9 | *INTERSPECIFIC COMPETITION AND COMPETITIVE EXCLUSION*

Objectives

- Program the Lotka-Volterra model of interspecific competition in a spreadsheet.
- Understand the competitive exclusion principle and how it relates to the model.
- Use the model to explore competitive exclusion and coexistence.
- Determine under what conditions two competing species can coexist, in terms of their competition coefficients, carrying capacities, and intrinsic rates of increase.

Suggested Preliminary Exercise: Logistic Population Models

INTRODUCTION

Our previous models of population dynamics considered only one population. As informative as those models were, it should be obvious that real populations do not exist in isolation, but share habitats with populations of other species. In many cases, coexisting species will interact by interspecific competition, predation, parasitism, mutualism, or other ecological interactions. More realistic models must take such interactions into account. In the 1920s, Vito Volterra and Alfred Lotka (1932) independently developed models of **interspecific competition** (competition between two species), and investigated the conditions that would permit competing species to coexist indefinitely. In this exercise, you will build a discrete-time version of their continuous-time models.

An important ecological generalization, the **competitive exclusion principle**, has grown out of the Lotka-Volterra model and from other sources. This principle states that *two species cannot coexist unless their niches are sufficiently different that each limits its own population growth more than it limits that of the other*. In other words, if there is too much niche overlap, one species will competitively exclude the other. In reality, whether two species coexist depends not only on their competitive interactions with each other, but also on their interactions with the abiotic environment and with other species not included in this simple model. Nevertheless, as with other models in this book, the competitive exclusion principle has proven fruitful in stimulating research and understanding ecological interactions in the natural world.

Model Development

To review, the geometric model of population growth, $N_{t+1} = N_t + RN_t$, includes no effect of competition. The population increases by RN_t in every time interval, without any limitations such as might be imposed by finite resources.

The logistic model of population growth includes **intraspecific competition** (competition between individuals of the same species). To keep things (relatively) simple, we will develop our model of interspecific competition beginning with this form of the logistic model:

$$N_{t+1} = N_t + RN_t \frac{K - N_t}{K}$$

Equation 1

where K is the carrying capacity, or largest sustainable population. The value of K is set by available resources and by each individual's resource demand. This version of the logistic model has intraspecific competition built into it in the term $(K - N_t)/K$. This term reduces the population growth rate in response to the addition of each new member of the population, representing the reduction in per capita birth rate, and increase in per capita death rate, caused by competition for limited resources. You can review Exercise 8, "Logistic Population Models," for more information about this model.

The Lotka-Volterra model of interspecific competition builds on the logistic model of a single population. It begins with a separate logistic model of the population of each of the two competing species.

$$\text{Population 1:} \quad N_{1,t+1} = N_{1,t} + R_1 N_{1,t} \frac{K_1 - N_{1,t}}{K_1}$$

$$\text{Population 2:} \quad N_{2,t+1} = N_{2,t} + R_2 N_{2,t} \frac{K_2 - N_{2,t}}{K_2}$$

Note the use of subscripts 1 and 2 to denote which species' population is being modeled. Each population has its own rate of increase R and carrying capacity K, and these may differ between the two species.

Next we build interspecific competition into each of these equations. In the model of population 1 above, we assume that each new member of population 1 reduces resources available to each member of population 1, and thus reduces population growth rate. In the two-species model, new members of population 2 will also reduce resources available to members of population 1—this is, after all, the meaning of interspecific competiton.

The simplest way to model this would be to modify the $(K_1 - N_{1,t})/K$ term into $(K_1 - N_{1,t} - N_{2,t})/K_1$. However, this assumes that each additional member of population 2 will affect population 1 exactly as much as an additional member of population 1. That is not necessarily the case, so we multiply $N_{2,t}$ in this term by a **competition coefficient**, α_{12} to express how much effect each additional member of population 2 has on population 1, relative to the effect of a new member of population 1. We modify the model for population 2 in a parallel way. The resulting Lotka-Volterra model of two-species competition is:

$$\text{Population 1:} \quad N_{1,t+1} = N_{1,t} + R_1 N_{1,t} \frac{K_1 - N_{1,t} - \alpha_{12} N_{2,t}}{K_1}$$

Equation 2

$$\text{Population 2:} \quad N_{2,t+1} = N_{2,t} + R_2 N_{2,t} \frac{K_2 - N_{2,t} - \alpha_{21} N_{1,t}}{K_2}$$

Equation 3

Note the subscripts on the competition coefficients: α_{12} expresses the effect of one member of population 2 on the growth rate of population 1; α_{21} expresses the effect of one member of population 1 on the growth rate of population 2.

In broad terms, the question Lotka and Volterra asked was, What will happen to the population dynamics of these two populations, given various values of the model parameters? Are there parameter values that will produce a winner and a loser,—one population that persists while the other goes extinct? This would be competitive exclusion. Will other values result in coexistence, in which both competing populations persist indefinitely? You will look for answers to these questions both analytically (algebraically) and graphically (using the spreadsheet).

Equilibrium Solutions

One approach to answering the questions posed above is to look for equilibrium solutions to Equations 2 and 3. If population 1 is at equilibrium, then $N_{1,t+1} = N_{1,t}$ and we can substitute $N_{1,t}$ for $N_{1,t+1}$:

$$N_{1,t} = N_{1,t} + R_1 N_{1,t} \frac{K_1 - N_{1,t} - \alpha_{12} N_{2,t}}{K_1}$$

Subtracting $N_{1,t}$ from both sides of the equation gives us

$$0 = R_1 N_{1,t} \frac{K_1 - N_{1,t} - \alpha_{12} N_{2,t}}{K_1}$$

In words, this equation says the population stops growing when it is at equilibrium, which should come as no surprise. This equation is satisfied if $N_{1,t} = 0$ or if $R_1 = 0$, but these solutions are trivial.

The equation is also satisfied by the more interesting case of

$$K_1 - N_{1,t} - \alpha_{12} N_{2,t} = 0$$

If we add $N_{1,t}$ to both sides and rearrange the terms, we get

$$N_{1,t} = K_1 - \alpha_{12} N_{2,t} \qquad \text{Equation 4}$$

Notice that this equation is in the general form of a linear equation, $y = a + bx$, and is therefore a straight line. We call this line a **zero net growth isocline**, or **ZNGI**, because anywhere along it, population 1 has zero net growth. In other words, this is an equilibrium solution for population 1.

Just as x and y in the general linear equation $y = a + bx$ can be used as coordinates for graphing, so we can use $N_{1,t}$ and $N_{2,t}$ as coordinates to graph Equation 4. We can graph this isocline by finding any two points along it and connecting them with a straight line. Two convenient points are where $N_{2,t} = 0$ and where $N_{1,t} = 0$.

If $N_{2,t} = 0$, then we solve for $N_{1,t}$. Equation 4 becomes

$$N_{1,t} = K_1 - \alpha_{12} 0$$

which reduces to

$$N_{1,t} = K_1$$

In words, if there are no members of population 2 in the habitat, population 1 will stabilize at its own carrying capacity, K_1. This seems a reasonable solution.

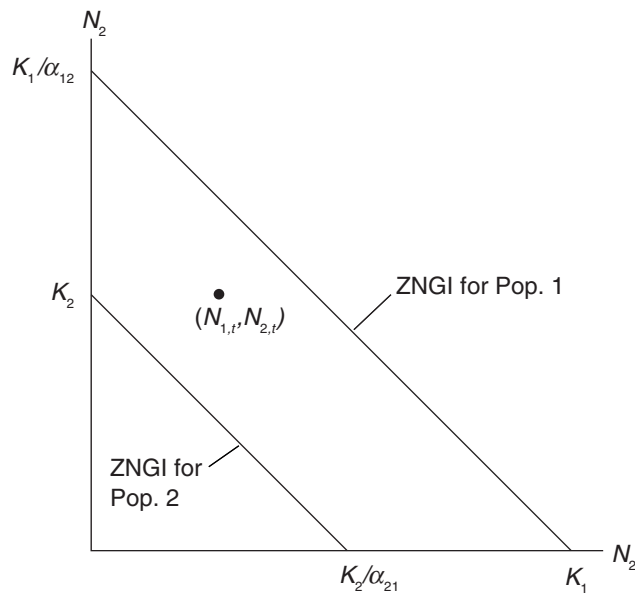If we set $N_{1,t} = 0$, and then solve for $N_{2,t}$. Equation 4 becomes

$$0 = K_1 - \alpha_{12} N_{2,t}$$

and adding $a_{12} N_{2,t}$ to both sides gives us

$$\alpha_{12} N_{2,t} = K_1$$

Dividing both sides by α_{12} gives us

$$N_{2,t} = K_1 / \alpha_{12}$$

Figure 1   Zero net growth isoclines (ZNGIs) generated by the Lotka-Volterra model of two-species competition. The point $(N_{1,t}, N_{2,t})$ represents the two populations at time t.

In words, if there are K_1/α_{12} members of population 2 in the habitat, there will be no resources left over for population 1, and its numbers will go to zero.

We can find a ZNGI and two points on it for population 2 in the same manner.

$$N_{2,t} = K_2 - \alpha_{21}N_{1,t}$$

$$\text{If } N_{1,t} = 0, \text{ then } N_{2,t} = K_2$$

$$\text{If } N_{2,t} = 0, \text{ then } N_{1,t} = K_2/\alpha_{21}$$

We can draw these isoclines on a linear graph of the two populations as shown in Figure 1. If we plot N_1 on the horizontal axis and N_2 on the vertical, then the solution points found become the intercepts of the isoclines on the axes.

We can graph the populations of the two species at any time by a point on a graph. If the point falls below and/or to the left of a species' isocline, that population will continue to increase. If the point falls above and/or to the right of a species' isocline, that population will decrease. In the case of the point shown in Figure 1, population 1 will increase and population 2 will decrease. As time passes, the point will move downward (population 2 decreases) and to the right (population 1 increases), and the point describing the two populations will trace some trajectory across the graph.

Notice that time does not appear on either axis of this graph. Figure 1 is called a **phase diagram**, and the space bounded by its axes is called **phase space**. You will plot the trajectory of two changing populations through the phase space and from that determine whether one species excludes the other, or if they coexist. The isoclines need not be arranged as shown in Figure 1; their arrangement will depend on the values of K_1, K_2, α_{12}, and α_{21}.

PROCEDURES

The questions Lotka and Volterra asked, and which you will answer in this exercise, are: What values of these parameters will cause population 1 to exclude population 2,

and vice versa? What parameter values will allow the two populations to coexist indefinitely? What do these outcomes, and their associated parameter values, mean in ecological terms?

As always, save your work frequently to disk.

INSTRUCTIONS	ANNOTATION

A. Set up the spreadsheet.

1. Open a new spreadsheet and set up titles and column headings as shown in Figure 2.

	A	B	C	D	E	F
1	*Lotka-Volterra Model of Interspecific Competition*					
2						
3		$N1$	$N2$		Parameters	
4		End points			$R1$ -->	1.00
5	$N1 = 0$ -->	0	1000	<-- $N2 = K2$	$K1$ -->	1200
6	$N1 = K2/a21$ -->	2000	0	<-- $N2 = 0$	$a12$ -->	0.75
7	$N1 = K1$ -->	1200	0	<-- $N2 = 0$	$R2$ -->	1.00
8	$N1 = 0$ -->	0	1600	<-- $N2 = K1/a12$	$K2$ -->	1000
9					$a21$ -->	0.50
10	Time (t)					
11	0					
12	1					
13	2					

Figure 2

Enter only the text items for now. These are all literals, so just select the appropriate cells and type them in.
You must leave cells B10 and C10 empty for your graphs to come out properly.
The values in cells B5 through C8 are the coordinates of the endpoints of the ZNGIs for the two species. How we got these values will be explained in subsequent steps.

2. Set up a linear time series from 0 to 50 in cells A11 through A61.

See the exercise "Spreadsheet Hints and Tips" for details.

3. Enter the values shown for the parameters.

These are in cells F4 through F9. Do not enter anything in cells B5 through C8 yet.

4. Enter zeros in cells B5, C6, C7, and B8.

These are ZNGI endpoints where each population is itself at zero. Cells B5 through C8 hold coordinates for the endpoints of the two ZNGIs. You must lay out these endpoint cells as shown for your graphs to work properly.

5. In cells B7 and C5, enter formulae to echo the carrying capacities of populations 1 and 2, respectively.

In cell B7, enter the formula **=F5**.
In cell C5, enter the formula **=F8**.
These are ZNGI endpoints where the competing population is at zero. When you change carrying capacities later in the exercise, your changes will automatically be carried over to the ZNGI endpoints.

6. Enter formulae to calculate the other ZNGI endpoints.

In cell B6, enter the formula **=F8/F9**. This corresponds to $N_{1,t} = K_2/\alpha_{21}$.
In cell C8, enter the formula **=F5/F6**. This corresponds to $N_{2,t} = K_1/\alpha_{12}$.

7. Enter initial population sizes ($N_{1,0}$ and $N_{2,0}$).

In cell B11, enter the value 100. In cell C11, enter the value 50. You will change these values later.

8. Enter formulae to calculate populations sizes at times $t = 0$ through $t = 50$.

In cell B12, enter the formula **=B11+$F$4*B11*($F$5-B11-$F$6*C11)/$F$5**. This corresponds to Equation 2:

$$N_{1,t+1} = N_{1,t} + R_1 N_{1,t} \frac{K_1 - N_{1,t} - \alpha_{12} N_{2,t}}{K_1}$$

In cell C12, enter the formula **=C11+$F$7*C11*($F$8-C11-$F$9*B11)/$F$8**. This corresponds to Equation 3:

$$N_{2,t+1} = N_{2,t} + R_2 N_{2,t} \frac{K_2 - N_{2,t} - \alpha_{21} N_{1,t}}{K_2}$$

Be sure to use absolute and relative addresses as shown.

9. Copy and paste the formulae in cells B12 and C12 down their columns through row 51.

See "Spreadsheet Hints and Tips" for details on copying and pasting.

B. Create graphs.

1. Graph N_1 and N_2 (vertical axis) against time (horizontal axis).

Use an XY graph (scatterplot). Include only cells A11 through C51 in the block of data to graph. Leave out the ZNGI endpoints (cells B5 through C8).
Use the *second* Chart Wizard dialog box to name your series so that they will be labeled properly in the legend.

In the dialog box (Figure 3), click the Series tab. Select Series1 and type "Pop 1" in the box to the right. Then select Series 2 and type "Pop 2" in the box. Your finished graph should resemble Figure 4.
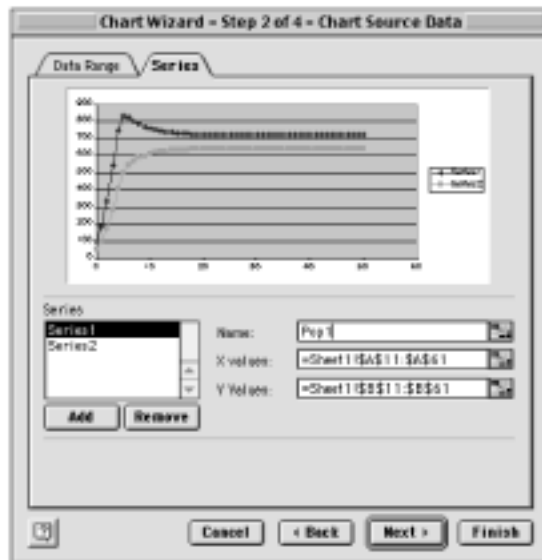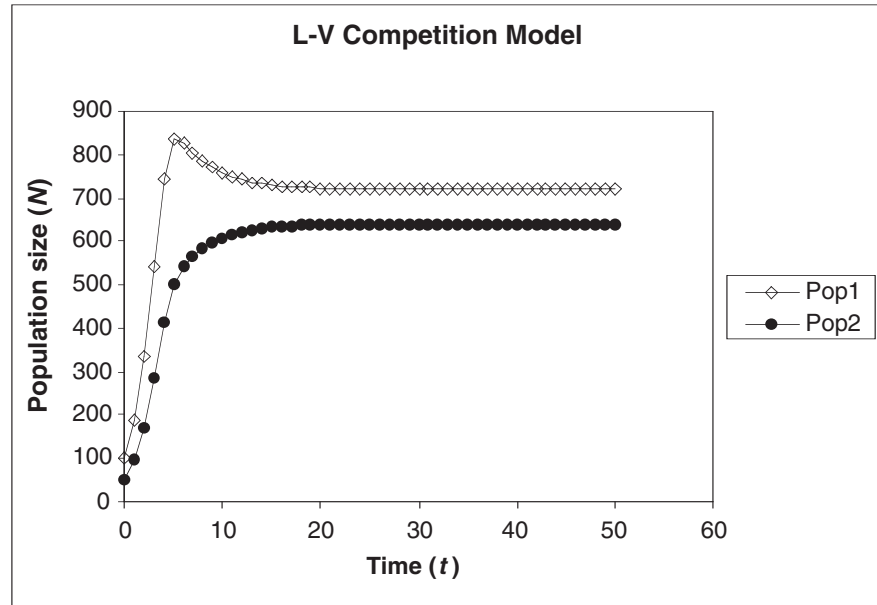

Figure 3

L-V Competition Model

Figure 4

2. Graph N_2 (vertical axis) against N_1 (horizontal axis).

Include cells B5 through C61 in the block to graph—in other words, this time *include* the ZNGI endpoints, but *leave out* "Time" (column A). Use an XY graph (scatterplot). Your graph should resemble Figure 5.

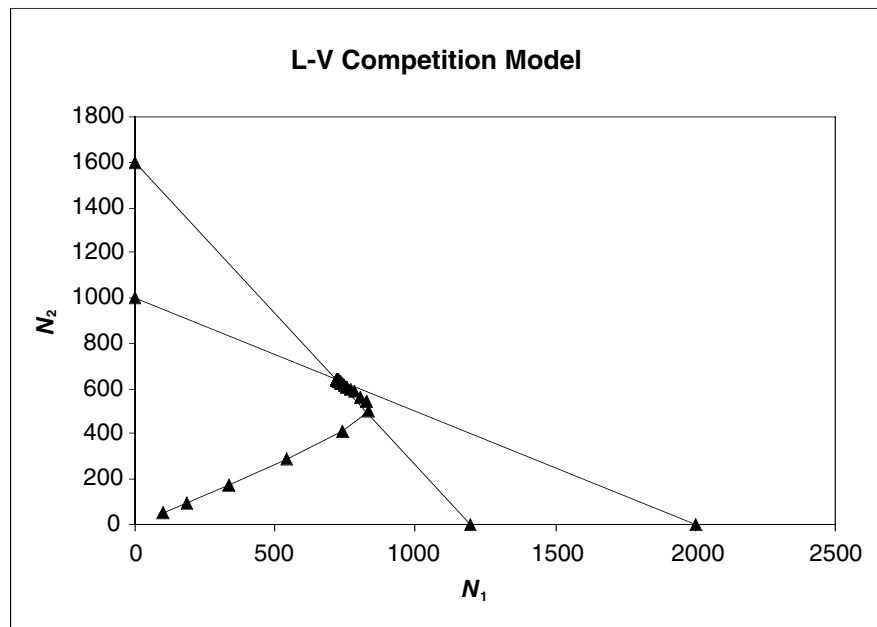**L-V Competition Model**

Figure 5

Unfortunately, the program does not label the ZNGI endpoints for you. You will have to identify each endpoint by its coordinates in the spreadsheet. In Figure 5, the top-left endpoint is $(0, K_1/\alpha_{12})$; the lower-left endpoint is $(0, K_2)$; the bottom-right endpoint is $(K_2/\alpha_{21}, 0)$; and the bottom-left endpoint is $(K_1, 0)$.

QUESTIONS

1. What parameter values will cause species 1 to exclude species 2 from the habitat? What do these values mean in ecological terms?

2. What parameter values will reverse this outcome? What do these values mean in ecological terms?

3. What parameter values will allow the two species to coexist indefinitely and stably? What do these values mean in ecological terms?

4. Are there parameter values under which the outcome depends on initial population sizes or rates of population growth? What do these values mean in ecological terms?

LITERATURE CITED

Lotka, A. J. 1932. The growth of mixed populations: two species competing for a common food supply. *Journal of the Washington Academy of Sciences* 22: 461–469.