterministic* (model elements do not vary across time) or *stochastic* (model elements vary randomly through time). Although stochastic models are more challenging to

build and interpret, they may more accurately reflect population behavior because demographic processes are inherently variable.

In exercises 12–15, we provide a series of problems in model building, interpretation, and population viability analysis for a U.S. federally-designated threatened plant species, the western prairie fringed orchid (*Platanthera praeclara*), which poses a variety of challenging but generalizable problems in population conservation. Because each exercise builds upon skills and knowledge gained from previous problems, we recommend doing the exercises in the order presented here.

NATURAL HISTORY AND CONSERVATION STATUS OF THE WESTERN PRAIRIE FRINGED ORCHID

The western prairie fringed orchid is a wetland species that was once locally common west of the Mississippi River in the tallgrass prairie biome (U.S. Fish and Wildlife

Service 1996). With widespread settlement of this region, more than 80% of the native prairie has been converted to cropland or otherwise developed (Klopatek et al. 1979), and many of the region's wetlands have been significantly altered or drained entirely (Dahl 1990). As a result, the orchid has disappeared from nearly 75% of the counties where it once was documented, and in 1989 was listed as a threatened species (U.S. Fish and Wildlife Service 1989). The three largest potential metapopulations of the orchid (collections of populations with a strong possibility of gene exchange) occur in the northern United States and southern Canada (fig. 12.1) (U.S. Fish and Wildlife Service 1996). Ninety percent of known orchids in the United States occur in Minnesota and North Dakota. Small, scattered populations occur in Iowa, Nebraska, Kansas, and Missouri.

Only a portion of the area on which orchid populations persist is managed specifically for orchid protection. Instead, multiple land use activities, including surface and groundwater diversion, livestock grazing,

Figure 12.1 Historic distribution of the western prairie fringed orchid (*Platanthera praeclara*) in the central United States and southern Canada, and 3 largest remaining metapopulations (solid dots) of greater than 3,000 plants each. (U.S. Fish and Wildlife Service, 1996.)



Figure 12.2 Vegetative life state of the western prairie fringed orchid growing among prairie grasses. (Photo courtesy of Carolyn Hull Sieg.)



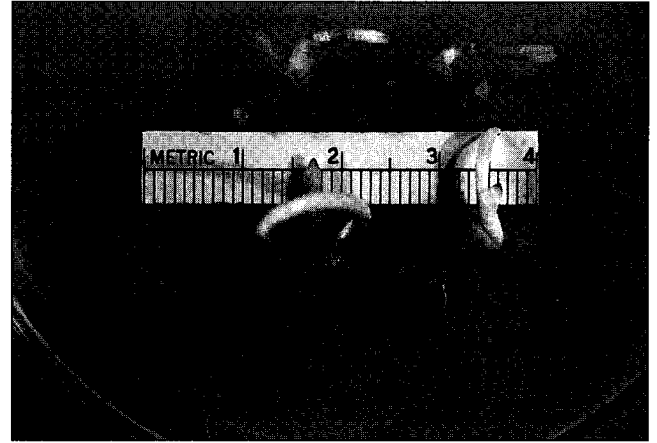
prescribed burning, production of hay, and wetland drainage to allow farming, are common and expected to continue. Some land management activities, depending on their timing and intensity, may be beneficial to the orchid by removing competing vegetation. Other land management activities, such as wetland drainage, are rarely beneficial. Thus, a thorough understanding of orchid life history is prerequisite to exploring possible population trajectories and evaluating the relative differences among effects that land-use decisions may have on population persistence.

The life history of the orchid includes two distinct aboveground stages. Vegetative plants are usually short (< 15 cm) and have only one or two leaves (fig. 12.2). Flowering plants are most conspicuous, growing up to 1.2 m tall, and producing a beautiful, branched flowering stalk with numerous cream-colored flowers (fig. 12.3). The lower petal of each flower is deeply 3-lobed and

Figure 12.3 Flowering life state of the western prairie fringed orchid. (Photo courtesy of Carolyn Hull Sieg.)



Figure 12.4 Protocorms and young seedlings of the western prairie fringed orchid. Tiny black dots are the dust-like seeds. (Photograph by Verla J. Nicholas.)



fringed, hence the orchid's common name. Both vegetative and flowering plants may appear aboveground the following growing season, persist in a dormant stage, or die. Although little is known about the orchid's pollination ecology, one or more species of hawk moths (Family Sphingidae) are the most likely pollinators. When successful pollination occurs, flowering plants may produce thousands of dustlike seeds (Hof et al. 1999). During the next growing season, a seed develops into an underground structure called a protocorm, which relies on mycorrhizae for its sustenance (fig. 12.4). In time, the protocorm develops into a seedling, and as the plant emerges from the ground it begins to photosynthesize. Germination, protocorm development, and transition to a seedling can occur within one growing season (Richardson et al. 1997).

STAGE-BASED DETERMINISTIC MODELS

Recovery efforts for rare species, especially plants, require a thorough understanding of all life-history stages, as well as detailed information on transition rates between stages. In addition, orchid conservation requires an understanding of environmental factors, such as precipitation levels, and land-management practices, such as livestock grazing, that affect population growth rates. Population modeling is one tool that can provide insights into these questions if multi-year data are available.

The Lefkovich, or stage-based model (Lefkovich 1965), is used for many species of plants, as well as many fishes and invertebrates, whose demographic rates are more closely related to developmental stage than age. The first step in developing a stage-based model is to identify the life-history stages of the species and the pathways of transition among the stages. Transition probabilities are then calculated from field data collected over several years. Matrix algebra is used to calculate several

useful statistics (Burgman et al. 1993), such as lambda (λ), or the geometric rate of increase. Lambda is the ratio of the population in year 2 to the population in year 1 ($\lambda = N_2/N_1$). That is, λ can be thought of as a multiplier of population increase from one time period to the next. Thus, a population in which $\lambda = 1.0$ is stable. When λ is > 1.0 , the population is growing. When λ is < 1.0 , the population size is declining. The value of λ provides a measure of the rate of increase or decline. For example, a population with $\lambda = 1.12$ is growing at a rate of 12% per year, whereas a population with $\lambda = 0.97$ is decreasing at a rate of 3% per year.

Be careful not to confuse λ with r , which is the *intrinsic rate of natural increase*—that is, a measure of the instantaneous rate of change of a population size per individual. λ and r are related by the formula

$$\lambda = e^r,$$

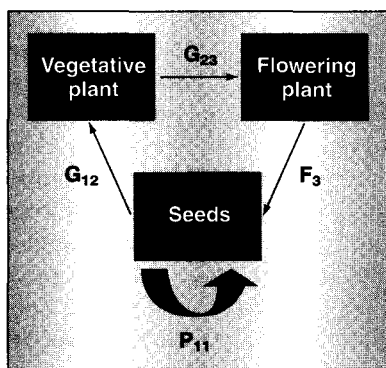
where e is the base of natural logarithms (approximately 2.7183). In these exercises, our model will generate and present values of λ , not values of r .

One assumption of deterministic models is that transition probabilities do not change over time. So, if you were interested in exploring how drought influences the population growth rate of a species, you could run a deterministic model using the vital rates (transition probabilities) measured in a drought and examine the effect of maintaining these transition rates for 10 to 20 years. It is unlikely that a drought would persist for 20 consecutive years, and a wet period persisting for 20 consecutive years would be equally unlikely. However, comparing the projected population growth rate of a species during dry conditions with that projected for a wet period provides insights into the underlying causes of variation in growth rates (Beissinger and Westphal 1998).

Constructing the Model and Matrices

Life-History Stages and Their Parameters

The life stages of an annual plant typically include vegetative plant, flowering plant, and seeds, which could be displayed as:



“P” represents the within-stage transition, or the probability that the plant will remain in the stage; “G” is a transition from one stage to another; and “F” is the number of seeds produced by a flowering plant. To begin, arrange the three life stages (seeds, vegetative plants, and flowering plants) in a matrix of rows and columns. Let column headings represent the plant’s present life stage and row headings its next (subsequent) life stage as shown in the following table. Subscripts shown in the preceding figure and in the table represent the column (first number) and row (second number). Thus, P_{11} is the probability that a seed will remain viable in the soil. The subscript 11 designates that this value belongs in the cell associated with the first row and first column of the matrix, which corresponds to the probability of the present seed remaining a seed in the next time interval. Similarly, G_{12} is the probability that a seed will germinate and become a vegetative plant; G_{23} is the probability that a vegetative plant will flower; and F_3 is the number of seeds that a flowering plant produces.

Next life stage	Present life stage		
	Seeds	Vegetative Plant	Flowering Plant
Seeds	P_{11}	—	F_3
Vegetative plant	G_{12}	—	—
Flowering plant	—	G_{23}	—

Assignment 12.A: Determining Transition Probabilities between Stages

Suppose that for our hypothetical annual plant, we have data from 650 vegetative plants that were marked and monitored in the field for 3 years. Of these 650 vegetative plants, 320 flowered. We measured seed production of 50 flowering plants, and over the 3 years, average seed production per plant was 23, of which 45% were viable.

We do not have data on germination rates of the seeds, but let us assume that 10% of the seeds germinate, and 20% of the seeds remain viable in the soil seedbank. Using these data, calculate and correctly insert the appropriate values in the following transition table. Remember that all transitions are represented as probabilities except for the number of seeds produced (F_3). When calculating probabilities, remember that if 10% of the seeds germinate, this reflects a probability represented as 0.1. Also remember that some cells may have no values because some transitions do not actually occur (for example, vegetative plants do not produce seeds).

Life-Stage Transition Probabilities for A Hypothetical Annual Plant

Next life stage	Present life stage		
	Seeds	Vegetative Plant	Flowering Plant
Seeds	—		
Vegetative plant		—	—
Flowering plant	—		—

The first step in developing a demographic model for the western prairie fringed orchid involves identifying the life stages. Based on the preceding discussion, and the knowledge you now have of the life history of the orchid, what are the aboveground and belowground stages of the orchid?

Aboveground: _____

Belowground: _____

Assignment 12.B: Constructing Transition Matrices for the Western Prairie Fringed Orchid

To identify all the transitions in the life history of the orchid, additional information is needed. The western prairie fringed orchid is a perennial plant that may persist for several years in some locations. A vegetative plant in year 1 may remain vegetative in year 2, become a flowering plant, or disappear. Likewise, a flowering plant in year 1 may be

vegetative or flower in year 2, or it may disappear. Plants that disappear may only be dormant, or they may be dead.

1. Construct a diagram similar to the one displayed earlier (see page 94) showing the life stages of the western prairie fringed orchid. Draw arrows on the diagram to indicate transitions. After you have completed your diagram, compare it with the one displayed in figure 12.5. Note that figure 12.5 combines the protocorm/seedling stages into 1 matrix element because growth from a protocorm to a seedling can occur within 1 growing season. Did you do this?

Figure 12.5 Visual representation of life-history stages and transitions in the western prairie fringed orchid.

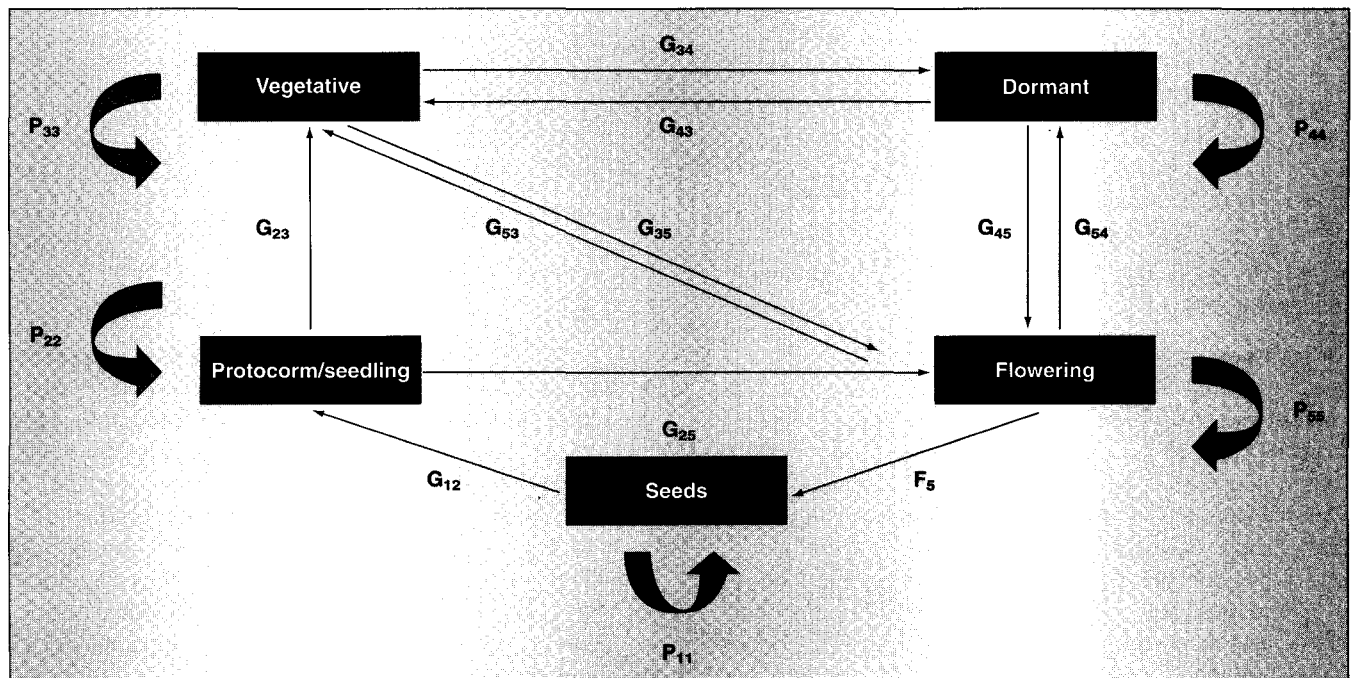


Table 12.1 A Generalized Transition Matrix for the Western Prairie Fringed Orchid

<i>Status next year</i>	<i>Present status</i>				
	Seeds	Seedling	Vegetative	Dormant	Flowering
Seeds	P ₁₁	—	—	—	F ₅
Seedling	G ₁₂	P ₂₂	—	—	—
Vegetative	—	G ₂₃	P ₃₃	G ₄₃	G ₅₃
Dormant	—	—	G ₃₄	P ₄₄	G ₅₄
Flowering	—	G ₂₅	G ₃₅	G ₄₅	P ₅₅

2. Using the diagram as a guide, construct a transition matrix for the orchid. Remember to label each row and column heading; then insert the appropriate symbol and subscript in each cell (row/column intersection). For example, the probability that a seedling in 1 year becomes a vegetative plant in the next year would be designated as G₂₃. Remember that some cells will have no values because some transitions never occur. After you have constructed your transition matrix, compare it to the one shown in table 12.1. Are they the same? Did you omit any life-history stages or transitions?

1. Using the following data, calculate the average transition probabilities for a vegetative plant becoming a flowering plant in the following year, and calculate the overall average for the 4 years.

	Number of Vegetative Plants in Year 1	Number of Vegetative Plants That Flowered in Year 2	Probability of a Vegetative Plant Flowering in Year 2
1990–91	74	0	_____
1991–92	54	10	_____
1992–93	154	53	_____
1993–94	361	12	_____
Average			_____

Assignment 12.C: Calculating Population Data

To complete the transition matrix for the western prairie fringed orchid with real values, we need detailed information on both aboveground and belowground transitions. For the aboveground transitions, we use data collected over 5 years on 16 sites on the Shenyenne National Grassland in southeastern North Dakota (USA) (adapted from Sieg and King 1995). Beginning in 1990, vegetative and flowering plants in 16 belt transects were permanently marked and numbered. Each year, the status of the previously marked plants was recorded, and new plants were marked.

2. Estimates of fruit set were made by permanently marking 635 flowering plants between 1995 and 1998. At the end of each growing season, the number of plants that produced viable fruits was recorded, as was the number of viable fruits/plant. Assume that each flowering plant produces an average of 1.2 fruits/plant and each fruit produces an average of 21,618 seeds, of which an average of 53% are viable (Richardson et al. 1997; Hof et al. 1999). Calculate the average number of viable seeds produced per flowering plant: _____

- Using the data we have calculated so far, fill in the G_{35} (average probability that a vegetative plant will become a flowering plant) and F_5 (number of viable seeds produced/flowering plant) cells in the following table. The other aboveground data were calculated in a similar manner, and are provided. In addition, we have estimated the probability of seedlings becoming vegetative and flowering plants, based on the appearance of new plants and the following belowground data.

- What is the probability of a vegetative plant being dormant the following year?

Present status

<i>Status next year</i>	Seeds	Seedling	Vegetative	Dormant	Flowering
Seeds	P_{11}	—	—	—	—
Seedling	G_{12}	P_{22}	—	—	—
Vegetative	—	0.0301	0.2806	0.0815	0.2106
Dormant	—	—	0.5783	0.1015	0.6968
Flowering	—	0.0099	—	0.0299	0.1025

Belowground Transitions

We use data from seed packets, buried in the ground and then retrieved the following year, to approximate transition probabilities for seed germination rates and development into protocorms and seedlings (Richardson et al. 1997; Hof et al. 1999). For this model, we assume that protocorms do not persist beyond 1 year.

We do not have data on seed viability in the soil, but for now will assume that 50% of the seeds produced remain viable in the soil. Thus, the resulting matrix is as follows:

- How does the probability of a vegetative plant, remaining vegetative, compare with the probability of a flowering plant reappearing as a flowering plant the next year?

Present status

<i>Status next year</i>	Seeds	Seedling	Vegetative	Dormant	Flowering
Seeds	0.5	—	—	—	$F_5 = 13,749$
Seedling	0.0015	0.00	—	—	—
Vegetative	—	0.0301	0.2806	0.0815	0.2106
Dormant	—	—	0.5783	0.1015	0.6968
Flowering	—	0.0099	0.1411	0.0299	0.1025

With this preliminary analysis and calculation of our transition variables, we are ready to run our first model. Before doing so, however, answer the following questions to clarify your thinking and ensure that you are in command of your data:

Stop and Reflect

- What is the average probability of a vegetative plant reappearing as a vegetative plant the following year?

RUNNING THE MODEL

The model we now will employ can simulate 3 different environmental conditions: average, wet, and dry. The matrix of transition variables we created earlier in assignment 12.B was for average conditions. However, recall that the orchid is adapted to wet environments. Thus, deviations from average conditions (wet or dry) will affect the values of transition variables. An EXCEL workbook (pva_workbook_010803.xls) has been created in advance and placed in a file on your workbook website at www.mhhe.com/conservation. Click on the "PVA excel file" link to reach the EXCEL spreadsheet. The EXCEL workbook contains four exercises. The worksheet titled

exercise 12 has three matrices, AVERAGE, WET, and DRY, which reflect the effects of average, wet, and dry climatic conditions based on actual field data. Be sure to access the appropriate matrix for each of the following exercises.

Assignment 12.D: Predicting Outcomes for Average Conditions

We are now ready to run our first model, using the matrix we created in assignment 12.B.

1. Open the EXCEL workbook file and click on "Enable Macros" when prompted.
2. Switch to the exercise 12 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*: Enter 22. (Note: This variable tells the program the number of time intervals to be estimated in the analysis. The longer the projection, the less confidence we have in the estimates. Many authors recommend using shorter time intervals (i.e., 10 or 25 years instead of 100 to 200 years) to minimize error propagation (Beissinger and Westphal 1998)).
 - b. *Stage names*: Highlight column A, rows 4 through 8, or type A4:A8.
 - c. *The stage parameter for lambda calculations*: Select "Flowering plants." (Note: Although lambda can be calculated for any stage, the population growth rate of flowering plants is most relevant to the persistence of this species.)
 - d. *Initial values*: Highlight column B, rows 4 through 8, or type B4:B8. (Note: These values are approximated from field data collected on the western prairie fringed orchid [Sieg and King 1995; Hof et al. 1999; Richardson et al. 1997]).
 - e. *Ceiling values*: Select "Cancel."
 - f. *Specification of first Lefkovitch matrix*: Highlight the average matrix (just the numbers in the matrix, not the headings).
 - g. *Next matrix*: Select "Cancel."
 - h. *Specify element standard deviations?* Select "No."
6. The program now provides a summary of the model specifications: Make sure it says:
 - Sequence length is 22.
 - Stage names from Exercise 12!A4:A8.
 - Initial stage parameter values from Exercise 12!B4:B8.
 - Lefkovitch matrices from Exercise 12!B14:F18.
 - i. *Begin computations?* Select "Yes."
 - j. *Plot selected population parameters?* Select "Yes."
 - k. Select "Flowering plants."

The model projections will be printed on two worksheets. Change the names of these worksheets to "average" and "average plot," respectively, as you need to look at them again. To change the name on a worksheet, right-click on the name of the worksheet (on the tab), select "Rename," and type in the new name.

Assignment 12.E: Predicting Outcomes for Wet Conditions

In this simulation, we use transition rates summarized from data on 16 sites in a wet year.

1. Switch to the exercise 12 worksheet. Follow the instructions for assignment 12.D (steps 2–4), except this time, at step 4f, when you are asked for the first Lefkovitch matrix, select the WET model matrix (b21:f25).
2. Save the results, and name worksheets as "wet" and "wet plot."

Assignment 12.F: Predicting Outcomes for Dry Conditions

In this simulation, we use transition rates summarized from data on 16 sites in a dry year. Again follow steps 1–4 from Assignment 12.D, except this time, at step 4f, when you are asked for the first Lefkovitch matrix, select the DRY model matrix (b28:f32). Save the results, and name worksheets as "dry" and "dry plot."

QUESTIONS AND ASSESSMENT

After you have completed your runs, answer the following questions:

1. What is the terminal value of lambda (in year 22) under average, wet, and dry conditions?
2. What is the projected population of flowering plants at the end of each of these 22-year simulations?
3. What do these values suggest about population persistence?

4. What are the limitations of a deterministic model?
What elements of biological reality does it omit?

5. In general, what kinds of questions could a conservation biologist, armed with this model, answer about this or other similar populations that the same biologist could not answer without the model? In what specific ways does the model increase and improve the skills of the conservation biologist to accomplish conservation goals?

SYNTHESIS

Models should never be confused with the real world, but they can be very useful in helping us understand it. This understanding often comes as much from building the model as from running the finished product. In this exercise, our model-building effort clarifies our understanding of the population's life history and helps us determine what data to collect and how to use it. Running the model tells us how the size of the population may vary through time and how such variation may be affected by environmental conditions.

Models do not make decisions, but when used skillfully, they inform decision makers. Similarly, models do not conduct research, but appropriately applied and interpreted, they guide conservation biologists in selecting subjects for research that have high value in understanding population processes. Models are not substitutes for fieldwork. Indeed, a model that is not based on carefully collected field data would have little value. But models do provide one very appropriate use for such data that, properly applied, can be used to make intelligent estimates of future population trends, not simply provide a summary of past population events.

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