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SOURCE-SINK DYNAMICS

Objectives

- Set up a population model of two subpopulations that interact through dispersal.
- Determine how birth, death, and dispersal between source and sink habitat affect population persistence.
- Determine how the initial distribution of individuals among source and sink habitat affects population dynamics.
- Examine the conditions in which a source-sink system is in equilibrium.

Prerequisite Exercise: Geometric and Exponential Population Models

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INTRODUCTION

If you could spend your life anywhere in the world, where would it be? A Hawaiian island? The Peruvian Andes? The French Riviera? Midtown Manhattan? A village in Bosnia? The rain forest of Madagascar? The Gobi Desert? New Zealand's South Island? In thinking about your choice, it becomes obvious that all habitat patches are not created equal.

For any given species, some habitats are superior to others for individual survival and reproduction. The fact that patch quality is heterogeneous (mixed) and that individuals of a population occupy different kinds of patches is an important consideration in predicting the population dynamics of a species. **Source-sink theory** addresses the issue of such heterogeneity. **Sources** are areas or locations where local reproductive success is greater than local mortality (Pulliam 1988). Alas, not all patches are optimal, and some individuals of a population may be forced to occupy poorer quality patches that lead to low birth rates and high death rates. These areas or locations are called **sinks**, because the populations occupying them will spiral "down the drain" to extinction unless they receive immigrants from other locations—usually a source.

Why would individuals disperse from a high-quality source habitat to a low-quality sink habitat? Because resources are limited, not all individuals can obtain breeding sites in the source. Individuals unable to find a breeding site in the source emigrate to the sink because, from a fitness perspective, even a poor-quality breeding site may be better than none at all (Pulliam 1988).

If we want to project the size of a population in which some individuals reside in source habitats and others reside in sink habitats, we need to consider the pop-

ulation dynamics of each source and sink **subpopulation**, and then consider how the distribution of individuals in sources and sinks influences the dynamics of the greater source-sink system. How can such a population be modeled? If you have completed Exercise 7, "Geometric and Exponential Population Models," you may recall that the most basic way to describe population growth is through the equation

$$N_{t+1} = N_t + B_t - D_t + I_t - E_t \qquad \text{Equation 1}$$

where

N_t represents the size or density of the population at some arbitrary time t
N_{t+1} represents the population size one arbitrary time unit later
B_t represents the total number of births in the interval from time t to time $t+1$
D_t represents the total number of deaths in the same time interval
I_t represents the total number of immigrants in the same time interval
E_t represents the total number of emigrants in the same time interval

Birth, death, immigration, and emigration are the four "biggies" in population dynamics. In concert, they determine whether a population will grow or decline over time, and are often called the **BIDE factors**. If you have completed the exercise "Geometric and Exponential Population Models", you modeled a population in which dispersal was neglible, and hence I and E were set to 0. However, in source-sink dynamics, the movement of individuals from one population to another must be considered, and changes in numbers over time must therefore include the movements of individuals into the population (immigration, I) and the movement of individuals out of the population (emigration, E). To make population projections of a source-sink system, we need to know the numbers of individuals in each habitat type, as well as the BIDE factors for each habitat type. Thus, two equations are needed: one for the source population, and one for the sink. We will consider these equations for a population that grows in discrete time, rather than for a continuously growing population.

To begin, let's think about a single habitat, say, the source. What controls the total number of births (B), immigrants (I), deaths (D), and emigrants (E) in the source habitat? If we switch from *total* numbers to *per capita* rates, we can do some fruitful modeling. A **per capita rate** is a per individual rate; the per capita birth rate is the number of births per individual in the population per unit time, and the per capita death rate is the number of deaths per individual in the population per unit time. Similarly, per capita immigration and emigration rates are the number of immigrants and emigrants per individual per unit time.

Per capita birth rate and immigration are easy to understand; they are the number of new individuals per individual that enter the population through birth or immigration. Per capita death and emigration rates may seem strange at first because they reflect the number of deaths or emigration events per individual per unit time, and usually these things happen to individuals only once. But you can think of these rates as each individual's risk of dying in a given unit of time, or the chance of exiting the population through dispersal in a given unit of time.

Keeping in mind that per capita rates are per individual rates, we can translate raw numbers (B_t, I_t, D_t, and E_t) into per capita rates, which we will represent with lower-case letters (b_t, i_t, d_t, and e_t) to distinguish them from raw numbers. All we have to do is divide the raw numbers by N_t, the population size at time t:

$$b_t = \frac{B_t}{N_t} \text{ and } B_t = b_t N_t$$

$$i_t = \frac{I_t}{N_t} \text{ and } I_t = i_t N_t$$

$$d_t = \frac{D_t}{N_t} \text{ and } D_t = d_t N_t$$

$$e_t = \frac{E_t}{N_t} \text{ and } E_t = e_t N_t$$

Because we assume constant per capita rates, we can make one further, minor modification to our equation by leaving off the time subscripts on b, i, d, and e. Thus,

$$N_{t+1} = N_t + bN_t + iN_t - dN_t - eN_t \qquad \text{Equation 2}$$

We can further simplify this model by factoring N_t out of the birth, immigration, death, and emigration terms:

$$N_{t+1} = N_t + (b + i - d - e)N_t \qquad \text{Equation 3}$$

The term $(b + i - d - e)$ is so important in population biology that it is given its own symbol, R and is called the **geometric rate of natural increase**. Thus*

$$R = b + i - d - e$$

Substituting R into Equation 3 gives us

$$N_{t+1} = N_t + RN_t \qquad \text{Equation 4}$$

We can calculate the *change* in population size, ΔN_t, by subtracting N_t from both sides of this equation:

$$N_{t+1} - N_t = RN_t$$

Because $\Delta N_t = N_{t+1} - N_t$, or the difference in population size over time, we can substitute and write

$$\Delta N_t = RN_t \qquad \text{Equation 5}$$

In words, the rate of change in population size is proportional to the population size, and the constant of proportionality is R. We can convert this to per capita rate of change in population size if we divide both sides by N_t:

$$\Delta N_t / N_t = R \qquad \text{Equation 6}$$

In words, the parameter R represents the per capita rate of change in the size of the population. If you'd like to determine how R will affect population size from one time step to the next, you can start with Equation 4, and then factor N_t out of the terms on the right side to get

$$N_{t+1} = (1 + R)N_t \qquad \text{Equation 7}$$

The quantity $(1 + R)$ is often given its own symbol, λ, or the **finite rate of increase**, and so we can write

$$N_{t+1} = \lambda N_t \qquad \text{Equation 8}$$

When $\lambda = 1$, the population size remains constant (unchanged) over time; when $\lambda > 1$, the population increases geometrically; and when $\lambda < 1$, the population declines geometrically.

Now let's return to the topic of sources and sinks. Without dispersal, a source can be defined as a subpopulation where $\lambda > 1$. This occurs only when $b > d$. A sink can be defined as a subpopulation where $\lambda < 1$, which occurs when $d > b$. With dispersal (immigration and emigration), a source or sink subpopulation is in dynamic equilibrium (not changing) when $B + I - D - E = 0$. Thus, because births are greater than deaths in a source population, to maintain an equilibrium number of individuals, the source must export individuals to other locations ($b > d$ and $e > i$). In contrast, for a sink to be in equilibrium, it must import individuals because deaths outnumber births ($d > b$ and $i > e$).

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*In Exercise 7, R was defined simply as $b - d$ because in that exercise i and e were assumed to be 0.

How is the equilibrium size of the greater population (source and sink) determined? If there are many habitats, the population reaches equilibrium when the total surplus in all the source habitats equals the total deficit in all the sink habitats. Some basic take-home points from Pulliam's (1988) source-sink model are:

- At equilibrium, the *number of individuals* in the overall, greater population is not changing.
- Each source and sink subpopulation can be characterized by its "strength," depending on its intrinsic rate of growth and the number of individuals present. Within-subpopulation dynamics (*b*, *i*, *d*, *e*) are important in determining the overall equilibrium population size, since the numbers of individuals on each patch and their growth rates are implicit in the model.
- The source-sink status of a subpopulation may have little to do with the size (number of individuals) within the subpopulation. Sinks can support a vast number of individuals and sources can be numerically very small. However, sources must have enough individuals with a high enough per capita production to support sink populations.

PROCEDURES

In this exercise you will develop a simple source-sink model in which dispersal occurs from the source to the sink when the source reaches its carrying capacity. We will consider only the female portion of the population and assume that there are plenty of males available for reproductive purposes. Once the model is constructed, you will be able to explore how the different BIDE parameters, population sizes, and carrying capacities influence the source-sink system. As always, save your work frequently to disk.

INSTRUCTIONS	ANNOTATION

A. Set up the basic spreadsheet.

1. Open a new spreadsheet and set up headings as shown in Figure 1.

	A	B	C	D	E	F
1	*Source - Sink Model*					
2						
3				**Constants**		
4		**Source**			**Sink**	
5		$N_0 =$	10		$N_0 =$	100
6		$K =$	25		$b =$	0.4
7		$b =$	0.5		$d =$	0.5
8		$d =$	0.2			
9		$i =$	0.1			

Figure 1

2. Enter the starting number of individuals, N_0; carrying capacity, K; and BIDE rates for the source and sink habitat as shown in Figure 1.

In our source-sink model, we will assume that the source has a carrying capacity (see Exercise 8, "Logistic Population Models") because not all individuals can occupy prime habitat. In the source, the birth, death, and immigration rates are constants that can be modified. The emigration rate, *e*, is not a constant but is calculated as the per capita number of individuals that leave the source after the carrying capacity has been reached. We will assume that the sink has no carrying capacity and that "poor quality" habitat is plentiful. The immigration rate into the sink, *i*, is not a constant but is calculated as the per capita number of individuals that disperse from the source to the sink habitat.

B. Project population size in a source over time.

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

	A	B	C	D	E	F	G	H	I	J
12					**SOURCE**					
13			Total	Total	Total	Total	Total	Delta		
14	Year	N-Source	births	deaths	immigrants	emigrants	source	*N*	*R*	λ

Figure 2

2. Set up a linear series from 0 to 20 in cells A15–A35.

Enter 0 in cell A15.
Enter **=1+A15** in cell A16. Copy this formula down to cell A35.

3. In cell B15, link the starting number of individuals in the source population to cell C5.

Enter **=C5** in cell B15.

4. In cells C15–E15, enter formulae to compute *B*, *D*, and *I* (the total numbers of births, deaths, and immigrants) in the source population.

Remember that the numbers of births, deaths, and immigrants in the source depends on the per capita rates given in cells C7–C9, as well as the number of individuals currently in the population, N_t. Enter the following formulae:

- C15 **=B15*C7**
- D15 **=B15*C8**
- E15 **=B15*C9**

5. In cell F15, use an IF function to compute the total number of emigrants from the source as the number of individuals in excess of the source's carrying capacity.

Enter the formula **=IF(B15+C15-D15+E15>C6,B15+C15-D15+E15-C6,0)**. This formula is long, but is really a simple **IF** formula with three parts, each part separated by a comma.

The first part is the criterion; our criterion is **B15+C15-D15+E15>C6**, which tells the spreadsheet to evaluate whether $N_t + B - D + I$ is greater than the source's carrying capacity (which is given in cell **C6**). If this criterion is **TRUE**, the program carries out the second part of the formula. If this criterion is **FALSE**, it carries out the third part of the formula.

Thus, if the number of individuals in the source is below carrying capacity (i.e., the criterion is **FALSE**), the number of emigrants from the source will be 0, and the spreadsheet will return the number 0 in cell F15. If the number of individuals in the source is above *K* (the criterion is **TRUE**), the number of emigrants from the source is computed as **B15+C15-D15+E15-C6.**

6. In cell G15, compute the total number of individuals in the source as $N_0 + B + I - D - E$.

We entered the formula **=B15+C15-D15+E15-F15**.

7. In cell H15, enter a formula to compute Δ*N*.

Enter the formula **=C15-D15+E15-F15**. The formula **=G15-B15** gives the same result. (Remember that you can generate the delta symbol, Δ, by typing in a capital D, selecting it, and changing its font to Symbol.)

8. In cell I15, compute *R* as Δ*N*/*N* to generate the *per capita* rate of population change.

Enter the formula **=H15/B15**.

9. In cell J15, compute λ as *R* + 1.

Enter the formula **=1+I15**. Note that λ can also be computed as N_{t+1}/N_t. You can generate the λ symbol by typing in the letter l, then selecting this letter on the formula bar, and changing its font to the symbol font. Interpret your results before proceeding.

10. In cell B16, enter a formula to compute *N* in year 1.

Enter the formula **=B15+C15+E15-D15-F15**. You could also simply enter **=G15**.

11. Select cell B16 and copy its formula down to row 35. Select cells C15–J15 and copy their formulae down to year 20, row 35.

12. Save your work. The first portion of your spreadsheet should now look like Figure 3.

	A	B	C	D	E	F	G	H	I	J
12					**SOURCE**					
13			Total	Total	Total	Total	Total	Delta		
14	Year	N-Source	births	deaths	immigrants	emigrants	source	*N*	*R*	λ
15	0	10.0	5.0	2.0	1.0	0.0	14.0	4.0	0.40	1.40
16	1	14.0	7.0	2.8	1.4	0.0	19.6	5.6	0.40	1.40
17	2	19.6	9.8	3.9	2.0	2.4	25.0	5.4	0.28	1.28
18	3	25.0	12.5	5.0	2.5	10.0	25.0	0.0	0.00	1.00
19	4	25.0	12.5	5.0	2.5	10.0	25.0	0.0	0.00	1.00
20	5	25.0	12.5	5.0	2.5	10.0	25.0	0.0	0.00	1.00

Figure 3

C. Project population size in the sink over time.

1. Set up new spreadsheet headings as shown in Figure 4.

	K	L	M	N	O	P	Q	R
12				**SINK**				
13		Total	Total	Total	Total	Delta		
14	N-Sink	births	deaths	immigrants	sink	N	R	λ

Figure 4

2. In cell K15, link the starting number of individuals in the source population to cell F5.

Enter the formula **=F5** in cell K15.

3. Enter formulae in cells L15–M15 to compute the total births and deaths in the sink.

Enter the following formulae:
- L15 **=K15*F6**
- M15 **=K15*F7**

4. In cell N15, enter a formula to link emigants from the source to immigrants into the sink.

Enter the formula **=F15**.

5. In cells O15–R15, enter formulae to compute the total population size of the sink; Δ*N*; *R*; and λ.

We entered the following formulae:
- O15 **=K15+L15-M15+N15**
- P15 **=O15-K15** or **L15-M15+N15**
- Q15 **=P15/K15**
- R15 **=K16/K15** or **=Q15+1**

6. Enter an **IF** formula in cell K16 to compute the population size in year 1.

We entered the formula **=IF(K15+L15-M15+N15<0,0,K15+L15-M15+N15)**. This **IF** formula is used to keep the population from falling below 0 and generating negative population sizes. The formula simply says that if the total population in the sink is less than 0, return the number 0; otherwise, return the total population size of the sink.

7. Select cell K16 and cells L15–R15, and copy their formulae down to year 20 (row 35).

8. Your sink projections should now look something like those in Figure 5. Save your work.

	K	L	M	N	O	P	Q	R
12	**SINK**							
13		Total	Total	Total	Total	Delta		
14	N-Sink	births	deaths	immigrants	sink	*N*	*R*	λ
15	100	40	50.0	0.0	90.0	-10.0	-0.10	0.90
16	90.0	36	45.0	0.0	81.0	-9.0	-0.10	0.90
17	81.0	32.4	40.5	2.4	75.3	-5.7	-0.07	0.93
18	75.3	30.136	37.7	10.0	77.8	2.5	0.03	1.03
19	77.8	31.1224	38.9	10.0	80.0	2.2	0.03	1.03
20	80.0	32.01016	40.0	10.0	82.0	2.0	0.02	1.02

Figure 5

D. Project and graph population sizes for the source-sink system.

1. Set up new headings as shown in Figure 6

	S	T
12	**SYSTEM**	
13		
14	N-Total	λ-Total

Figure 6

2. In cell S15, compute the total population size as the sum of the source individuals and sink individuals.

Enter the formula **=G15+O15.**

3. In cell T15, enter a formula to compute λ for the entire source-sink system.

Enter the formula **=S16/S15.**

4. Copy cells S15–T15 down to year 20 (row 35).

5. Graph the numbers of individuals in the source, sink, and total population over time. Your graph should resemble Figure 7.
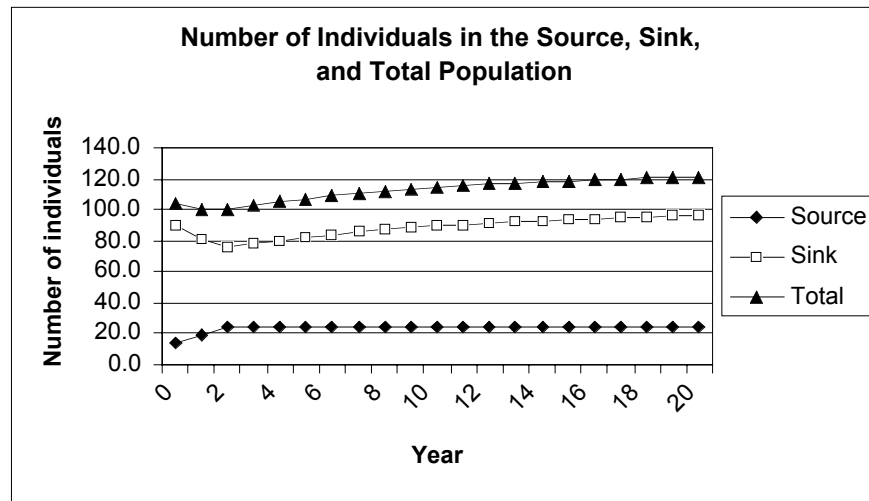

Figure 7

6. Graph the proportion of the total population in source and sink habitat over time. Your graph should resemble Figure 8.

Select cells G15–G35, then press the Control key or the key and select cells O15–O35. Use the 100% Stacked Column option, and label your axes fully.
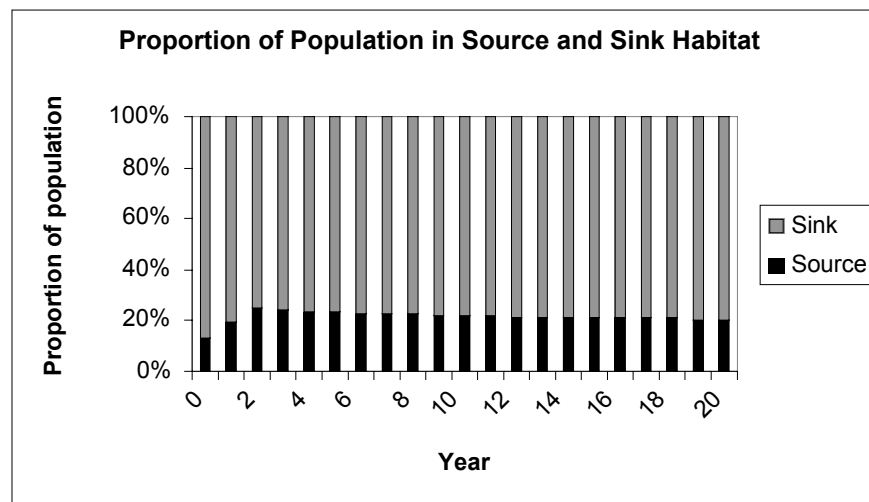

Figure 8

QUESTIONS

1. Keeping the parameters as you set them at the beginning of the exercise, and examining the graphs created in the last step, answer the following questions:

• At what year does the source reach an equilibrium state?
• At what year does the sink reach an equilibrium state?
• How does the proportion of the total population in source and sink habitats change over time? Why do the proportions change?

2. Extend your population projections to 100 years. Copy the formula in row 35 down to row 115. Update your graphs to include the 100-year projection, and answer the questions in question 1 again.

3. The definition of a sink is that it is incapable of sustaining itself over time without the influx of individuals from source habitats. What happens if the source population is extirpated? Set cell C5 to 0, and interpret your model results.

4. With your model programmed, you can change various parameters and watch how the parameters effect the population over time.

   • What happens to the greater population if you increase the starting number of individuals in the source? Increase the value of cell C5 from 10 to 100 in increments of 10. Interpret λ for the source, sink, and greater population.
   • What happens to the greater population if you increase the starting number of individuals in the sink? Increase the value of cell F5 from 100 to 1000 in increments of 100. Interpret λ for the source, sink, and greater population over time. What is the equilibrium population size?
   • What if you increase survival rate (i.e., lower the death rate, cell C8) in the source habitat?
   • How does carrying capacity, K, affect overall population growth? What happens when you increase or decrease this factor in the source?

5. Field biologists seldom have the opportunity to estimate the birth and survival rates for many organisms. Instead of basing habitat quality on these parameters, quality is often associated with density (number of individuals per unit area). Modify your model to show that density may be a misleading indicator of habitat quality.

6. In Pulliam's 1988 model, b (cell C7) changes and is a function of number of breeding sites/total breeders. Thus, if the number of total breeders is large, b, the per capita birth rate, is low. And if the number of total breeders is less than total sites available in source, b is maximum. How can this be incorporated into your model, and how does this change affect your model results?

LITERATURE CITED

Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132: 652–661.