

Patchy Prairies

Introduction

If you had visited the Willamette Valley of Oregon a few hundred years ago, you would have seen an expansive mosaic of upland and wetland prairie habitats dominated by perennial bunchgrasses and showy wildflowers. Although the habitat was suitable for shrubs and trees, periodic burning by the native Kalapuya killed encroaching woody species. The open prairie habitat they maintained supported a rich variety of plants and animals, including many endemic species.

Today, urbanization and agriculture have spread throughout the region, reducing native prairie to less than 1% of its original range. Fire suppression on the remaining prairie remnants has allowed invasion by both woody species and by non-native plants, degrading those habitats and making them less suitable for native species. The loss, fragmentation, and degradation of habitat have, as you can imagine, reduced the populations of many species to low enough levels to warrant their listing as threatened or endangered species. One such species is Fender's blue butterfly.

Although adult Fender's blue butterflies can feed on nectar from a number of different flower species, they rely on only a few species for reproduction. Specifically, Kincaid's lupine and, to a lesser extent, two other lupines, are the only plants on which Fender's blue larvae can feed. If females can't lay eggs on these plants, they leave no offspring. Unfortunately, habitat loss, fragmentation, and invasion by woody and exotic species have left only relatively small, scattered populations of Kincaid's lupine. These patches are now so widely separated that many butterflies are unable to disperse from one patch to another. Today, Fender's blue populations fluctuate between 2,000 and 6,000 individuals among a dozen prairie remnants scattered throughout the Willamette Valley.

Beginning in the 1990s, a partnership of local, state and federal agencies, along with The Nature Conservancy and other Non-Governmental Organizations (NGO's) came together to form the West Eugene Wetlands Partnership (now the Rivers to Ridges Partnership) with the goal of conserving and restoring 3,000 acres of wetland and upland prairie west of Eugene Oregon—an area that includes most of the remaining Fender's blue butterflies.

The most immediate problem facing Fender's blue butterflies is that suitable patches of Kincaid's lupine are small and widely separated. With funds available to restore a limited amount of habitat, habitat managers must decide on a restoration plan. They could select an existing, large patch and add to it; with more food and larval host plants, the population within the patch should grow larger. That plan, however, leaves a large number of butterflies at risk if the patch is disturbed; for example, periodic fires could kill larvae that overwinter at the soil surface. One alternative is to restore continuous strips of habitat—known in conservation biology as *habitat corridors*—between existing patches. In theory, butterflies could then use these corridors as “habitat highways” to disperse among patches. Finally, rather than creating corridors among patches, managers could restore new patches of habitat between existing patches, thereby decreasing the distance between patches. The new patches might act as *stepping stones* for dispersing butterflies, allowing them to move more easily among patches.

Habitat corridors and stepping-stones both increase connectivity of habitat patches. But which is best for Fender's blue? Unfortunately, the answer requires a great deal more information about the butterfly's behavior and life history than is available. And, because this is an endangered species, implementing an extensive program of experimentation to obtain the data we need is out of the question. How, then, do we proceed?

The good news is that ecologists have developed simulation models that can help direct our research. A simulation model uses a collection of rules that dictate the actions and behaviors of a system. Although simulation models don't capture all of the complexity of real systems, they allow us to conduct experiments that can help us predict how a system will behave under different conditions. They can also help us identify the most critical data we need to understand the system.

In this lab, you will use and modify a simulation model of butterflies in a patchy prairie system to investigate the challenges of the Fender's blue butterfly and to explore the utility of models to develop and test possible conservation strategies.

Exercise 1: Virtual Blues

- [1] Start the program by double-clicking the **SimBio Virtual Labs** icon on your computer or by selecting it from the Start Menu on your computer. When **SimBio Virtual Labs** opens, select **Patchy Prairies** from the list.

You will see a number of different panels on the screen; these will be explained as needed for the exercises in the lab.

- [2] The top menu bar has a drop-down menu from which you will select individual exercises as you proceed through the lab. Be sure that **Virtual Blues** is selected.

- [3] Click on the names of each species in the **Library Panel** in the bottom right corner of the screen to bring up pages for each. Use the library to complete the following questions:

[3.1] Approximately how long is the adult stage of the Fender's blue butterfly?

[3.2] How do Kincaid's lupine disperse seeds? Would you consider this an example of long-distance dispersal? Explain.

- [4] The **Parameters Panel** above the **Library** lets you select between two patch configurations. Click on each to see what the habitat arrangements look like. As you toggle between configurations, the **Prairie Habitat Area** box beneath the habitat patches indicates the total area (in hectares) of prairie habitat in the configuration being displayed.

[4.1] How many hectares of prairie are there in the **Large Far** configuration?

[4.2] How many hectares of prairie are there in the **Small Near** configuration?

[5] Select the **Large Far** patch configuration. In the bottom left corner of the screen, a **Control Panel** allows you to start, stop, and reset the simulation. Click the **GO** button to start the simulation. Observe the action and answer the following questions.

[5.1] Do the simulated butterflies appear to go through the same life history stages as real butterflies? If not, what stages are missing?

[5.2] At the bottom of the screen you will see that TIME ELAPSED is displayed in “Weeks”. Does this seem realistic? Why or why not?

[5.3] When simulated butterflies die, they disappear. You should be able to tell that the simulated butterflies are more likely to die when they are outside of prairie patches than when they are inside of prairie patches. Do you think this is biologically reasonable? Explain.

[5.4] A **Moving Average** of the total number of butterflies in the system (calculated every 10 “weeks”) is displayed above the graph. Assuming there is no immigration or emigration, what evidence is there for butterfly reproduction?

Clearly, this simulation is not completely realistic! Nobody knows enough about Fender’s blue butterflies to create a 100% realistic model. However, the simulation captures aspects of butterfly biology and the prairie system that biologists think are the most important for answering questions about habitat restoration. Following is a description of how the simulation model in this lab works. You may find it useful to refer back to this description as you work through the lab.

Virtual Butterflies in Make-Believe Prairies: A Peek Under the Hood

HABITAT

The landscape consists of two different environmental types: prairie habitat, which are patches of prairie where the lupine host plant grows, and non-prairie habitat. Each week, new host plants (i.e., food) are added to prairie habitat according to a food density parameter, which is the number of individuals per unit area per week that are added.

BEHAVIOR

Butterflies move, eat, reproduce, and die.

MOVEMENT

In prairie habitat, butterflies look for food and move toward it. Outside a patch (non-prairie), butterflies move according to their heading, but can turn a bit with a specified probability per week. Flight speed is different in prairie vs. non-prairie, as is the probability that a butterfly will change heading (turn probability). When a butterfly inside a patch encounters the edge, it may cross the edge into non-prairie or turn around, according to the leave prairie probability. Butterflies tend to avoid neighbors; crowding sensitivity is the radius of avoidance. If a neighbor is within this distance, the individual tries to move away from the neighbor.

EATING

Food consists of the larval host plant (though the larval stage is not specifically modeled). There's no food in non-prairie. If a butterfly finds and eats food, it gains energy. Each week, some energy is subtracted from the butterfly's energy store. If the butterfly runs out of energy, it dies.

REPRODUCTION

Butterflies can only mate in prairie habitat, only when their energy level exceeds a threshold, and only with other individuals that are nearby. They have two successful offspring per mating event, and each parent donates half its energy store to offspring. Parents can reproduce repeatedly until they die.

DEATH

Butterflies die one of three ways. They can starve to death. They can die randomly in non-prairie environments (death probability). They can die of old age.

[6] Make a prediction based on what you now know about the model.

[6.1] Do you think the total number of butterflies supported by the two habitat configurations (**Large Far** and **Small Near**) should be the same or different? Explain.

[7] To determine whether you were correct, you'll need to collect some data. First click the **RESET** button in the **Control Panel** to return the simulation to its original settings. With the **Large Far** configuration selected. Click the **STEP 100** button to advance the simulation 100 weeks.

★ *Note: If you slide the speed button to the right, the simulation runs faster.*

[7.1] When the simulation stops, record the current moving average for the total population size (i.e., the number in the right corner above the graph) in the first row of Data Table 1 below. Then repeat the procedure two more times, completing the table.

DATA TABLE 1:
BUTTERFLY POPULATION SIZE IN LARGE FAR PATCHES AFTER 100 WEEKS

POPULATION SIZE	
Run 1	
Run 2	
Run 3	

[7.2] What is the average population size of the three runs for the Large Far configuration?

★ *Note: You have a handy dandy Calculator tool at the bottom right-hand side of your screen.*

[8] Repeat the steps above for the **Small Near** patch configuration.

[8.1] Switch to the **Small Near** configuration and complete the table below, following the same procedure as above.

DATA TABLE 2:
BUTTERFLY POPULATION SIZE IN SMALL NEAR PATCHES AFTER 100 WEEKS

POPULATION SIZE	
Run 1	
Run 2	
Run 3	

[8.2] What is the average population size of the three runs for the **Small Near** configuration?

[9] The average sizes for the two configurations were probably similar, although there likely was a good deal of variation between runs. Random variability is part of what adds to the realism of the simulation. (The real world is quite messy!) Because the simulated system includes random variability, when you collect data, it will be important to conduct replicate runs. To simplify this process, you will likely find the **Automator** tool (to the left of the **Calculator** tool) to be quite useful.

[10] Once again, select the **Large Far** configuration. Then click on the **Automator** tool, popping up the automator window. The default settings let you conduct 20 simulation runs for 100 weeks each. At the end of each run, the average butterfly count across all runs completed will be updated in the lower right corner of the **Automator** window. The number of times that all of the butterflies in the system go extinct is also tracked, and the overall extinction rate will be updated in the lower left corner. Click the **AUTOMATE** button to initiate your experimental runs.

[10.1] When the **Automator** stops after the completion of 20 runs, record your results for the **Large Far** configuration in the first row of Data Table 3.

DATA TABLE 3:
AVERAGE NUMBER OF BUTTERFLIES AND EXTINCTION RATES AFTER 100 WEEKS
(20 REPLICATES)

CONFIGURATION	AVERAGE COUNT	EXTINCTION RATE
Large Far		
Small Near		

[11] Select the **Small Near** configuration and use the **Automator** to collect data for 20 runs.

[11.1] When the **Automator** stops after the completion of 20 runs, record your results for the **Small Near** configuration in the second row of Data Table 3.

[11.2] Which configuration, **Large Far** or **Small Near**, supports the largest, most stable butterfly population with the current model settings?

You should have confirmed that the difference between the two configurations is not very large; however, the **Large Far** configuration should consistently slightly outperform the **Small Near** configuration. This is due to “edge effects”; when you divide an area into two, you necessarily increase the total amount of perimeter. (You can easily convince yourself of this with pencil and paper.) The relative amount of edge is greater in the **Small Near** configuration. With more edge, more butterflies will randomly encounter edge, and thus more butterflies will leave prairie habitat (which has food) and enter the environment that does not have any food. If this doesn’t make sense, review the “peek under the hood” description of how the simulation model works.

[12] Click on the **TEST YOUR UNDERSTANDING** button and answer the question that appears in the pop-up window.

The next exercise explores how adding more complexity to the system can influence the outcome of your **Large Far** vs. **Small Near** comparison.

Exercise 2: Hot and Bothered

Real habitats are subject to periodic disturbances that can impact local populations. We know that fire was a historically important disturbance in Fender habitat. Controlled burning prevents prairies from being invaded by woody and exotic species and is thus often used by land managers to restore and maintain the prairie plant communities. Unfortunately, fire kills butterflies. In this exercise, you will explore how factoring in disturbance (in the form of fire) changes the relative survival success of butterflies in the **Large Far** vs. **Small Near** scenarios.

- [1] Select **Hot and Bothered** from the **Select an Exercise** drop-down box. You should notice that the **Parameters Panel** now includes an option that allows you to play with fire.
- [2] In the **Parameters Panel**, select the **Large Far** configuration and choose **Periodic Fires** as the Disturbance. **RUN** the simulation to see fires moving through prairie habitat.

In the model, fires start about every 40 (virtual) weeks. They spread from plant to plant inside the prairie, burning up to half (or so) of the total prairie habitat. Fires kill all butterflies and lupine in the burned area. Watch the simulation for a few hundred weeks or until you feel confident that you can answer the following questions.

- [2.1] **Why are the burned patches in the **Large Far** configuration not recolonized by butterflies?**

- [2.2] **Given what you saw, when there are periodic fires, do you think more butterflies will survive in the **Small Near** or **Large Far** configuration? Explain.**

- [3] **RESET** the simulation and test your prediction. Use the **Automator** tool to run the simulation 20 times for each configuration to answer the questions below.

DATA TABLE 4:
AVERAGE NUMBER OF BUTTERFLIES AND EXTINCTION RATES AFTER 100 WEEKS WITH PERIODIC FIRES (20 REPLICATES)

CONFIGURATION	AVERAGE COUNT	EXTINCTION RATE
Large Far		
Small Near		

- [3.1] Which patch configuration resulted in a higher average butterfly count after 100 weeks?
- [3.2] Butterflies in both configurations followed the same behavior rules. Fires in both configurations were about the same size, occurred at the same rate, and resulted in localized patch extinctions. What aspect of butterfly behavior resulted in one configuration being better for butterflies than the other when fires periodically burned patches?
- [3.3] Your answer in [3.1] was based on average butterfly count as a measure of population success and persistence. Does extinction rate show the same pattern?
- [4] Click on the **TEST YOUR UNDERSTANDING** button and answer the question in the pop-up window.

You've now seen that simulated model outcome depends on what factors are considered. If patches are not burned periodically, one might conclude from using the simulation model that a few large isolated prairie patches is better for butterfly persistence than many smaller patches close to each other. These "what if" experiments would not be possible in the real world.

As mentioned earlier, we don't know everything about butterfly behavior. When we create models, we have to make some guesses. When management decisions are based on simulations, it's very important to know which guesses could affect our decisions.

The next exercise lets you determine whether the simulated system is particularly sensitive to how butterflies are modeled.

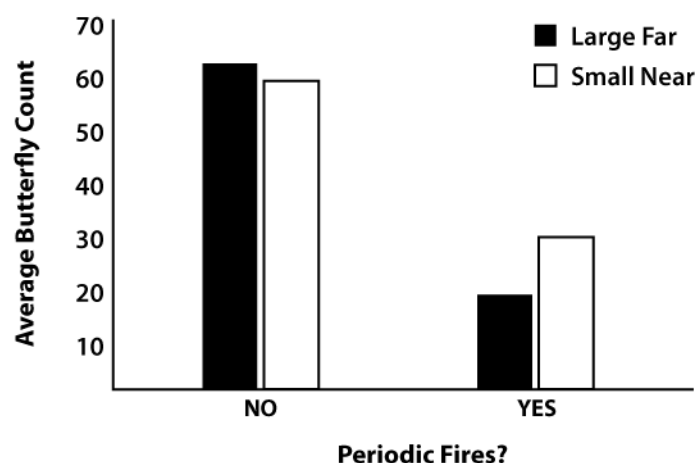
Exercise 3: Sense and Sensitivity

In the previous exercise, you discovered that the habitat configuration resulting in the largest, most stable population of simulated butterflies depends critically on whether or not the prairie patches periodically burn. This is because the simulated butterflies cannot fly far enough to recolonize burned patches in the **Large Far** configuration. As you might imagine, patterns that emerge from the modeled system depend on the particular rules that modeled individuals follow.

The rules individuals follow in simulation models involve many parameters. For example, a parameter called **leave prairie probability** dictates the probability that a butterfly encountering the patch edge will leave the prairie and enter the surrounding, unfavorable environment. If that probability is 0, no butterflies will ever leave prairie patches. If it is 0.5, there is a 50–50 chance that a butterfly encountering the edge of a patch will leave that patch. Similarly, the **turn probability** parameter dictates the probability that a butterfly will change direction as it flies through non-prairie between patches. As a modeler, you likely do not know the actual probabilities for butterflies leaving prairie patches or changing direction when they fly outside their habitat. Values the modeler used for these parameters were based on her best guesses after researching what is known about Fender's blue butterflies.

In this exercise, you will determine when a modeled system is sensitive to a parameter. The process you will use is called a **sensitivity analysis**, which is a very important tool to modelers—and to land managers who have access to models.

You actually already conducted a sensitivity analysis, when you simulated prairies with and without fire. If you were to plot data from your simulations, it might look something like this:



The above graph illustrates that the results from the simulation are sensitive to whether fire is included in the model. Moreover, the degree of sensitivity depends on the way butterfly habitat is configured—large far patches are more sensitive than small near patches.

- [1] Select **Sense and Sensitivity** from the **Select an Exercise** drop-down box. Notice that the **Parameters Panel** now includes sliders for adjusting the **Leave prairie probability** and **Turn probability (NP)**.

★ *Note: “NP” stands for “non-prairie”; parameters with the NP designation only apply to butterflies when they are outside of prairie patches. If you see a P designation, it means the parameter only applies to butterflies when they are inside of prairie patches.*

- [2] Make sure that the **Turn probability** parameter is set to its default value (0.2) and that the **Periodic Fire** Disturbance regime has been selected.
- [3] To begin, see whether under the **Large Far** patch configuration the model is sensitive to the **Leave prairie probability** parameter setting. That is, if **Leave prairie probability** is set to different values, does your model output (i.e., average butterfly count) change?
- [4] Select the **Large Far** patch configuration and set the **Leave prairie probability** parameter to 0.1. Use the **Automator** tool to run the simulation 20 times for 100 weeks each.

- [4.1] Record the average butterfly count in the first column of the first row (Large Far) of **Data Table 5**.

DATA TABLE 5:
AVERAGE BUTTERFLY COUNTS FOR DIFFERENT LEAVE PRAIRIE PROBABILITIES AFTER 100 WEEKS WITH PERIODIC FIRES (20 REPLICATES)

PATCH CONFIGURATION:	LEAVE PRAIRIE PROBABILITY = 0.1	LEAVE PRAIRIE PROBABILITY = 0.5	LEAVE PRAIRIE PROBABILITY = 0.9
Large Far			
Small Near			

- [5] Repeat for **Leave prairie probabilities** of 0.5 and of 0.9, recording the average butterfly count for each of those probabilities in the appropriate cells in **Data Table 5**.
- [6] Examine your data and consider whether your results at different parameter values are very different. Of course, there will always be some random variability in your data; it would be better to do 1,000 or 10,000 runs per parameter value, but that would take a very long time. For the purpose of this investigation, let's say this model is sensitive to a parameter if the average butterfly count changes by more than 15 butterflies as the parameter changes.

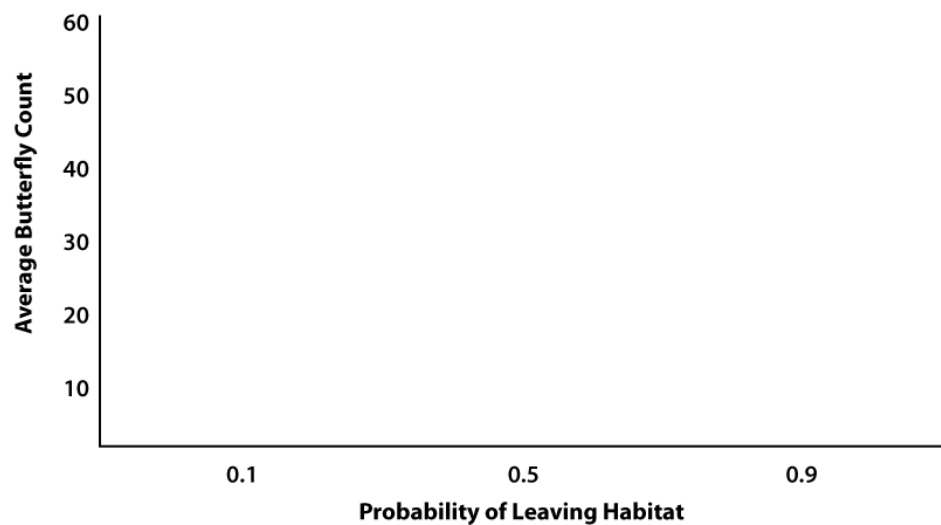
[6.1] Based on your data, is the simulation model sensitive to the **Leave prairie probability**? Explain.

[7] Change the patch configuration to **Small Near** and use the **Automator** as above to conduct a sensitivity analysis of the **Leave prairie probability** parameter with the **Small Near** configuration.

[7.1] Record your average butterfly counts in the appropriate cells of Data Table 5 above.

[7.2] Is the model sensitive to the **Leave prairie probability** parameter with the **Small Near** configuration? Explain.

[7.3] Use the axes below to graph your data for both configurations. Refer to the graph in the introduction of this exercise to see how make this graph. Include a legend showing which data represent **Large Far** and **Small Near**.



[8] Your graph (probably) illustrates two things about the simulation model. First, it should show that the model is especially sensitive to the **Leave prairie probability** parameter with the **Small Near** patch configuration. However, it should also show something that is biologically very important.

[8.1] Based on your graph, when there are periodic fires, can you say definitively whether your simulated butterflies are better off with small near patches than they are with large far patches (as you found in the previous exercise)? Explain.

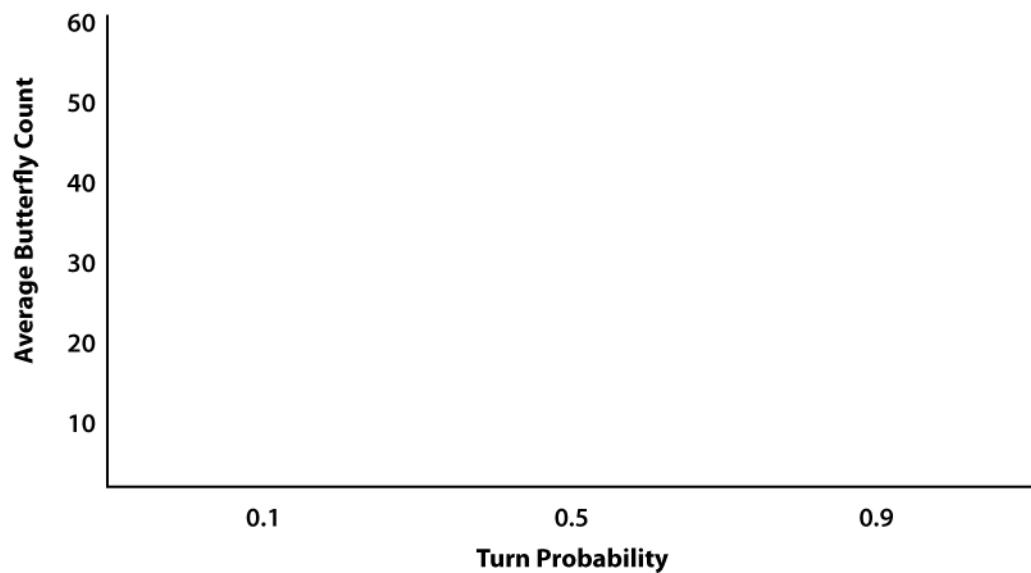
[9] Follow the same basic approach to conduct a sensitivity analysis of the **Turn probability** parameter. First click the **Restore Default Parameters** button to return the **Leave prairie probability** to its default value. Make sure the **Periodic Fires** checkbox is checked, and use the **Automator** to collect the data necessary to complete **Data Table 6**.

[9.1] Fill in the data table below with the data that you collect.

DATA TABLE 6:
AVERAGE BUTTERFLY COUNTS FOR DIFFERENT TURN PROBABILITIES AFTER 100
WEEKS WITH PERIODIC FIRES (20 REPLICATES)

PATCH CONFIGURATION:	TURN PROBABILITY = 0.1	TURN PROBABILITY = 0.5	TURN PROBABILITY = 0.9
Large Far			
Small Near			

[9.2] Graph your results using the axes below (and include a legend).



[9.3] What does your sensitivity analysis tell you about the **Turn probability** parameter?

[9.4] Based on these results, to which parameter is the model more sensitive: **Leave prairie probability** or **Turn probability**? Explain your choice.

[9.5] Do your sensitivity analyses tell you whether the model is sensitive to either parameter when there is no disturbance (i.e., no periodic fires)? Explain.

[9.6] Based on this sensitivity analysis, if you were asked to use this model to decide between the **Large Far** and **Small Near** patch configurations for butterflies, and you could send a field biologist out to collect data before you settled on which parameter settings to use in your simulations, what would you tell the biologist is the most important field data to collect?

[10] Click on the **TEST YOUR UNDERSTANDING** button and answer the question in the pop-up window.

Exercise 4: Connections

Now that you're a simulation model expert, you have been approached by the Rivers to Ridges Partnership. They have asked you to apply your excellent modeling skills to the task of developing and testing possible conservation strategies for Fender's blue butterflies. Their ultimate goal is to give Fender's blues the best possible chance at long-term persistence.

Several prairie patches in the Partnership's study area already support small, vulnerable populations of Fender's blue butterflies and Kincaid's lupine. The Partnership's strategy is to construct a butterfly reserve system around these existing patches. They have decided they want to restore land to prairie habitat so that the small butterfly populations will be connected to each other in some way, allowing butterflies to disperse from one remnant patch to another. You are going to help them figure out (1) where to consider restoring prairie, and (2) what aspects of butterfly biology to study in order to confidently choose the best reserve design.

The partnership is considering three different ways to connect remnant patches:

Patch enlargement adds prairie habitat to existing patches, so that the distance between patches is reduced enough to facilitate patch-to-patch butterfly dispersal.

Corridors are bands of prairie habitat that link one existing patch to another.

Stepping stones are smaller patches placed between existing patches. Stepping stones offer stopover points (or "refueling stations") for dispersing butterflies.

PART ONE

- [1] Select **Connections** from the **Select an Exercise** drop-down menu. You will see four irregularly shaped prairie patches, representing the existing patches in the Rivers to Ridges reserve. The total **Prairie Habitat Area** is 70 hectares.

You will also see two new parameters on the **Parameters Panel**, as well as a **Periodic Fires** checkbox. These will be discussed in more detail later. You can always restore parameters to default values using the **RESTORE DEFAULT PARAMETERS** button.

In the next steps, you will practice using tools to create hypothetical reserves where prairie patches are connected using patch enlargement, corridors, or stepping stones. Start with a stepping stones configuration.

- [2] Select the **ADD PRAIRIE** tool from the **Tools Panel** (bottom of the screen) by clicking the "+" button immediately to the right of the **BINOCULARS** button.

- [3] Draw a small rectangle with your mouse in the middle of the prairie patch group. You will see the area turn green, indicating that it is a “stepping stone” of prairie habitat.
- [4] Continue making stepping stones wherever you like until the total **Prairie Habitat Area** is 85 hectares. At this point you’ve created 15 additional hectares of prairie.

If you added too much prairie and need to remove some habitat, select the **REMOVE PRAIRIE** tool by clicking the “-” button in the **Tool Panel** and draw a rectangle around the chunk of prairie to remove. You will see it revert to non-prairie, turning brown. Be careful not to destroy any of the original prairie habitat with the **REMOVE PRAIRIE** tool!

If you want to completely start over, click the blue **RESTORE DEFAULT PATCHES** button below your prairies. This will reload the original four patches in the study area.

- [5] Once you are satisfied with the stepping stone configuration, you can save it to experiment with later. Click the **SAVE PATCHES** button, name the patch configuration (for example, “Stepping Stones Config 1”) and then click OK. You will see this name appear under **My Saved Patches**.
- [6] Click **RESTORE DEFAULT PATCHES** to return to the original patches and then follow steps 2–5 to create and save two more prairie configurations; one representing patch enlargement and one representing corridor options. Each configuration should have a **Prairie Habitat Area** of 85 hectares.

Remember, with corridors, the prairie habitat must be completely contiguous (i.e., touching) between patches. With patch enlargement, no new patches are created.

- [6.1] **Which of your configurations (patch enlargement, corridors, or stepping stones) do you think will result in the largest, most stable population of Fender’s blue butterflies? Explain.**

- [7] Make sure parameters have their default settings and that **Periodic Fires** is unchecked (that is, fires are suppressed). Then conduct a quick experiment to see if your prediction was correct.

- [8] As before, use the **Automator** to collect butterfly population persistence data from the simulation for each of your three patch connection options. You will need to decide whether to focus on extinction rate or average butterfly count (or both) as a measure of persistence. You will also need to decide how many runs to conduct, and how long each run should be.

[8.1] Briefly describe your experimental methods:

[8.2] In the space below, create a table to record your data. Then run your experiment and record your results in the table.

[8.3] Which configuration resulted in the largest, most stable population of butterflies? Was this what you predicted? Explain.

PART TWO: On Your Own

In Part One of this exercise, your answer to the question of which connector type works best for Fender's blue butterflies was based on default parameter values and fire suppression. Is it possible that under different circumstances the best means of patch connection would be different?

As you know, the simulation model you are using includes “best guess” values for parameters. These values can be determined more accurately by field research, which is exactly what the River to Ridges Partnership intends. But field research is costly, in terms of both time and money, so they want to focus on critical parameters. Your next task is to conduct a sensitivity analysis to decide which parameters are critical to determining the best means of patch connection.

As before, you can vary **Leave prairie probability** and **Turn probability (NP)**. You can also vary **Death probability (NP)** and **Crowding sensitivity (P)**. **Death probability (NP)** is exactly what it sounds like—the additional probability that a butterfly in its non-preferred environment will die in one week (butterflies can also die of starvation or old age). **Crowding sensitivity (P)** is a measure of how tolerant butterflies are of each other while in prairie patches: the higher the crowding sensitivity, the more likely they will move away from one another.

You can evaluate simulation outcomes with and without periodic fire. As you've already learned, fire was a key element maintaining the original prairie habitat required by Fender's blue butterflies. It is also a valuable management tool because controlled burning can prevent woody and exotic species from invading restored habitat. But fire can be unpopular when habitat restoration occurs in areas that also include housing developments, private businesses, and public parks. Sometimes suppressing fire creates broader public support for restoration efforts—an important consideration in real-world conservation endeavors.

- [1] Your final challenge is to design and conduct your own sensitivity analysis to identify critical parameters that affect optimal patch connection choice. When you are done, you will present your findings as a letter and short report to the River to Ridges Partnership, as explained below.

Your instructor may provide some guidelines on what to investigate. If not, you will need to (a) state clearly what questions you are asking and (b) plan a systematic approach for answering your chosen questions. This is an open-ended investigation: you will not be able to investigate every possible question so choose questions that are interesting to you! There are no wrong answers.

Play around with the model, to determine what model behavior is interesting, different, and research-worthy in this prairie system. Make additional patch connection plans as needed. (Each must be restricted to 85 hectares of prairie habitat.)

Make some decisions about your research. Record answers to the following questions in your notebook, so that you can organize your research and refer back when preparing your report.

- [1.1] **What habitat configurations do you choose? Make sketches or save screen shots for your report.**
 - [1.2] **What fire regime(s) do you choose to simulate?**
 - [1.3] **Which parameters and parameter values will you investigate?**
 - [1.4] **What number and duration of runs will you conduct for each combination of habitat configuration, fire regime, and parameter value?**
 - [1.5] **Which measure(s) of persistence will you record?**
- [2] Construct data tables for your results. Conduct your sensitivity analysis using the **Automator**. Record your results as you obtain them.
- [3] Analyze your results. Share your findings with the Rivers to Ridges Partnership by writing a letter explaining what you think their top research priorities should be and why. Construct your letter however you think will best make your case.

Consider including the following:

- A short explanation of how you used the butterfly simulation model to investigate the patch connection design challenge.
- An outline of your methods, including which habitat configurations, fire regimes, parameter values, and measure(s) of persistence you examined.
- Graphs of your data (such as those you made in Exercise 3: Sense and Sensitivity), where appropriate.
- Which parameters or fire regimes affected the optimal patch connection design (that is, which model parameters you designate as critical).
- A preliminary recommendation for optimal patch connection design, with justification, if one can be made. If you cannot recommend a specific design at this time, consider stating so and explaining why.
- The top priority (or priorities) for field research to be conducted. That is, what should be studied in order to recommend a specific habitat restoration plan for Fender's blue butterflies?

Wrap-up

Habitat Fragmentation and the Need for Connectivity

Habitat loss is the primary anthropogenic (human-induced) cause of loss of biodiversity. As we humans convert more and more natural habitat for our own uses, we not only reduce the amount of habitat suitable for other species, but we also subdivide remaining habitat into fragments. If individual fragments become too small and/or too isolated, a species may become vulnerable to extinction even if the total amount of its habitat appears sufficient. Such is the case with Fender's blue butterfly and its larval host plant, Kincaid's lupine.

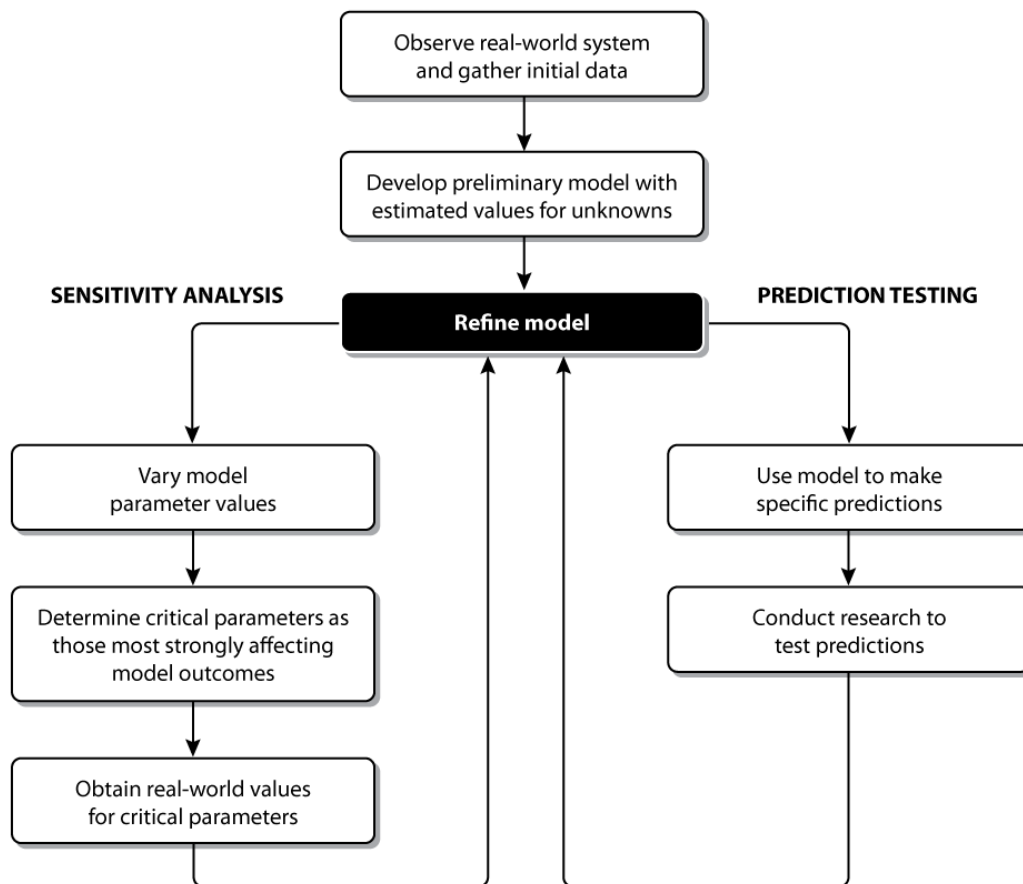
As an individual habitat fragment becomes smaller, organisms living in it face a number of challenges. Most obviously, smaller patches support smaller populations, which incur a higher risk of local extinction. Smaller populations are more likely to succumb to stochastic events such as severe storms, disease outbreaks, and droughts. Inbreeding and loss of genetic diversity can reduce fitness, further threatening species. Small habitat patches also have a relatively high ratio of edge to core habitat, increasing **edge effects**, as you saw in Exercise 1 (Virtual Blues). Depending on the nature of the core habitat and its surroundings, edge effects can include: increased sunlight, temperature, and aridity at the patch's border; the establishment of predator and/or competitor populations that would otherwise not have access to core habitat; and invasion by exotic species.

One way to mitigate the effects of habitat fragmentation is to facilitate dispersal for threatened species. Habitat patches can be connected in a few basic ways, all of which have been used in habitat restoration efforts. As a general rule, corridors are more restrictive. Land necessary to construct corridors is often unavailable for restoration, badly degraded, and/or expensive to restore. In addition, corridors carry risks: they facilitate movement not only of target organisms but also of parasites, pathogens, invasive exotics, and disturbance. Stepping stones, in contrast, might already be available as existing patches too small to support sustained populations but well-positioned to connect larger patches. Logistics and practicality aside, understanding the biology of the target species is crucial in determining which strategy will be best.

Modeling and Its Role in Conservation

With so many factors involved in determining an optimum recovery strategy for endangered species, and so much about their biology often unknown, developing sound restoration plans is extremely difficult at best. And, given the stakes, using a trial-and-error approach is hardly an option. This is why modeling can play a significant role, as it has for Fender's blue butterflies.

The big picture is illustrated in the figure below. Model development begins as scientists observe some system of interest (a group of individuals, a population, a community, a landscape, etc.). Based on initial data, modelers develop a preliminary mathematical model that describes the basic system. At this point, the goal is to refine the model so that it truly embodies the essential system behavior. You've practiced one method—sensitivity analysis—in this lab. By varying model parameters, you determined which most strongly affected the model's outcomes. In the real world, such results would drive research to obtain better values for these critical parameters.



Another important method for refining models is prediction testing—which is exactly what it sounds like. In this case, the model outcome is treated as a prediction for what should happen in real life if the model has captured the system's essential properties. The predictions are compared with empirical observations and the results are used to refine the model further.

A sufficiently refined model can be put to work to guide habitat restoration efforts. Models are used to answer such questions as whether corridors or stepping stones is the better option, and how corridors or stepping stones should be configured to assist dispersal.

Modeling Fender's Blue Butterfly

Dr. Cheryl Schultz and her colleagues have been using precisely this approach for the restoration of Fender's blue butterfly in Western Oregon. With their first, simplest model based on field data of movement behavior, they determined that butterflies were not sufficiently habitat-specific for corridors to be useful. Stepping stones seemed viable, as long as patches were no more than about 1 km apart (Schultz 1998). Later investigations into how butterflies respond to edge habitat suggested that butterflies stayed in small patches for shorter periods of time than they did in larger patches (Schultz and Crone 2001). Combined with additional work on fecundity and survival, Schultz and Crone were able to determine that high-quality habitat patches of less than about 5 hectares would be too small to support persistent populations, if those populations were isolated from other patches (Schultz and Crone 2003).

Fender's blue researchers then developed a complex model that allowed them to include the sizes and locations of existing and potential habitat patches within the West Eugene Wetlands restoration area and to make more specific, detailed recommendations for restoration work. In addition, that model also resulted in new insights, particularly about the relationship between connectivity and population dynamics. They discovered, for example, that when nearby patches are restored, populations in small patches that would normally remain well under carrying capacity will grow to near carrying capacity. Conversely, as population size increases within a patch, individuals are more likely to move to new patches—population size thus influences connectivity (McIntire et al. 2007). None of these results would have been obtainable without combining long-term field research with a variety of modeling approaches.

So where does that leave Fender's blue? In 2010, the U.S. Fish and Wildlife Service published its Recovery Plan for the Prairie Species of Western Oregon and Southwestern Washington. Developed in part based on the modeling work described above, this document sets out a plan for ensuring the long-term recovery of 5 species, including Fender's blue butterfly and Kincaid's lupine. The projected cost of implementation through 2035 (the earliest projected date for the recovery of Fender's blue) is \$16,590,000, however, so the plan's success is far from certain.

Annotated References

Crone, E. E. and C. B. Schultz. 2003. Movement behavior and minimum patch size for butterfly population persistence. Pages 561-576 in C. Boggs, P. Ehrlich, and W. Watt

Crone and Schultz collected and analyzed movement and demographic data to establish a minimum patch size of 2 ha for Fender's blue butterfly population persistence.

Crone, E. E. and C. B. Schultz. 2008. Old models explain new observations of butterfly movement at patch edges. *Ecology* 89: 2061-2067.

Crone and Schultz emphasize the utility of the biased correlated random walk model of movement behavior to explain edge-mediated butterfly behaviors.

McIntire, E. J. B., C. B. Schultz, and E. E. Crone. 2007. Designing a network for butterfly habitat restoration: where individuals, populations, and landscapes interact. *Journal of Applied Ecology* 44: 725-736.

McIntire and colleagues built a full, demographically complex, spatially-explicit landscape model to address the specific questions of (a) whether Fender's blue butterflies can persist with certain scenarios of prairie restoration, and (b) whether certain non-ideal patches were suitable for inclusion in the reserve design.

Schultz, C. B. 1998. Dispersal behavior and its implications for reserve design in a rare Oregon butterfly. *Conservation Biology* 12: 284-292.

Schultz studied Fender's blue butterfly dispersal and movement. She determined that successful reserve connectivity should have inter-patch distances of 1.0 km or less. She also suggested that corridors were not warranted because butterflies readily leave natal habitat.

Schultz, C. B., and E. E. Crone. 2001. Edge-mediated dispersal behavior in a prairie butterfly. *Ecology* 82: 1879-1892.

Schultz and Crone measured Fender's blue butterfly behavioral responses to edges and modeled dispersal in different ways to determine that only models including appropriate edge-mediated movement behavior accurately predicted residence time in patches.

Schultz, C. B. and E. E. Crone. 2005. Patch size and connectivity thresholds for butterfly habitat restoration. *Conservation Biology* 19: 887-896.

Schultz and Crone used two models to evaluate previous minimum patch size (2 ha) and connectivity (1 km) recommendations. The models yielded different predictions: the non-mechanistic incidence function model suggested patch size and connectivity were equally important, but the spatially explicit individual-based model predicted that small connected patches were of higher restoration value than were larger, more isolated patches.

U.S. Fish and Wildlife Service. 2010. Recovery Plan for the Prairie Species of Western Oregon and Southwestern Washington. U.S. Fish and Wildlife Service, Portland, Oregon. xi + 241 pp.

This USFWS document includes recovery plans for both Fender's blue butterfly and Kincaid's lupine. Cheryl Schultz and Tom Kaye (currently of the Institute for Applied Ecology) are co-leaders of the Recovery Team.