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EDGE EFFECTS AND ECOLOGICAL TRAPS

Objectives

- Understand the concept of an ecological trap
- Set up a population model for populations in edge and core habitat.
- Be able to differentiate between “trap” and “sink” habitat.
- Evaluate how selection for edge and core habitat affects population persistence.

Suggested Preliminary Exercises: Geometric and Exponential Population Models; Logistic Population Models; Source-Sink Dynamics

INTRODUCTION

As we have said in earlier exercises, not all habitats are created equal. Some habitats are higher in quality for reproduction or survival than others; yet individuals appear to occupy or even “select” both kinds of habitat to carry out their life histories. Bobolinks (*Dolichonyx oryzivorus*), for example, are long-distance migratory songbirds that breed in grassland habitats in North America. In the springtime, they set up territories in both native prairies and in hayfields. Bobolinks that nest in prairies tend to have higher reproductive success (number of offspring produced per female per year) than Bobolinks that nest in hayfields because hayfields are often harvested before young can successfully fledge the nest. When the hay is harvested early in the breeding season, nests are destroyed and Bobolink reproductive success plummets. Yet Bobolink population densities on hayfields can be equal to or greater than on native prairies (Bollinger and Gavin 1992). This may be because hayfields look like prime nesting habitat in the early spring when Bobolinks begin to establish breeding territories. If Bobolinks actually “prefer” hayfields to native prairie, the hayfields may be an **ecological trap**.

What exactly is an ecological trap? Most organisms occur in both low- and high-quality habitats. If you have completed the Source-Sink exercise, you know that **source** populations occupy high-quality habitats that promote high birth and survival rates. In contrast, **sink** populations occupy habitats that have low birth and survival rates—so low that the population would go extinct in the absence of immigrants from the source. Just because a habitat is low in quality for a given species, however, does not mean it is an ecological trap. The essence of an ecological trap is that it is low in quality for reproduction or survival and cannot sustain a popu-

lation, yet it is *preferred* over other available, higher-quality habitats (Donovan and Thompson 2001). For example, if a landscape consists of 60% high-quality habitat and 40% low-quality, sink habitat, but more than 40% of the individuals actively “select” the poor habitat for breeding, the low-quality habitat may function as a trap. This assumes that individuals are “free” to choose habitats and are able to breed where they choose. Low-quality habitat that is not preferred beyond its availability is not likely to have the same effect on a population as an ecological trap, but low-quality habitat may lead to extirpation if it becomes a dominant habitat for reproduction and survival (Donovan and Thompson 2001).

Habitat edges have long been hypothesized as “ecological traps” for songbirds (Gates and Gysel 1978). **Edges** are defined as borders between two different habitat types, such as an agricultural field that abuts a forest. In contrast, core habitat is habitat that is buffered some distance from an edge. Birds sometimes occur in higher densities along edges, perhaps because edge habitat offers a variety of foods and niches that core (interior) habitats may lack. However, birds nesting in edges often experience greater reproductive failure than birds nesting in core habitats. In a landscape that consists of edge and core habitat, how much edge can there be and still allow population persistence? How does habitat “selection” for edge habitat influence how much edge can remain on the landscape?

In this exercise, you’ll set up a model to explore these questions. You will model an organism that breeds in edge and core habitats, where each habitat type has its own, unique reproductive and survival parameters. We will assume that our census of the population occurs just after individuals breed, and that only females are censused. We will assume that any young birds censused in year t have some probability of surviving to the following year; those individuals that survive select breeding territories in year $t+1$ and attempt to raise their first clutch of offspring. This selection of breeding habitat will be set by a selection coefficient in the model. Those individuals that are able to secure breeding territories in their preferred habitat will continue to select that breeding habitat throughout their reproductive life. At times, the preferred habitat will be at the carrying capacity, and some individuals will not be able to secure a breeding location. These individuals will attempt to find a breeding location in their non-preferred habitat. If the non-preferred habitat is also full, they will disperse out of the population. Once adults settle into a breeding territory, they will reproduce at rates that are specific to the habitat type—core habitats will have higher per capita birth rates than edge habitats. Immediately after young are produced a census is taken, and the total numbers of adults and young in the system are counted. We are interested in the equilibrium population size, as well as understanding the conditions that lead to population extirpation.

How can we write equations to reflect such a life history? To begin, we can write very simple equations expressing the relationship between population size and two demographic processes, birth and survival.

Let

N_t represent the number of breeding adults and young in the population at some arbitrary time t

N_{t+1} represent the number of breeding adults and young in the population one arbitrary time-unit later

B_t represent the total number of births in a particular habitat type

N_a represent the total number of breeding adults in the population in a particular habitat type

K represent the carrying capacity of a given habitat type

b represent the per capita birth rate for a particular habitat type

s_j represent the per capita survival rate of juveniles, or the probability that an offspring born in year t will survive to counted as an adult in the next time unit

s_a represent the per capita survival rate of adults, or the probability that an adult in year t will survive to counted again as an adult in the next time unit

In our record keeping, we will need to count the number of young produced in a given habitat (edge or core). The total number of young produced at time t will be represented by a capital B . It is computed as the per capita birth rate (b) times the number of adults breeding in the habitat. This is simply

$$B_t = b \times N_t \quad \text{Equation 1}$$

It follows that we need to count the number of adults that breed in a given habitat, N_t . The numbers of adults that breed in a habitat are supplied from two places. The first source of adults is the adults that were in the habitat in the previous year (year $t - 1$) that survived to be counted in the same habitat as adults in year t :

$$N_{a(t)} = N_{a(t-1)} \times s_a \quad \text{Equation 2}$$

The second source of adults in year t in a particular habitat consists of young born in year $t - 1$ that survived to be counted as first-time breeders *and* that secured a breeding territory in the habitat. Remember that young are produced in *both* habitat types; those produced in the edge habitat will survive to adulthood with some probability, and those produced in the core habitat will survive with some probability. Upon the arrival of the breeding season, the individuals that survived to breeding age will be pooled together, and some portion will select edge habitat for breeding, and the other portion will select core habitat. The proportion that attempt to breed in the core habitat type is designated by α . The remaining individuals attempt to breed in the edge habitat type ($1 - \alpha$). If we designate the edge habitat with a subscript e and a core habitat with a subscript c , we can compute the total number of individuals that attempt to secure their first breeding locations in the core habitat as

$$N_{a(c,t)} = (N_{a(c,t-1)} \times b_c \times s_{j(c)} + N_{a(e,t-1)} \times b_e \times s_{j(e)}) \times \alpha \quad \text{Equation 3}$$

The term in parentheses in Equation 3 simply gives the total number of new adults (born last year) seeking breeding locations. And the total number of individuals that attempt to secure their first breeding locations in the edge habitat is

$$N_{a(e,t)} = (N_{a(c,t-1)} \times b_c \times s_{j(c)} + N_{a(e,t-1)} \times b_e \times s_{j(e)}) \times (\alpha - 1) \quad \text{Equation 4}$$

Equations 3 and 4 thus provide the number of new adults attempting to breed in each habitat type. With many species, breeding habitats have carrying capacities, such that not all individuals that attempt to secure a territory will be successful. We will assume for this model that such individuals will attempt to breed in the non-preferred habitat type if the preferred habitat is full. If both habitats are full, individuals leave the system and are no longer considered in the model.

PROCEDURES

You will use formulae based on equations 1–4 to develop a two-habitat model and explore how habitat selection affects population persistence. This model is a modification of Pulliam’s original source-sink model (1988). The basis of an ecological trap is that it is attractive to individuals ($\alpha >$ the proportion of poor-quality habitat in the landscape), and is low in quality in terms of s_a , s_j , and b . These parameters, as well as the amount of each kind of habitat in the landscape, play a critical role in determining whether the population will persist or go extinct. The model you are about to develop will allow you to explore these relationships.

As always, save your work frequently to disk.

INSTRUCTIONS

A. Set up the model parameters.

1. Open a new spreadsheet and set up headings as shown in Figure 1. Enter 800 in cell D5 and 200 in cell F5.

2. Calculate the proportion of core and edge habitat in cells D6 and F6.

3. Enter 100 in cells D7 and F7.

4. Enter the per capita birth and survival parameters shown in cells D8–D10 and F8–F10.

5. Enter the maximum density of females per hectare as shown in cells D11 and F11.

6. Calculate K for the core habitat in cell D12 and edge habitat in cell F12.

ANNOTATION

	A	B	C	D	E	F	G
1	Edge Effects and Ecological Traps						
2							
3				Model Input Parameters			
4				Core		Edge	
5	Amount of habitat (hectares) =			800		200	
6	Proportion of habitat =			0.8		0.2	
7	Initial population size =			100		100	
8	Birth rate = b =			1.2		0.5	
9	Adult survival = s_a =			0.6		0.6	
10	Juvenile survival = s_j =			0.4		0.3	
11	Number of females / 1 ha =			1		2	
12	K = total females =			800		400	
13	Selection coefficient = α =			0.8		0.2	= $1-\alpha$

Figure 1

We'll start with a landscape that consists of 800 hectares of core habitat and 200 hectares of edge habitat.

Enter the formula `=D5/(D5+F5)` in cell D6.

Enter the formula `=F5/(D5+F5)` in cell F6.

We calculate the proportion of core and edge habitats as the amount of each type divided by the total habitat.

We'll start with a population of 100 adults in core habitat and 100 adults in edge habitat. Remember that the number of adults in any given year consists of adults that were breeders in the previous year that survived to breed again, plus "first year" adults that will breed for their first time.

The birth rates, b , are number of offspring per adult female per year. There are two survival rates, s_a and s_j . The first rate is the probability that an adult in the previous year will survive to breed again. The second rate is the probability that a young born in the previous year will survive to breed for the first time as an adult. These values in concert establish how suitable the core and edge habitats are. Because we are modeling edge effects, where there is a decrease in fitness associated with edge habitat, the parameter values should reflect edge as a lower quality habitat than core.

The density of females will dictate the number of individuals per unit area that can breed in edge and core habitat. Since edge is considered a potential "ecological trap," we will start by assuming that there is something about the edge habitat (food abundance, perhaps) that can accommodate more females per hectare than core habitat.

Enter the formula `=D11*D5` in cell D12.

Enter the formula `=F11*F5` in cell F12.

K is the total carrying capacity of the core and edge habitats. It is a function of both the total amount of habitat, as well as the maximum density of breeders in a habitat.

7. Enter the selection coefficients shown in cells D13 and F13.

8. Save your work.

B. Set up the populations for year 0.

1. Set up new headings as shown in Figure 2.

2. Set up a linear series from 0 to 50 in cells A19–A69.

3. In cell C19, enter =D7. Enter =F7 in cell H19.

4. Calculate the total births in core habitat (cell D19) and edge habitat (cell I19).

5. In cell B19, calculate the total number of individuals in the system (edge and core).

6. Save your work.

C. Set up the populations for years 1–50.

1. In cell E20, enter a formula to calculate the potential new adults to core habitat.

2. In cell J20, calculate the potential new adults in edge habitat.

The selection coefficient establishes how “attractive” edge and core habitats are to dispersing individuals. In this model, only the individuals born last year and survive to breeding age select habitats. Once the habitat has been selected, older individuals remain in that habitat type for life. A selection coefficient of 0.8 for core habitat indicates, for example, that 80% of the new adults will seek breeding locations in the core habitat, and 20% of the new adults will seek breeding locations in the edge habitat.

We are now ready to track the dynamics of our edge and core populations for 50 years.

	A	B	C	D	E	F	G	H	I	J	K	L
16					CORE				EDGE			
17			Total	Total	New Adults			Total	Total	New Adults		
18	Year	Total	adults	births	Potential	Success	Unsuccessful	adults	births	Potential	Success	Unsuccessful

Figure 2

Enter 0 in cell A19.

Enter =1+A19 in cell A20 and copy the formula down to cell A69.

We’ll start with 100 adults in the core habitat and 100 adults in the edge habitat. Later in the exercise, you will change the starting number of adults and determine how these initial numbers affect your model.

Enter the formula =C19*\$D\$8 in cell D19.

Enter the formula =H19*\$F\$8 in cell I19.

These are the spreadsheet version of Equation 1, $B_t = b \times N_t$ for each habitat type. The total number of births in a particular habitat is the number of adults (females) times the birth rate for that habitat.

Enter the formula =C19+D19+H19+I19 in cell B19.

Remember that our census occurs immediately after the breeding season, so the total count of individuals will include both adults and young.

Enter the formula =(D19*\$D\$10+I19*\$F\$10)*\$D\$13 in cell E20.

This formula is a version of Equation 3, $N_{a(c,t)} = (N_{a(c,t-1)} \times b_c \times s_{j(c)} + N_{a(e,t-1)} \times b_e \times s_{j(e)}) \times \alpha$. The formula sums the total number of young produced last year in the each habitat type (adjusted by the survival probabilities for the each habitat), and then multiplies this total by α , the selection coefficient for the core habitat. The potential new adults to the core habitat are the total number of individuals born last year that survived to the current year. The column is labeled “potential adults” because not all individuals seeking a breeding location will necessarily attain a breeding location; it depends on how many returning adults there are and how “full” the habitat is relative to K .

Enter the formula =(D19*\$D\$10+I19*\$F\$10)*\$F\$13 in cell J20.

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3. In cell F20, use an IF formula to determine the number of successful new adults to the core habitat.

Enter the formula `=IF(C19*D9+E20<D12,E20,D12-(C19*D9))` in cell F20. This formula tells the spreadsheet to determine whether $C19 * \$D\$9 + E20 < \$D\12 . The left side of the inequality which is the number of adults from the previous year multiplied by their survival probability plus the number of potential immigrants. IF this number is less than K for the core habitat (given in cell $\$D\12), then the program returns the value in cell E20, so all of the new adults attempting to breed in the core successfully attain breeding habitats. If the term $C19 * \$D\$9 + E20$ is *not* less than K , then only a fraction of the immigrants will successfully attain breeding locations in the core. How is this fraction determined? The term $\$D\$12 - (C19 * \$D\$9)$ tells us. It is the carrying capacity minus the number of returning adults. This result gives the number of "openings" available to the new breeders.

4. In cell K20, calculate the number of successful immigrants to the edge habitat.

We used the formula `=IF(H19*F9+J20<F12,J20,F12-(H19*F9))` in cell K20.

5. In cells G20 and L20, calculate the number of unsuccessful new adults.

Enter the formula `=E20-F20` in cell G20.
Enter the formula `=J20-K20` in cell L20.
The immigrants that were unsuccessful will attempt to attain a breeding territory in the non-preferred habitat type. Their success in the non-preferred habitat type will also depend on K , and is accomplished in the next step. If K is full in both habitats, the unsuccessful new breeders will disperse out of the system and will not be considered in the model.

6. In cell C20, enter a formula to calculate the total number of adults censused in the core in year 1.

Enter the formula `=IF(C19*D9+F20+L20<D12,C19*D9+F20+L20,D12)` in cell C20.
The total number of adults censused in the core is the total number of adults from the previous year that survived, plus any new adults that successfully attained a breeding location (individuals born last year and are now considered adults). The new adults include those that attempted to breed in preferred source habitat that successfully attained a breeding territory (cell F20), plus any unsuccessful new adults that attempted to breed in the edge habitat but were unsuccessful (cell L20). The IF formula in cell C20 examines the total adults, old and new. If the total is greater than K in the core (cell D12), the total returned will be K ; otherwise it will simply be the sum of the returning and new adults.

7. Calculate the total edge adults in cell H20.

Enter the formula `=IF(H19*F9+K20+G20<F12,H19*F9+K20+G20,F12)` in cells D20 and I20.
This is similar to the formula you entered in cell C20. The new adults include those that successfully attained a breeding territory in edge habitat, plus those individuals that attempted to breed in the core but did not locate a territory.

8. Calculate the total births for year 1 in cells D20 and I20.

Enter the formula `=C20*D8` in cell D20.
Enter the formula `=H20*F8` in cell I20.

9. Compute the total number of individuals in the edge-core system in year 1 in cell B20..

Enter `=C20+D20+H20+I20` in cell B20. Copy cells B20–L20 down to year 50.

10. Save your work.

D. Create graphs.

1. Graph the total adults, total core adults, and total edge adults as a function of time.

Use the line graph option and label your axes fully. Your graph should resemble Figure 3.

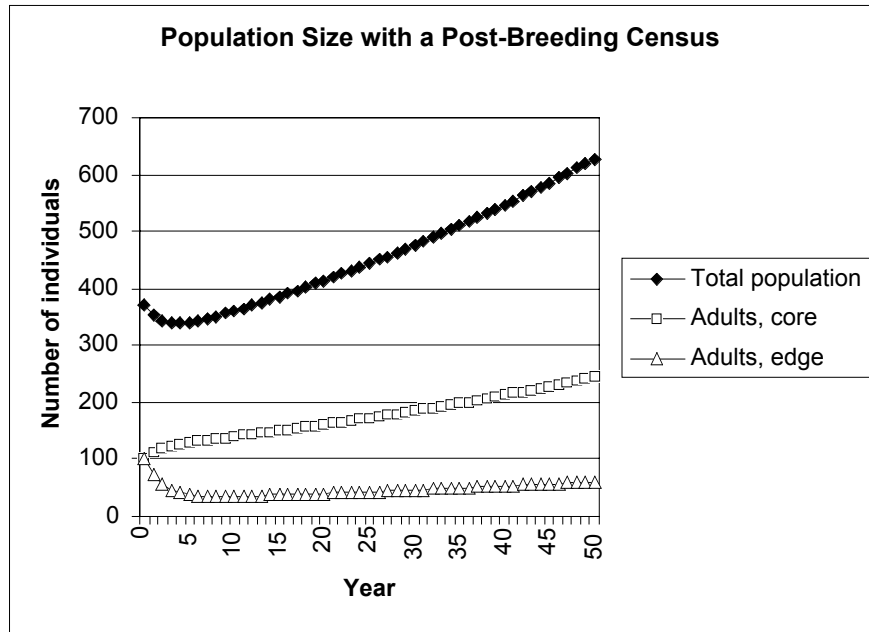


Figure 3

2. Graph the number of potential and successful new adults to edge and core habitats as a function of time.

Your graph should resemble Figure 4. Here, success indicates success in attaining a breeding territory. In both cases, "Potential" equals "Successful" and the lines overlap completely.

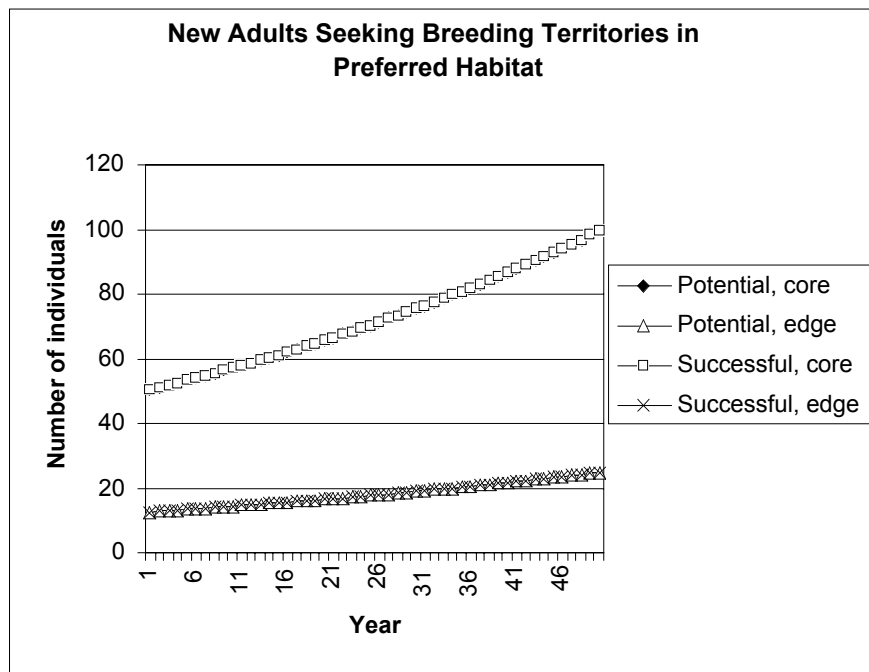


Figure 4

3. Save your work.

QUESTIONS

1. Fully interpret your model results. Given the initial parameters, describe the population growth of each habitat type: does the population increase, decrease, or remain stable in the short term and in the long term? Is the entire system (core plus edge) increasing, decreasing, or remaining stable? Does the population reach an equilibrium point in 50 years? Why or why not?
2. The essence of an ecological trap is that it is poor in quality compared to other habitat types, *and* that it is selected beyond its availability in the landscape. Keep your survival and fecundities at the initial levels, but change the selection coefficient to 0.7. Thus, although the system contains 80% core habitat, only 70% of new adults actively seek out core for breeding, while the other 30% actively seek out edge for breeding. How do the dynamics of the system change?
3. Assume that the selection of habitats is 0.5 for core and 0.5 for edge. In other words, it's a coin flip to dispersing individuals as to which habitat they will attempt to breed in. Also assume that survival values in the edge are 0.5 times that of the core as shown below. What levels of reproduction are needed in the core habitat to sustain the population? Enter values from 2.0 to 2.75 in cell D8 in increments of 0.25 and examine your graphs. Interpret the population dynamics under these conditions.

	A	B	C	D	E	F	G
3				Model Input Parameters			
4				Core		Edge	
5	Amount of habitat (hectares) =			800		200	
6	Proportion of habitat =			0.8		0.2	
7	Initial population size =			100		100	
8	Birth rate = b =					0.5	
9	Adult survival = s_a =			0.5		0.25	
10	Juvenile survival = s_j =			0.4		0.2	
11	Number of females / 1 ha =			1		2	
12	K = total females =			800		400	
13	Selection coefficient = α =			0.5		0.5	= $1 - \alpha$

4. Enter a formula in cells D13 and F13 so that individuals select core and edge habitat in the proportions that are available (given in cells D6 and F6). Keep the birth rate at 2.75 in the core habitat. How much loss of core habitat can the system tolerate and still remain viable? Given this required amount of core habitat, are there any conditions in which this population can persist if the edge functions as a trap?
5. Examine the literature and look for potential examples of ecological traps. Do your model results apply to the organisms studied? How can you adjust your model to mimic the life-history of the organism studied and examine potential affects of ecological traps?
6. Ask an interesting questions about habitat amount and habitat selection and use your model to answer it.

LITERATURE CITED

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