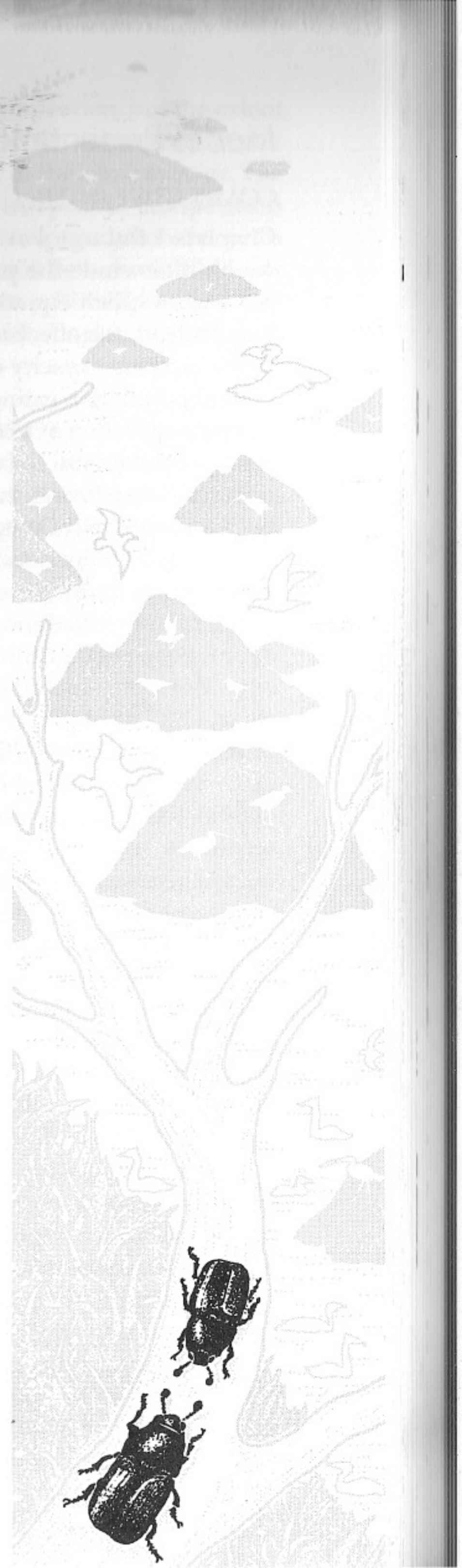
CHAPTER 5

Competition



Model Presentation and Predictions

COMPETITIVE INTERACTIONS

Chapters 1 through 4 examined single-species population growth. Although we didn't exclude the possibility that other species were important, we did not write explicit equations for populations of predators, prey, or competitors. Instead, the effects of other species were contained in constants such as *K*, the carrying capacity of the environment (Chapter 2), or p_e, the probability of local population extinction (Chapter 4). In this chapter, we will introduce a second population of a competing species and model the growth of two interacting populations.

Before introducing the model, we need to specify exactly what we mean by "competition." **Competitive interactions** are those in which two species negatively influence each other's population growth rates and depress each other's population sizes. This general definition encompasses a variety of population interactions. **Exploitation competition** occurs when populations depress one another through use of a shared resource, such as food or nutrients. Examples include tropical reef fish that graze on the same kinds of algae, and desert plants that compete for a limited supply of water.

Interference competition occurs when an individual or population behaves in a way that reduces the exploitation efficiency of another individual or population. Examples include song birds that maintain well-established breeding territories, and ant colonies that kill invaders at food patches. Even plants engage in a form of interference competition known as **allelopathy**. Many plant species, particularly aromatic herbs, release toxic chemicals that poison the soil for competitors. The key element in interference competition is that species supress one another directly, not only through their indirect use of resources.

Interference competition leaves more resources for the winner to consume, so it may evolve as an adaptation when exploitation competition is severe. As an analogy for understanding these two kinds of interactions, exploitation competition is when you and a friend are sitting at a table drinking the same milkshake with straws. The "winner" in exploitation competition is the one who consumes the most milkshake. Interference competition is when you reach over and pinch your friend's straw!

Pre-emptive competition is a third category that has elements of both exploitation and interference. In pre-emptive competition, organisms compete for space as a limiting resource. Examples include birds that use tree holes for nesting and intertidal algae that must attach to stable rock surfaces. Unlike food or nutrients that are used exploitatively, space is a renewable resource that is "recycled"—as soon as an organism dies or leaves, the space is immediately available for use by other individuals.

We need to consider not only the mechanism of competition, but the extent to which competition occurs within and between species. **Intraspecific competition** is competition that occurs among members of the same species. The logistic equation (Equation 2.1) is a model of intraspecific competition because the per capita growth rate diminishes as the population becomes more crowded. **Interspecific competition** is competition between individuals of two or more different species. In this chapter we will build a model of interspecific competition that is a direct extension of the logistic equation.

THE LOTKA–VOLTERRA COMPETITION MODEL

In the 1920s and 1930s, Alfred J. Lotka (1880–1949) and Vito Volterra (1860–1940) described a simple mathematical model of interspecific competition that is the framework for competition studies in ecology. The model treats populations of two competing species, which we will designate as N_1 and N_2. Each population grows according to the logistic, with its own intrinsic rate of increase (r_1 or r_2) and its own carrying capacity (K_1 or K_2). As in the logistic model, population growth is reduced by intraspecific competition:

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1}{K_1} \right) \qquad \text{Expression 5.1}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2}{K_2} \right) \qquad \text{Expression 5.2}$$

In our new model, the population growth rate is further depressed by the presence of the second species. For now, assume that the growth is reduced by some function (f) of the number of individuals of the competitor:

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - f(N_2)}{K_1} \right) \qquad \text{Expression 5.3}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - f(N_1)}{K_2} \right) \qquad \text{Expression 5.4}$$

These expressions show that population growth rate is depressed by both intraspecific and interspecific competition. There are many complicated functions that we could use in Expressions 5.3 and 5.4, but the simplest formula is to multiply the population size of the competitor by a constant number:

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha N_2}{K_1} \right) \qquad \text{Equation 5.1}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - \beta N_1}{K_2} \right) \quad \text{Equation 5.2}$$

COMPETITION COEFFICIENTS

The **competition coefficients** α and β are critical to understanding the Lotka–Volterra model. α is a measure of the effect of species 2 on the growth of species 1. If $\alpha = 1$, then individuals of the two species are interchangeable—each has an equal effect in depressing the growth of species 1. On the other hand, suppose that $\alpha = 4$. Each individual of species 2 that is added to the environment depresses the growth of N_1 by the same amount as adding four individuals of species 1. Thus, α is a measure of the relative importance *per individual* of interspecific and intraspecific competition. If $\alpha > 1$, the per capita effect of interspecific competition is greater than the per capita effect of intraspecific competition. If $\alpha < 1$, the intraspecific competition is more important—population growth of species 1 is depressed more by the addition of an individual of N_1 than by addition of an individual of the competing species. Finally, notice that if $\alpha = 0$, there is no competitive effect, and Equation 5.1 reduces to the single-species logistic equation (Equation 2.1). Thus, we can define α as the per capita effect of species 2 on the population growth of species 1, *measured relative to the effect of species 1.*

Similar reasoning applies to the interpretation of β, which is the per capita effect of species 1 on the population growth of species 2. It is important to realize that α and β need not have the same values. Competitive effects in nature often are asymmetrical—adding an individual of one species may severely depress the population growth of a second species, whereas the reverse is not true. Although both species in our model coexist in the same location, remember that they each have separate carrying capacities (K_1 and K_2), and intrinsic rates of increase (r_1 and r_2). Although r_1 and r_2 do not affect the outcome of competition in this model, we will see in the next section that the carrying capacities and competition coefficients are critical for determining species coexistence.

A useful way to understand α and β is to return to the analogy we developed in Chapter 2 (Krebs 1985): the carrying capacity of the environment for species 1 is a square frame that holds a limited number of flat tiles (individuals). In our competition model, the tiles come in two different sizes, representing the two different species (Figure 5.1). Continuing the analogy, α is the relative area of the two tiles. For example, if $\alpha = 4$, then a single individual of species 2 consumes four times the remaining resources of the environment as a single individual of species 1. So, a tile of species 2 has four times the area of a tile of species 1. At equilibrium, the frame is filled with a mix of the two kinds of tile. In the next section we will solve for these equilibrium densities.

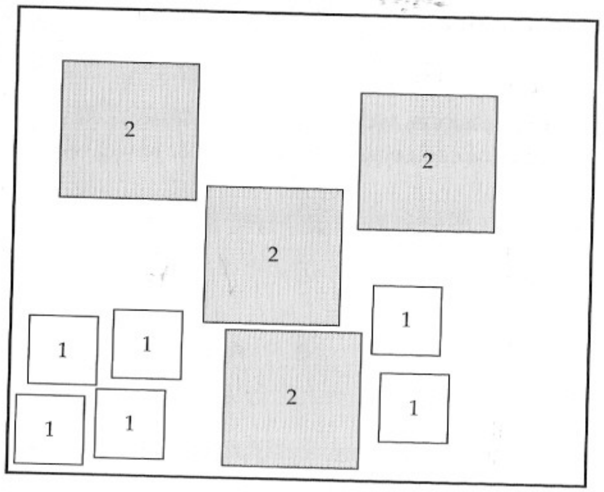


Figure 5.1 A graphical analogy for interspecific competition. The heavy square frame represents the carrying capacity for species 1 (K_1). Each individual consumes a portion of the limited resources available and is represented by a tile. Individuals of species 2 reduce the carrying capacity four times as much as individuals of species 1. Hence, the tiles for species 2 are four times larger than those for species 1, and $\alpha = 4.0$. (After Krebs 1985.)

EQUILIBRIUM SOLUTIONS

As in all our previous analyses, we find the equilibrium population densities ($\hat{N}$) by setting the differential equations equal to zero and solving for N:

$$\hat{N}_1 = K_1 - \alpha N_2 \quad \text{Equation 5.3}$$

$$\hat{N}_2 = K_2 - \beta N_1 \quad \text{Equation 5.4}$$

These results make intuitive sense. The equilibrium for N_1 is the carrying capacity for species 1 (K_1) reduced by some amount due to the presence of species 2 (αN_2). But we have trouble putting numbers into these solutions—the equilibrium for species 1 depends on the equilibrium for species 2, and vice versa! We can make progress by substituting the equilibrium for N_2 into Equation 5.3, so that the answer will be entirely in terms of N_1:

$$\hat{N}_1 = K_1 - \alpha(K_2 - \beta \hat{N}_1) \quad \text{Expression 5.5}$$

Similarly, we can substitute the equilibrium for N_1 into Equation 5.4:

$$\hat{N}_2 = K_2 - \beta(K_1 - \alpha\hat{N}_2) \qquad \text{Expression 5.6}$$

For each of these expressions, we carry out the multiplication, move all the N terms to the left side of each equation, and arrive at the following solutions:

$$\hat{N}_1 = \frac{K_1 - \alpha K_2}{1 - \alpha\beta} \qquad \text{Equation 5.5}$$

$$\hat{N}_2 = \frac{K_2 - \beta K_1}{1 - \alpha\beta} \qquad \text{Equation 5.6}$$

Note that for both species to have an equilibrium population size greater than zero, the denominator of each expression must usually be greater than zero. Thus, it is usually the case that the product $\alpha\beta$ must be less than 1 for both species to coexist.

THE STATE SPACE

Although Equations 5.5 and 5.6 tell us the equilibrium conditions for the Lotka–Volterra competition models, they do not provide much insight into the dynamics of competitive interactions, or whether these equilibrium points are stable or not.

We can understand these equations much better by using the **state-space graph**, a special kind of plot. In the state-space graph, the x axis represents the abundance of species 1, and the y axis represents the abundance of species 2. This graph takes a bit of getting used to, but it is an important tool in multispecies models. We will use it again in Chapter 6, when we explore predator–prey models.

What do points in state space represent? A point in this graph represents a *combination of abundances* of species 1 and species 2. The abundance of species 1 can be read from the x axis and the abundance of species 2 can be read from the y axis. If our point falls on the x axis, then only species 1 is present and the abundance of species 2 is zero. For points on the y axis, only species 2 is present. So, the full collection of points in this graph represents all the different combinations of species 1 and species 2 that we could put together.

We use the state-space graph to understand the population dynamics of two competitors. Imagine two competing species whose populations are changing size with time. At each point in time, we could represent their abundances by a single point in the state space (Figure 5.2a). As both populations change in size (Figure 5.2b), we would trace a line in the state space. The final equilibrium point is the end of this line, and if either species goes extinct, this point falls on one of the two axes of the state-space graph.

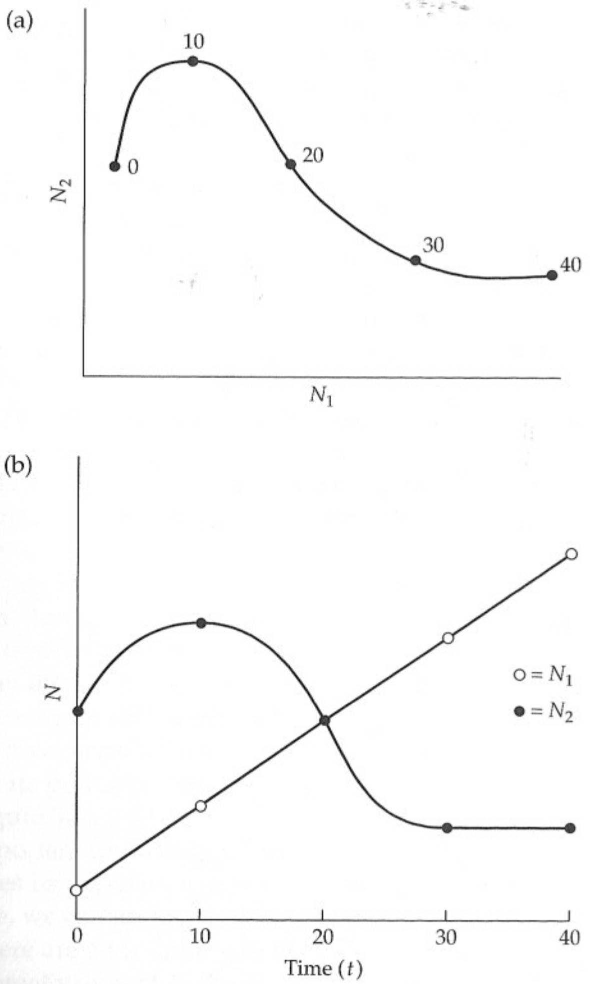


Figure 5.2 (a) A state-space graph. The axes of the state space are the abundances of the two species (N_1 and N_2). As abundances change through time, a curve is traced from left to right. The numbers on the curve indicate time, beginning at 0 and ending at 40. (b) Translation of the state-space graph in (a). The abundances of each species are read from the state-space graph at different times. Note that species 2 first increases and then decreases, whereas species 1 shows a continuous increase in population size.

How can we use the state-space graph to help us understand the Lotka–Volterra equations? We will first plot Equation 5.3 in the state space. Equation 5.3 is the equilibrium solution for species 1, and its graph is a straight line.

This line represents the combinations of abundances of species 1 and species 2 for which there is zero growth of species 1. At any point on this line, the carrying capacity for species 1 is entirely "filled" with individuals of both species. This line is an **isocline**: a set of abundances for which the growth rate (dN/dt) of one species is zero.

The isocline for species 1 intersects the axes of the state-space graph in two places. The intersection on the x axis is at a value of K_1. This equilibrium point represents the case in which species 2 is absent and species 1 has grown to its own carrying capacity. The other point is the intersection on the y axis. Here, species 1 is essentially extinct, and the carrying capacity of species 1 is entirely filled with individuals of species 2. The equilibrium solution at this point is K_1/α individuals of species 2 and zero individuals of species 1. Between these extremes are combinations of both species that fall on the isocline (Figure 5.3).

The isocline for species 1 splits the state space into two regions. If we are to the left of the isocline, the joint abundance of N_1 and N_2 is less than the carrying capacity for species 1, so N_1 will increase. An increase in N_1 in the state space is represented as a *horizontal* arrow pointing to the right. The arrow is horizontal because the abundance of species 1 is represented on the x axis. When you work with state-space graphs, pay close attention to which species' isocline you are plotting. Any point to the left of the isocline for species 1 generates a horizontal right-pointing arrow. Under these circumstances, we know that species 1 has a positive growth rate, so its population will increase in size. In contrast, if we are to the right of the isocline, the joint abundance of N_1 and N_2 exceeds the carrying capacity of species 1. In this case, the growth rate of N_1 is negative, and the population decreases. The decrease is represented as a left-pointing horizontal arrow in the state space. Finally, if we are at a point precisely on the isocline, N_1 neither increases nor decreases, and there is no movement in the horizontal direction.

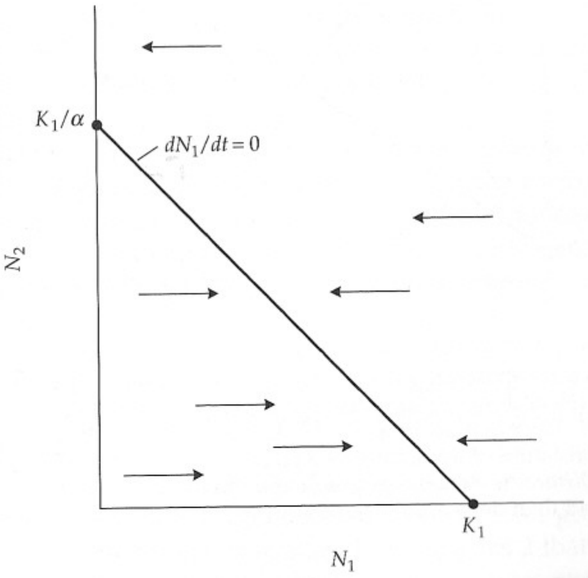


Figure 5.3 The linear isocline for species 1 in the Lotka–Volterra competition model. The isocline defines the combination of abundances for which species 1 shows zero growth. For points to the left of this line, the population of species 1 increases, indicated by the right-pointing horizontal arrow. For points to the right, the joint abundance of species 1 and species 2 exceeds the isocline for species 1, so its population decreases, indicated by the left-pointing arrows.

Now we plot the isocline for species 2 in the state space. The isocline of species 2 intersects the y axis at a value of K_2 and intersects the x axis at a value of K_2/β. The first case is one in which species 1 is absent and species 2 has grown to its carrying capacity. In the second case, species 2 is absent, and its carrying capacity is occupied by K_2/β individuals of species 1. Once again, the isocline for species 2 splits the state space into two regions. If we are below the isocline, the joint abundance of species 1 and species 2 is below K_2, and N_2 will increase. Because species 2 is on the y axis, positive growth of species 2 is represented as a *vertical* arrow pointing up in state space. Similarly, if we are above the isocline, the carrying capacity of species 2 is exceeded; its population decreases, represented by a downward-pointing arrow (Figure 5.4).

It is important to recognize that there is a unique isocline for each species that dictates its population growth. By plotting both isoclines together in the state space, we can understand the dynamics of two-species competition. Of course, there are an infinite number of isoclines we could build, simply by using different values of K_1, K_2, α, and β. Fortunately, there are only four qualitatively different ways we can plot the isoclines. These four patterns represent the four possible outcomes of competition in the Lotka–Volterra equations.

GRAPHICAL SOLUTIONS TO THE LOTKA–VOLTERRA COMPETITION MODEL

Case 1: Species 1 wins in competition. Figure 5.5 shows one possible configuration of the two isoclines in the state space: the isocline for species 1 lies entirely above the isocline for species 2. In this case, the state space is split into three regions. If we are in the lower left-hand region of the graph, we are below the isoclines of both species, and both species can increase. This is represented by a horizontal and vertical arrow joined at their base. The joint movement of these two populations is represented by the vector sum, which is an arrow that points towards the upper right-hand corner of the graph.

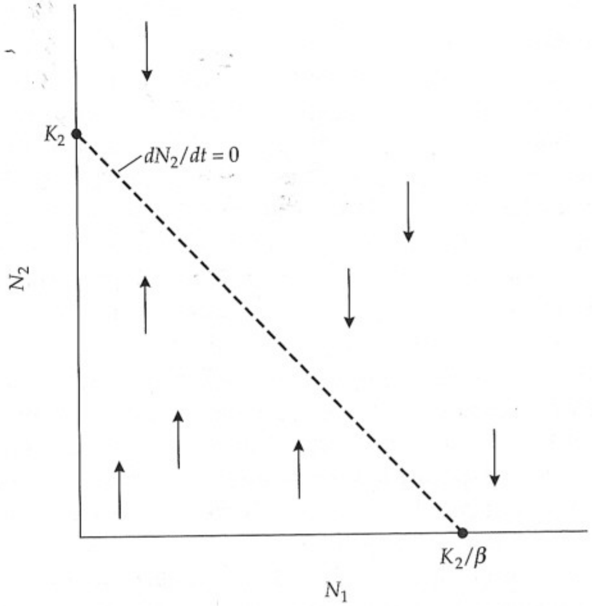


Figure 5.4 The isocline for species 2 in the Lotka–Volterra competition model. Note that the arrows point vertically for species 2, because its abundance is measured on the *y* axis of the state space graph.

Conversely, if we are in the upper right-hand region of the state space, we are above the isoclines of both species. Both populations will decrease, and the joint vector points towards the origin of the graph.

Things get more interesting in the interior region. Here, we are *below* the isocline of species 1, so its population increases in size, and the horizontal arrow points to the right. However, we are *above* the isocline of species 2, so its population decreases, and the vertical arrow points down. The joint vector points down and to the right, which takes the populations towards the carrying capacity of species 1. Eventually, species 2 declines to extinction, and species 1 increases to K_1. Notice that, no matter what combination of abundances we start with, the arrows always point towards this outcome. If the isocline of species 1 lies above that of species 2, species 1 always wins in competition, and species 2 is driven to extinction.

Case 2: Species 2 wins in competition. If we graph the isocline of species 2 above that of species 1, then we reverse the conditions and species 2 wins in competition (Figure 5.6). The only difference in this graph is the vector in the interior region. In this case, we are *above* the isocline of species 1, which generates a horizontal arrow to the left, but we are *below* the isocline of species 2, which gener-

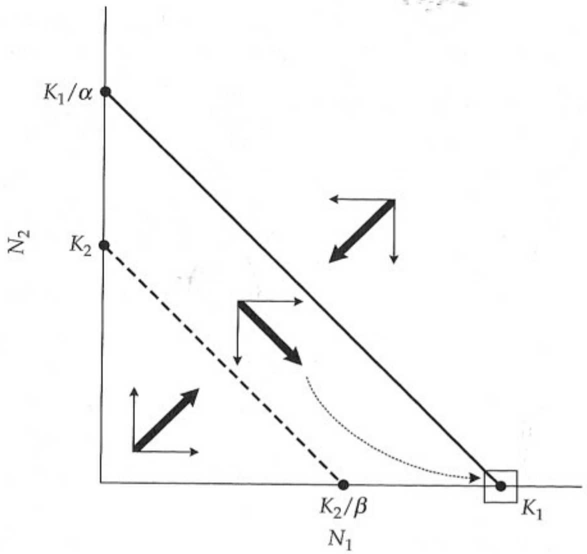


Figure 5.5 Case 1: Competitive exclusion of species 2 by species 1. The thin arrows show the trajectories of each population, and the thick arrow is the joint vector of movement. Competition results in the exclusion of species 2 and an equilibrium for species 1 at carrying capacity. The box indicates a stable equilibrium point.

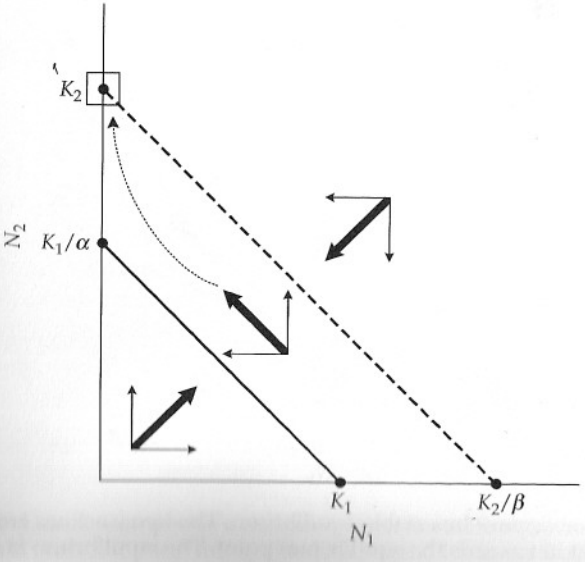


Figure 5.6 Case 2: Competitive exclusion of species 1 by species 2.

ates a vertical arrow pointing up. The joint vector points up and to the left, taking us towards the equilibrium point at K_2, with N_1 going extinct.

Case 3: Coexistence in a stable equilibrium. The remaining two cases are slightly more complex, because they involve isoclines that cross, dividing the state space into four regions. Nevertheless, the analysis is exactly the same. We simply plot the vectors in each of the four regions to determine the outcome (Figure 5.7). First, note that because the two isoclines cross, there must be an equilibrium point—the crossing of the isoclines represents a combination of abundances for which both species 1 *and* species 2 have achieved zero growth. The state space analysis reveals whether that equilibrium is stable or not.

As in our previous two examples, the region close to the origin is one of joint growth of both populations, and the region in the upper right-hand corner of the graph is one of joint decrease. The vectors in these regions point towards the equilibrium intersection. If we are in the region of the graph on the lower right, we are *above* the isocline of species 1, but *below* the isocline of species 2. Here, the joint vector points towards the center, as N_1 decreases along the horizontal axis and N_2 increases along the vertical axis. Finally, if

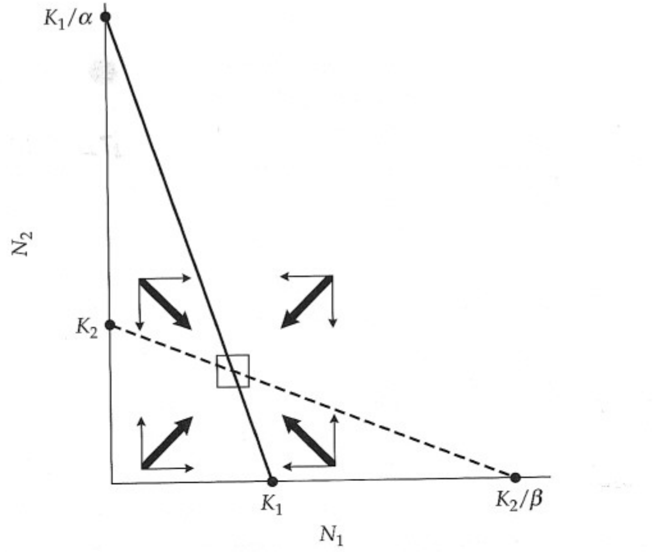


Figure 5.7 Case 3: Coexistence in a stable equilibrium. The two isoclines cross, and the joint vectors point in towards the equilibrium point. The equilibrium is stable because if the populations are displaced, they will always return to their equilibrium sizes.

we are in the region of the graph on the upper left, we are *above* the isocline of species 2, but *below* the isocline of species 1, and the joint vector again points towards the center.

This is a **stable equilibrium** in which all roads lead to Rome—no matter what the initial abundances of the two species are, both populations will move towards the joint equilibrium value. Although this equilibrium is stable and both species coexist, note that each species persists at a lower abundance than it would in the absence of its competitor. Competition reduces the population size of each species, but neither can drive the other extinct.

Case 4: Competitive exclusion in an unstable equilibrium. This final case is the one in which the isoclines cross in the opposite way (Figure 5.8). Once again, both populations increase in the sector closest to the origin, and both populations decrease in the upper right-hand region. But the pattern changes in the two remaining slivers of state space. In the lower right-hand region, we are *below* the isocline of species 1, but *above* the isocline of species 2. In this region of the graph, the populations move *away* from the joint equilibrium and towards K_1. Similarly, in the fourth region of the state space, we are *above* the isocline for N_1, but *below* that for N_2. The populations move away from the joint equilibrium and towards K_2.

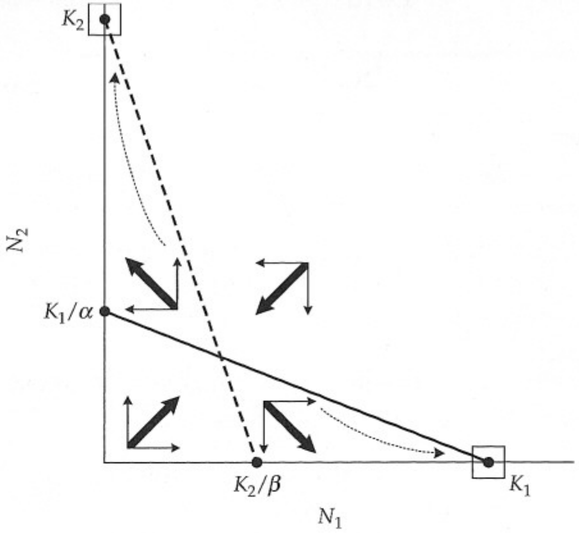


Figure 5.8 Case 4: Competitive exclusion in an unstable equilibrium. The two isoclines again cross and form an equilibrium point. However, the joint vectors point away from this equilibrium. If the populations are displaced, one species or the other will win in competition, depending on the starting abundances.

Case 4 represents an **unstable equilibrium**. If the populations are displaced from the joint equilibrium, they will eventually end up in one of the two regions of the graph that will take them to competitive exclusion. Thus, both species cannot persist in the long run, and one will be driven to extinction by competition. However, the winner is difficult to predict. The population that has a numerical advantage is the one that will probably win in competition, but the outcome depends on the initial position in the state space, and the relative growth rates of the two competitors (r_1 and r_2).

THE PRINCIPLE OF COMPETITIVE EXCLUSION

Now that we understand the four graphical solutions to the Lotka–Volterra competition equations, we will take another look at the algebraic solutions. We can reason that species 1 will always persist if it can invade under the worst possible circumstances. The worst scenario for species 1 is that its own abundance is close to zero ($N_1 \approx 0$), and the abundance of its competitor is close to carrying capacity ($N_2 \approx K_2$). If N_1 can achieve a positive per capita growth rate $[(dN_1/dt)(1/N_1) > 0]$ under these circumstances, then it should always be able to invade (MacArthur 1972). Plugging these conditions into Equation 5.1 gives:

$$\left(\frac{dN_1}{dt}\right)\left(\frac{1}{N_1}\right) = r_1\left(\frac{K_1 - 0 - \alpha K_2}{K_1}\right) \qquad \text{Expression 5.7}$$

Since r_1 is always positive, the following inequality must hold for N_1 to increase:

$$\frac{K_1 - \alpha K_2}{K_1} > 0 \qquad \text{Expression 5.8}$$

which reduces to:

$$\frac{K_1}{K_2} > \alpha \qquad \text{Expression 5.9}$$

If species 1 is to successfully invade, the ratio of the carrying capacities must exceed the competitive effect of species 2 on species 1. In other words, if species 2 is a strong competitor, species 1 must have a relatively large carrying capacity to persist.

Using Equation 5.2, we can go through a similar calculation to arrive at the following inequality for the persistence of species 2:

$$\frac{K_2}{K_1} > \beta \qquad \text{Expression 5.10}$$

Flipping the inequality makes this directly comparable with Expression 5.9:

$$\frac{1}{\beta} > \frac{K_1}{K_2} \qquad \text{Expression 5.11}$$

Table 5.1 Algebraic inequalities defining the ability of species to invade and the outcome of competition in the Lotka–Volterra equations.

(a)

Inequality	*Outcome*
$\frac{K_1}{K_2} > \alpha$	Species 1 invades
$\frac{K_1}{K_2} < \alpha$	Species 1 cannot invade
$\frac{K_1}{K_2} < \frac{1}{\beta}$	Species 2 invades
$\frac{K_1}{K_2} > \frac{1}{\beta}$	Species 2 cannot invade

(b)

Species 1 invades	*Species 2 invades*	*Inequality*	*Outcome*
Yes	No	$\frac{1}{\beta} < \frac{K_1}{K_2} > \alpha$	Species 1 wins (Case 1)
No	Yes	$\frac{1}{\beta} > \frac{K_1}{K_2} < \alpha$	Species 2 wins (Case 2)
Yes	Yes	$\frac{1}{\beta} > \frac{K_1}{K_2} > \alpha$	Stable coexistence (Case 3)
No	No	$\frac{1}{\beta} < \frac{K_1}{K_2} < \alpha$	Unstable equilibrium (Case 4)

Now we have expressions for whether N_1 will invade or not, and whether N_2 will invade or not. Putting these expressions together generates four algebraic inequalities that define the four graphical solutions to the Lotka–Volterra equations. For example, if species 1 can invade ($K_1/K_2 > \alpha$), but species 2 cannot ($1/\beta < K_1/K_2$), then we have defined the conditions for case 1, in which species 1 always wins in competition. If both species are able to invade, we have the stable coexistence of case 3, whereas if neither species can invade, we have the unstable equilibrium of case 4 (Table 5.1).

These inequalities give us insight into one of ecology's enduring proverbs, the **principle of competitive exclusion**. Briefly stated, the principle is that "complete competitors cannot coexist" (Hardin 1960). In other words, if species are able to coexist, there must be some difference between them in resource use (Gause 1934).

If two species are very similar in their resource use, then α and β should be very close to 1. Suppose, for example, that $\alpha = \beta = 0.9$. From the inequality in Table 5.1, coexistence of these species requires that:

$$\frac{1}{0.9} > \frac{K_1}{K_2} > 0.9 \qquad \text{Expression 5.12}$$

$$1.1 > \frac{K_1}{K_2} > 0.9 \qquad \text{Expression 5.13}$$

Thus, if the species are very similar in their use of resources, there is only a narrow range of carrying capacities that will ensure stable coexistence. In contrast, suppose that $\alpha = \beta = 0.2$, indicating that species differ greatly in their use of common resources. In this case, coexistence will occur if:

$$5 > \frac{K_1}{K_2} > 0.2 \qquad \text{Expression 5.14}$$

In this case, the two species will coexist with a wide range of possible carrying capacities. Thus, our analysis of the Lotka–Volterra equations allows us to refine the competitive exclusion principle: the more similar species are in their use of shared resources, the more precarious their coexistence.

The Lotka–Volterra equations are the simplest two-species model of competition. As you might expect, it is even more difficult to obtain coexistence of species in models that have three or more competitors. For many years, ecologists have studied the "coexistence problem," and discovered that species often coexist in nature with little apparent difference in resource exploitation. In these circumstances, one or more of the following assumptions of the model has been violated.

Model Assumptions

As in the logistic and exponential growth models, we assume there is no age or genetic structure to the populations, no migration, and no time lags. The following assumptions also apply to the Lotka–Volterra model:

✔ ***Resources are in limited supply.*** The result of resource limitation is both intra- and interspecific competition. If resources are not limiting, then an infinite number of species can coexist, regardless of how similar they are in resource use.

✔ ***Competition coefficients (α and β) and carrying capacities (K_1 and K_2) are constants.*** If these parameters should change with time or density, it may be difficult to predict species coexistence.

✔ ***Density dependence is linear.*** Adding an individual of either species produces a strictly linear decrease in per capita population growth rate. This is reflected in the linear isoclines of the Lotka–Volterra model. Models with nonlinear isoclines have more complex stability properties that are not easy to deduce from simple state-space graphs.

Model Variations

INTRAGUILD PREDATION

Ecologists classify species interactions according to their effects on population growth rate. Thus, competition is defined as both species having a net negative effect on one another (–,–), mutualism as both species having a net positive effect (+,+), and predation or parasitism as one species gaining and the other species losing (+,–). These classifications are convenient and natural, and they reflect our model assumptions that interaction coefficients are constant and that there is no age structure in the populations.

But when we study the natural history of many animals, we find they cannot be classified simply as "predators" or "competitors." For example, lions prey on the young of cheetahs, wild dogs, and spotted hyenas, but also compete with these same species for prey. Flour beetles in the genus *Tribolium* compete for food, but at high densities they also consume one another's larvae. For many predators, diet is determined strictly by their size and what they can get their jaws around. As individuals age, their diets can change radically. Anyone who has tried to raise baby fish in an aquarium can appreciate that predation is often critically tied to body size. Individuals of a single species may act as prey, competitors, or predators, depending on their age and size. **Intraguild predation** (IGP) is the ecological interaction in which two competing species also interact as predator and prey. IGP is not an isolated phenomenon; it is common in terrestrial, marine, and freshwater communities, and probably represents the rule rather than the exception in nature (Polis et al. 1989).

How can we modify our simple competition model to take account of IGP? Suppose that two species compete according to the Lotka–Volterra equations, but species 1 is also a predator on species 2. This is a simple model that does not involve age structure, reciprocal predation, or cannibalism. However, it at least illustrates the way that IGP can modify ecological interactions. The growth equation for species 1 ("predator") is:

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha N_2}{K_1}\right) + \gamma N_1 N_2 \qquad \text{Equation 5.7}$$

This is identical to the original Lotka–Volterra model, except we have added an additional term. This addition represents the increase in growth rate that species 1 receives by feeding on species 2. The amount of this increase depends on the abundances of predator and prey (N_1N_2) and an interaction coefficient (γ). We will see a similar expression in Chapter 6 when we build a predator-prey model. The growth equation for species 2 ("prey") is:

$$\frac{dN_2}{dt} = r_2N_2\left(\frac{K_2 - N_2 - \beta N_1}{K_2}\right) - \delta N_1N_2 \qquad \text{Equation 5.8}$$

Again, growth of species 2 is described by the Lotka–Volterra model, but is further reduced because of losses due to predation by species 1. These losses also depend on the abundances of predator and prey (N_1N_2) and an interaction coefficient (δ). Note that the interaction coefficients for predator (γ) and prey (δ) need not be equivalent. The loss of an individual to predation usually does not correspond to a symmetrical gain for the predator population. Again, these ideas are explored more thoroughly in Chapter 6.

How does IGP affect the coexistence of species? The graphical effect of IGP is to rotate the isoclines. IGP does not change the carrying capacity for either predator or prey. Instead, it changes the abundance of the competitor that is necessary to cause extinction. Consequently, each isocline is rotated up or down, but remains fixed at the intercept on its own axis. For the predator, the isocline swings up, because it now requires more competitors to drive the predator to extinction than before (Figure 5.9a). For the prey species, IGP swings the isocline in towards the origin, because it now requires fewer competitors to cause extinction (Figure 5.9b).

IGP can either reinforce or reverse the outcome of competition, depending on the position of the isoclines and the amount of rotation (which is ultimately controlled by the interaction coefficients). For example, if the inferior competitor is also the prey species, IGP merely adds the insult of predation to the injury of competition and reinforces the extinction of species 2 (Figure 5.10a). But if the inferior competitor is the predator, IGP can change the outcome from competitive exclusion (case 1) to stable coexistence (case 3; Figure 5.10b). Other outcomes are possible, and IGP may provide insight into species coexistence when simple competition and predation models fail (Polis et al. 1989).

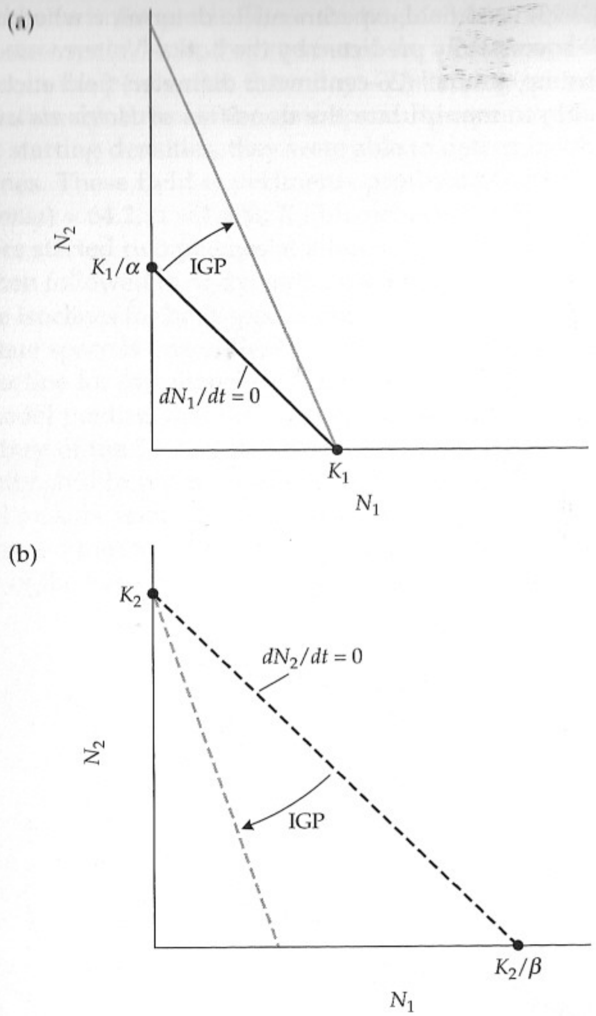


Figure 5.9 (a) Intraguild predation rotates the isocline of the "predator" species up, because it now requires more individuals of the competitor-prey to drive it to extinction. (b) Intraguild predation rotates the isocline of the "prey" species down, because it now requires fewer individuals of the competitor-predator to drive it to extinction.

Empirical Examples

COMPETITION BETWEEN INTERTIDAL SANDFLAT WORMS

In northern Puget Sound, many species of marine worms coexist in intertidal sandflats at very high densities. Abundances can be manipulated experimentally, allowing for a direct test of the Lotka–Volterra competition model. Gallagher et al. (1990) examined competition between juveniles of the polychaete *Hobsonia florida* and a number of closely related species of oligochaetes. Both *Hobsonia* and the oligochaetes coexist in dense aggregations in nature and feed on benthic diatoms.

Gallagher et al. (1990) used field experiments to determine whether such coexistence could be successfully predicted by the Lotka–Volterra model. By adding predatory shrimp to small (26-centimeter diameter) field enclosures, the authors were able to manipulate the densities of *Hobsonia* and the

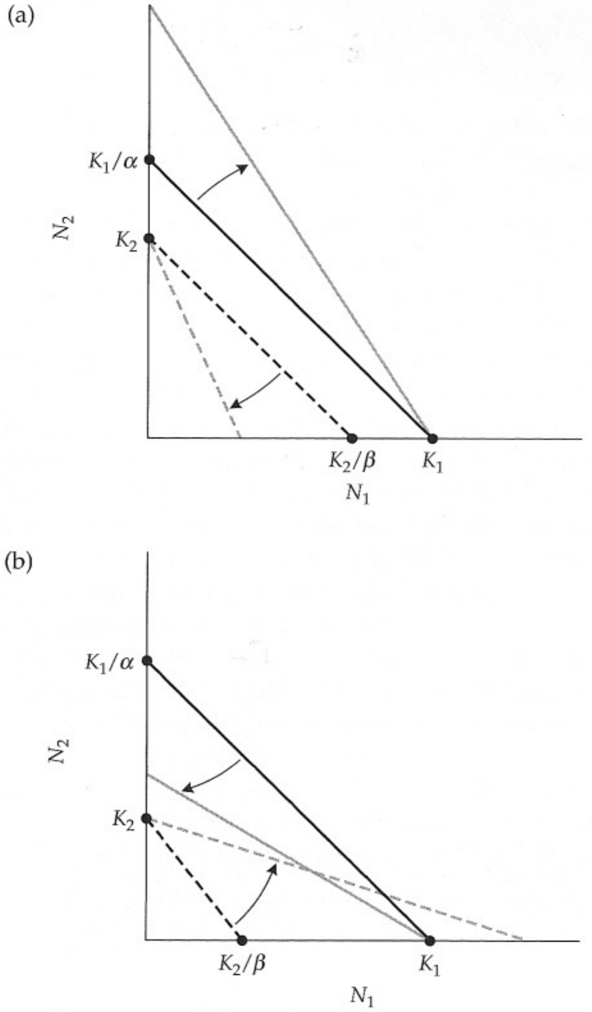


Figure 5.10 (a) Intraguild predation reinforces competitive exclusion. In this example, the superior competitor (N_1) is also the predator, so the shifted isoclines lead to the same outcome. (b) Intraguild competition reverses competitive exclusion. In this example, the inferior competitor (N_2) is now the predator. The isoclines shift from competitive exclusion (Case 1) to stable coexistence (Case 3).

oligochaetes in the patch. These starting densities represented a single point in the state space. Next, they measured the increase and decrease of each population in the patch after three days. These changes revealed the vector of population dynamics in the state space. By repeating this procedure for different starting densities, they were able to determine the placement of both isoclines. These field experiments produced the following estimates: K_1 (*Hobsonia*) = 64.2, α = 1.408; K_2 (oligochaetes) = 50.7, β = 0.754. Finally, the authors started two patches at a low initial abundance of both competitors and then followed their dynamics for 55 days.

The isoclines for both species are plotted in Figure 5.11. Superimposed on this state space is one of the trajectories for the 55-day experiment. Because the isocline for the oligochaetes lies slightly above the isocline for *Hobsonia*, the model predicts that the oligochaetes should win in competition. But the trajectory of the 55-day experiment did not reach the oligochaete carrying capacity, and in nature, both species coexist. The simple Lotka–Volterra model must be rejected for this system.

Why did the model fail to give us the correct predictions? Because the isoclines of the two species are very close to one another, the predicted time to

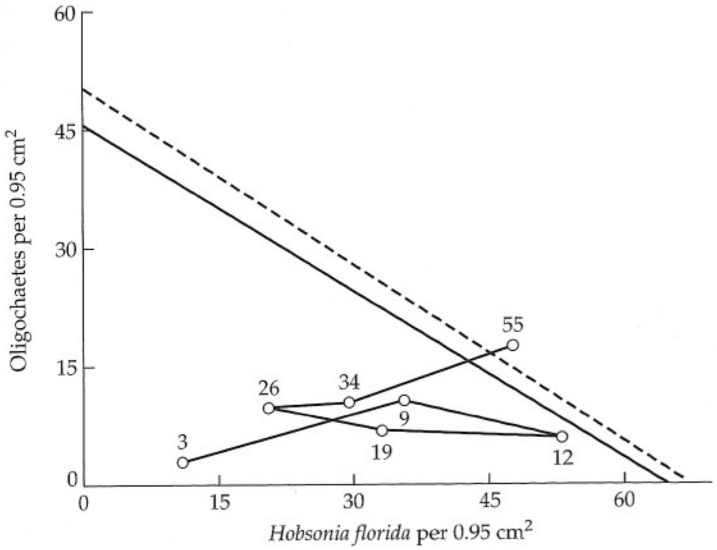


Figure 5.11 Competition between marine intertidal worms. The solid line is the estimated isocline for *Hobsonia florida*, and the dashed line is the estimated isocline for the oligochaetes. The line segments trace an experiment in the state space that was started with low abundances of both competitors. The numbers indicate the number of days since the start of the experiment. (From Gallagher et al. 1990.)

extinction is long. Moreover, there are seasonal changes in diatom abundance, so that the carrying capacities for each species are always changing. When carrying capacities change, the isoclines "wobble" through time, so that population trajectories may be continually changing. Under these conditions, there may not be enough time for one species to win in competition. Thus, the oligochaetes do not competitively exclude *Hobsonia* because the environment is always changing. As the ecologist G. Evelyn Hutchinson (1967) wrote: "The competitors of a given genus or other higher taxon are from time to time lined up, and sometimes the race begins, but as it might be in the works of Lewis Carroll, the event is always called off before it is completed and something entirely different is arranged in its place."

THE SHAPE OF A GERBIL ISOCLINE

Gerbils are mouselike rodents of the deserts of Africa and the Middle East. They are nocturnal seed foragers, and the coexistence of several gerbil species may depend on their use of common food and habitat resources. Abramsky et al. (1991) studied the coexistence of *Gerbillus allenbyi* and *G. pyramidum* in the western Negev desert of Israel.

Experimental studies of vertebrate competition are particularly difficult because of the large areas needed to enclose populations, and because competition is often mediated by subtle behavioral interactions. Abramsky et al. (1991) took advantage of the fact that *G. pyramidum* is considerably larger than *G. allenbyi* (mean mass = 40 grams versus 26 grams). The authors built enclosures that were 100 meters on a side (one hectare in area). Each enclosure was separated into two plots by a common fence. This fence had small gates to permit gerbils to move between the two sides. The gates were large enough to allow *G. allenbyi* through, but too small for *G. pyramidum* to pass. Thus, the fence acted as a semipermeable membrane, allowing *G. allenbyi* to "equilibrate" its density on the two sides based on the density of *G. pyramidum*.

Although the Lotka–Volterra competition model predicts changes in population growth rate, these are difficult to measure in short-term experiments on vertebrates. Moreover, the effects of competition on gerbil populations are likely to be expressed more immediately in changes in behavior and foraging activity. Instead of measuring gerbil density, the authors measured the "activity density" of each species by counting gerbil footprints in clean trays of sand that were placed in the plots each night. This index was correlated with density and foraging activity of individual gerbils.

The authors established one half of each enclosure with a high density of *G. pyramidum* and the other half with a low density. The density of *G. allenbyi* was allowed to equilibrate to these differences in competitor density. The resulting changes in activity of both species can be plotted in state space.

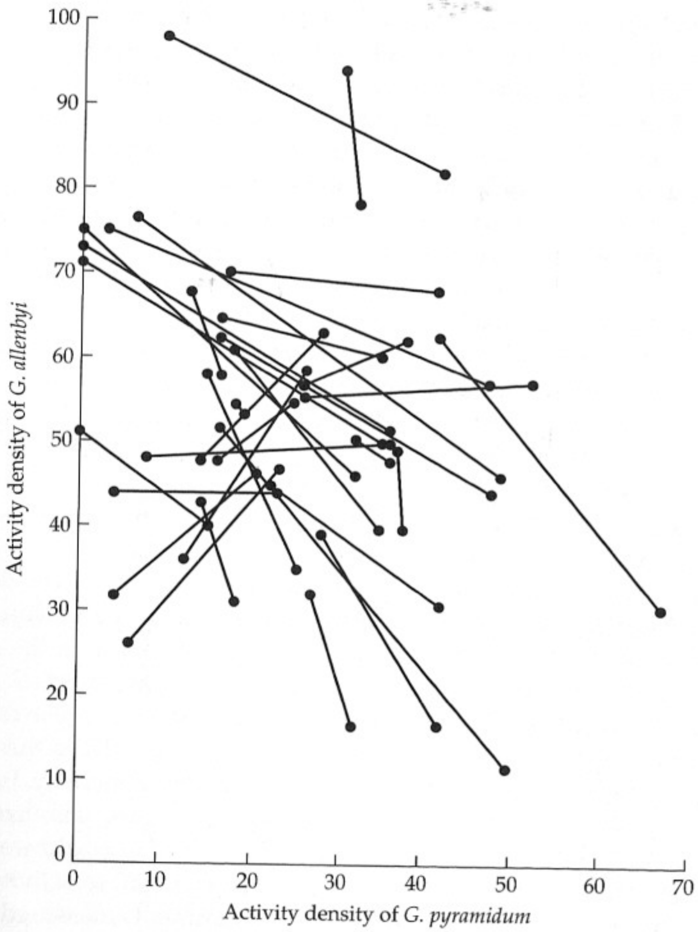


Figure 5.12 Results of gerbil competition experiments plotted in state space. Each line segment connects the points for the high-density and low-density plots in an experimental enclosure. Most of the segments have a negative slope, indicating a reduction in the activity density of *Gerbillus allenbyi* (*y* axis) in the presence of its competitor *G. pyramidum* (*x* axis).

Each line segment in this graph represents the activity density in the two halves of an enclosure. The slope of this line segment is a measure of the isocline of *G. allenbyi* in that area of the state space (Figure 5.12). Although there is considerable scatter in the data, most of these segments have a negative slope, indicating that high densities of *G. pyramidum* depressed the activity of *G. allenbyi*.

Figure 5.13 shows the isocline based on the "best fit" of all these line segments. In contrast to the predictions of the Lotka–Volterra model, the isocline for *G. allenbyi* is nonlinear, with steep declines at high and low densities of *G. pyramidum*, but a shallow slope at intermediate competitor densities.

Why isn't the isocline of *G. allenbyi* a straight line? The answer is that activity density depends not only on the abundance of competitors, but also on the availability and use of different habitats. In the Negev Desert, there are two habitat types that the gerbils use. "Semistabilized dunes" contain little perennial vegetation, many open patches of sand, and unstabilized sand dunes. "Stabilized sand" habitats are dominated by dense shrub cover, with large areas of stable soil crust and few open patches. Both habitat types were present in approximately equal abundance within each enclosure.

Under uncrowded conditions, both gerbil species preferred the semistabilized dunes. As intraspecific density increased, both species began to use the stabilized sand in greater frequency. *G. pyramidum* density induced a habitat shift in *G. allenbyi*, and this was responsible for the nonlinear isocline. Superimposed on the state space in Figure 5.13 are four lines ("isolegs") that are cutpoints for changes in habitat use of the two species. At low densities (regions I and II), both species preferred the semistabilized dunes, and increased densities of *G. pyramidum* led to a sharp decrease in the activity density of *G. allenbyi*. As the density of *G. pyramidum* increased, *G. allenbyi* did not decrease its activity, but instead shifted into the less preferred stabilized sand habitat. Consequently, the isocline is relatively flat in this region, reflecting habitat shift, rather than a reduction in activity density. But as its density increased, *G. pyramidum* was also forced to use the stabilized sand habitat. At high densities of *G. pyramidum*, *G. allenbyi* could no longer "escape" competition by moving to an unoccupied habitat, so activity density again dropped off steeply. Additional field experiments measured the isocline of *G. pyramidum* (Abramsky et al. 1994), and a mathematical analysis predicts stable coexistence of both competitors.

The Lotka–Volterra model generates simple predictions and provides a framework for field tests of competition. Nevertheless, it is very difficult to manipulate species densities in realistic field experiments, and it is still an open question as to whether resources are limiting. These studies show that even when resources are limiting, the model's simple predictions may fail because factors such as variable environments and habitat selection can also affect the outcome of interspecific competition.

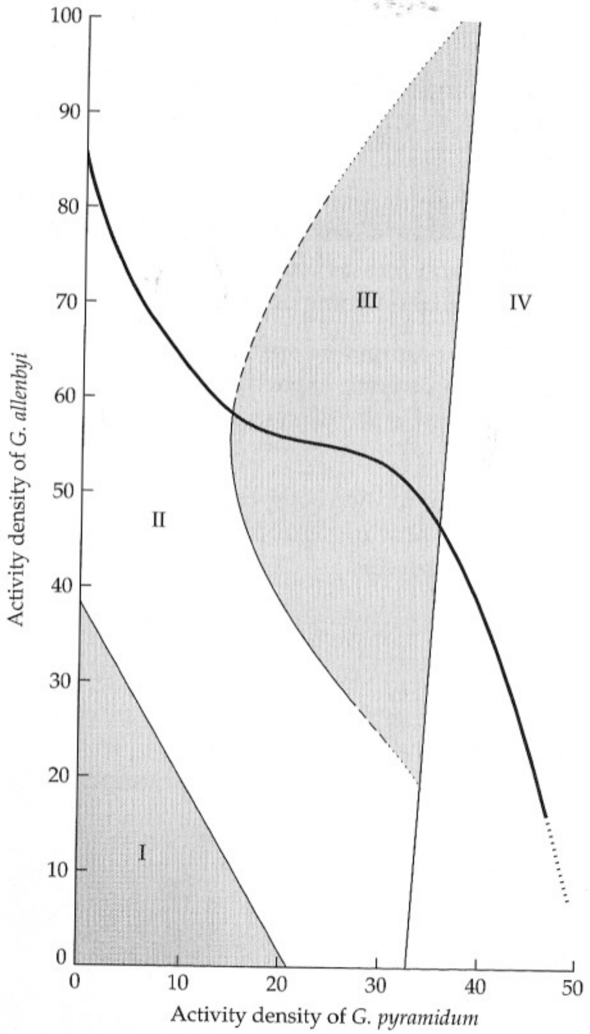


Figure 5.13 The isocline for *Gerbillus allenbyi*, estimated from the data in Figure 5.12. Note that the isocline (thick line) is not linear, but has a region of shallow slope at intermediate densities of *G. pyramidum*. This nonlinear isocline reflects the effects of competition and habitat selection. The thin lines divide the state space into regions based on habitat use. Region I: Both species use the preferred habitat, semistabilized dune. Region II: *G. allenbyi* is forced to use the less preferred habitat, stabilized sand. Region III: Increased use of the stabilized sand by *G. allenbyi*. Because *G. allenbyi* shifts to its less preferred habitat, its activity density can remain high, leading to a shallow slope for the isocline in this region of the state space. Region IV: *G. pyramidum* is forced into the stabilized dune habitat by intraspecific competition. Because *G. allenbyi* no longer has an escape to the unoccupied habitat, its activity density drops off sharply with increases in the activity density of *G. pyramidum*.

Problems

5.1. You are studying competition between red and black desert scorpions. For the red scorpion, $K_1 = 100$ and $\alpha = 2$. For the black scorpion, $K_2 = 150$ and $\beta = 3$.

Suppose the initial population sizes are 25 red scorpions and 50 black scorpions. Graph the state space and isoclines for each species, and plot these initial population sizes. Predict the short-term dynamics of each population and the final outcome of interspecific competition.

5.2. Suppose that, for two competing species, $\alpha = 1.5$, $\beta = 0.5$, and $K_2 = 100$. What is the minimum carrying capacity for species 1 that is necessary for coexistence? How large is the carrying capacity needed for species 1 to win in competition?

*5.3. Diagram the state space for two competing species in which there is a stable equilibrium. Show how intraguild predation could shift this to exclusion by the predatory species.

---

* Advanced problem