

14 Competitors

INTERSPECIFIC COMPETITION MAY BE OF TWO RELATED TYPES

Interspecific competition between two species occurs when individuals of one species suffer a reduction in growth rate from a second species due to their shared use of limiting resources (**exploitative competition**) or active interference (**interference competition**). In general, we do not expect interference competition to evolve unless this energetically costly squabbling potentially leads to some benefits to the aggressors (Case and Gilpin 1975). Such would be the case if an aggressor were able to protect some limited resource from being consumed in its territory by individuals of a competing species. For this reason, we might expect a correlation between the degree of interference competition between two species and the extent that they share critical resources. Moore (1978) studied interspecific aggression by mockingbirds inhabiting residential areas in South Carolina. In the fall and winter these birds defend territories containing trees and shrubs laden with small fruits. The level of aggression by mockingbirds to intruders in their territory is roughly proportional to the degree of frugivory in the diet of the intruding species, as indicated in Figure 14.1.

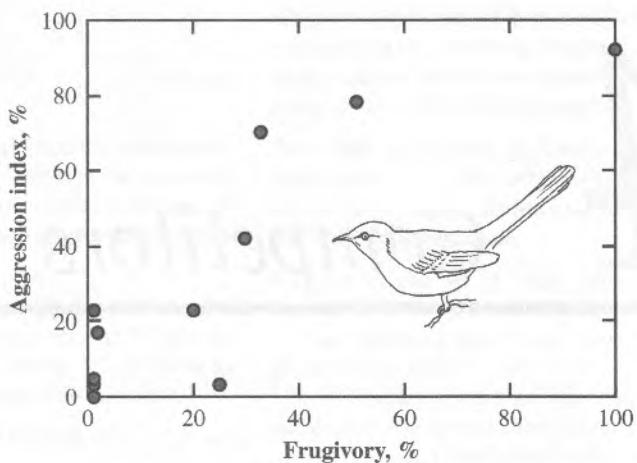
Typically, interference competition is asymmetric, with one species aggressively dominating the other. This dominance is often associated with larger body size (Lawton and Hassel 1981, Robinson and Terborgh 1995). In many vertebrates, interspecific aggression can lead to interspecific territoriality such that individuals defend their territories against intrusion from individuals of their own and other species. However, in other cases it can simply lead to the decline and local extinction of the inferior competitor across all habitats. Recall the example of the spreading Argentine ants in southern California from a study of Erickson (1971). In Chapter 2, we showed that the radius of their distribution across a field grew linearly with time. As they moved across this field and as their colony number increased, a native harvester ant, *Pogonomyrmex californicus*, declined, as illustrated in Figure 14.2. Since these two ant species eat different kinds of foods, the major cause of this competitive displacement can be ascribed to the dominance of the Argentine ant in interference competition. Here, however, this advantage isn't due to a larger body size—Argentine ants are substantially smaller than harvester ants. Rather the Argentine ants have larger colonies and a more coordinated fighting response in which several workers team up to defeat a single harvester ant. If these ants do not compete for food, why should they bother fighting? Perhaps because they compete for other resources such as available below-ground nest space.

LABORATORY EXPERIMENTS ON COMPETITION

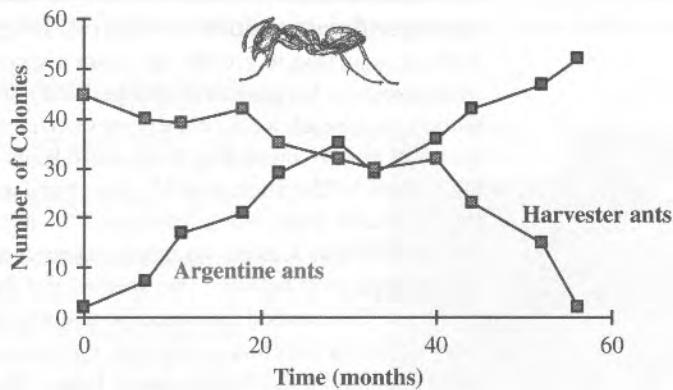
We now turn to some observations taken from laboratory experiments involving simple two-species competitive systems. In the laboratory it is possible to manipulate species densities and control external environmental conditions to focus on the role

Figure 14.1

Mockingbirds are generally more aggressive to other bird species which, like them, eat a large proportion of small fruit (from Moore 1978).

**Figure 14.2**

As the population of the introduced Argentine ants in an old field in Southern California increased, the seed-eating harvester ants, *Pogonomyrmex californicus*, declined (modified from Erickson 1971).



of particular interspecific interactions. These observations will guide us in developing a theory to predict the consequences of interspecific competition under different situations.

Paramecium

In Chapter 5 we showed—from the experiments of Gause (1934, 1936)—that population growth of the protozoan *Paramecium* provided a reasonable approximation to the continuous logistic equation. Gause and others also conducted experiments growing different species of *Paramecium* alone and then together. The time course of one set of experiments involving the species *P. aurelia* and *P. caudatum* when alone and grown together is shown in Figure 14.3.

The cell sizes of these two species are very different. Because *Paramecium caudatum* is 2.5 times larger than *P. aurelia*, its carrying capacity is less than one-half that of *P. aurelia*. In other experiments, Gause demonstrated that the carrying capacity of each species alone seemed to be a direct function of the amount of food (bacteria) added to the culture medium. Subsequently, Gause (1935) placed other species in competition, using somewhat different rearing conditions. In one set of experiments he found the results summarized in Figure 14.4.

As before, *P. caudatum* is competitively excluded in the presence of *P. aurelia*. However, it coexists with the equally small *P. bursaria*, which also has a larger carrying capacity, K . Clearly, K alone is not a predictor of competitive outcome. *Paramecium aurelia* can also coexist with *P. bursaria*. Upon closer inspection, Gause (1936) noticed that the coexisting species pairs subdivided space in the test tubes. *Paramecium bur-*

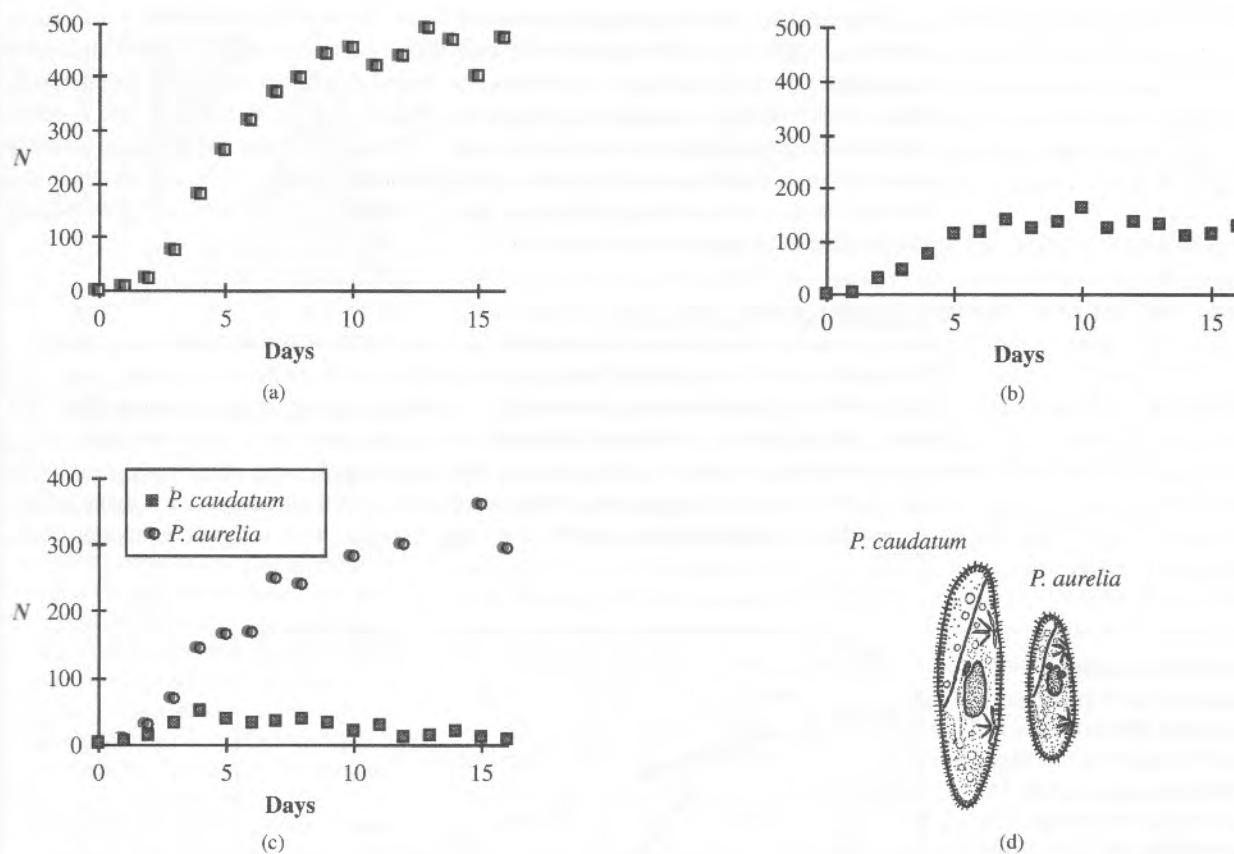


Figure 14.3

Paramecium numbers are expressed in numbers per 0.5 ml. Data and drawings are from Gause (1934, page 99 and Table 4).
 (a) $P. aurelia$ alone. (b) $P. caudatum$ alone. (c) $Paramecium aurelia$ out-competes $P. caudatum$ when the two are together.
 (d) $Paramecium caudatum$ is about 2.5 times larger than $Paramecium aurelia$ in cell volume.

Figure 14.4

Competitive outcomes with different species pairs of *Paramecium*. The diagonal gives estimates for r and K based on some single species experiments. The K 's are the number of individuals per 0.5 ml (recalculated from Gause 1935).

	Relative cell volume = 1	0.39	0.41
<i>P. caudatum</i>	<i>P. caudatum</i>	<i>P. aurelia</i>	<i>P. bursaria</i>
<i>P. aurelia</i>	<i>r</i> = 1.10 <i>K</i> = 80	<i>P. aurelia</i> wins	Coexist
<i>P. bursaria</i>	<i>r</i> = 1.00 <i>K</i> = 510	Coexist	
	<i>r</i> = 0.94 <i>K</i> = 400		

saria have tiny symbiotic green algae inside them. These algae, like all plants, produce oxygen that allows *P. bursaria* to live in the bottom of the tubes where oxygen levels are depleted by bacteria, which tend to sink. The other two *Paramecium* have higher oxygen requirements and are relatively more common in the upper parts of the tubes where oxygen levels are higher but food (bacteria) concentrations are lower.

For the species pairs that coexist, roughly the same equilibrium densities are reached regardless of the initial densities, as long as both species are simultaneously introduced into the medium. The four trajectories in Figure 14.5 all converge to the small region of phase space marked by the rectangle.

Vandermeer (1969) repeated some of these experiments with the same three species plus one other. His experimental conditions were somewhat different and, most important, he used a strain of *P. bursaria* that lacked symbiotic algae. He found conditions under which *P. caudatum* could coexist with *P. aurelia*, yet both would exclude *P. bursaria*, quite contrary to Gause's results. Altogether, these experiments indicate that food supply levels, oxygen levels, and the buildup of metabolic by-products in the culture media are important in limiting the growth of these species and determining competitive advantage or coexistence.

Tribolium Flour Beetles

Park (1954, 1962) conducted competition studies on flour beetles in the genus *Tribolium*. These small insects grow readily in vials containing common wheat flour and yeast. Their generation time is about 35 days, and population censuses were taken once a month. In one set of experiments Park explored the role of climatic conditions on the growth of the species when they were alone and then when they were together. Figure 14.6 presents the results. First, unlike the case with some *Paramecium*, Park

Figure 14.5

Four different initial conditions produce trajectories that converge on roughly the same equilibrium abundances of *Paramecium bursaria* and *P. caudatum*, the stippled box. The K 's show the carrying capacities of the two species when they are alone. After Gause (1936).

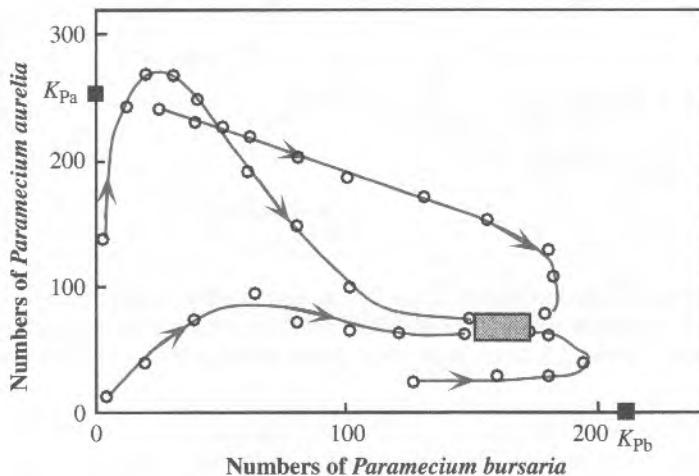
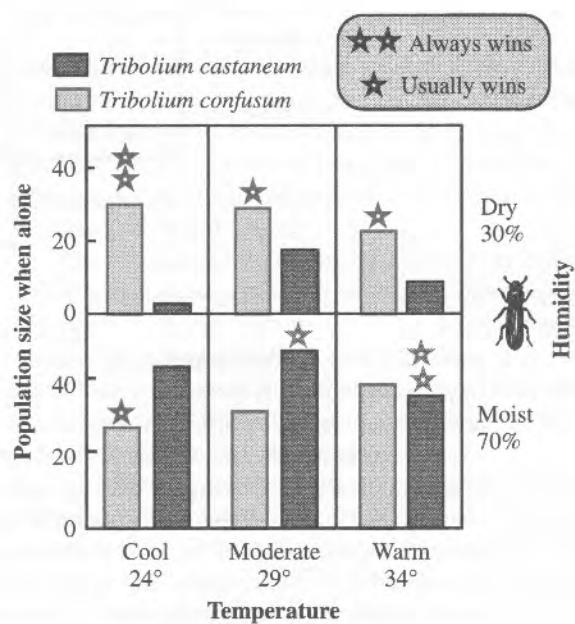


Figure 14.6

Flour beetle competition under different climatic conditions. The mean population size per gram of flour includes larvae, pupae, and adults, based on 15–40 replications of each experiment (standard errors are small and range from about 0.4 to 3.5 individuals). Each experiment was initiated with eight adults (four males and four females) of each species introduced into 8 grams of a flour/yeast mixture. After Park (1954).



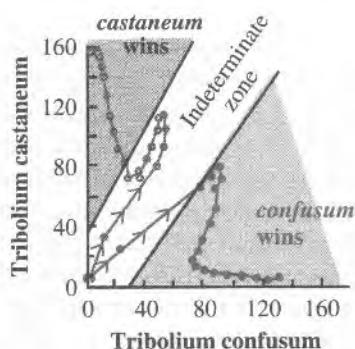


Figure 14.7

The head-start advantage of *Tribolium* competition. These results are for the cool/moist conditions shown in Figure 14.18. The outcome of competition is strongly influenced by the initial conditions. The regions display the qualitative outcome of competition starting from different initial abundances for the two species. In the "confusum wins" region, *confusum* outnumbers *castaneum* initially. When the two species are approximately equal in abundance, the outcome of competition is probabilistic. Two sample trajectories are shown, both from the same initial condition of eight beetles of each species. Each dot is a census 30 days apart. After Neyman et al. (1956).

found no conditions under which the two species could coexist, nor did both species become extinct. Instead, a clear winner and loser always emerged. Which species won, however, was not obviously related to its abundance or even relative abundance in the single species experiments. For example, under the cool/moist conditions, *T. castaneum* had a much higher mean density when alone but was the usual loser in competition. However, it occasionally would win, providing a degree of indeterminacy to the results.

This indeterminacy is typically seen when the initial numbers of each species are approximately equal as they were for this particular set of experiments (eight individuals of each species). For the same climatic conditions, the initial numbers make a big difference in determining the winner and loser. Either species, if given a strong numerical head start, becomes the favored species, as shown in Figure 14.7.

Several experiments by Park and others demonstrated that if the amount of flour is increased, the carrying capacity of each species is increased in a roughly linear fashion. Consequently, equilibrium densities (numbers per gram of flour) remain roughly constant for the same environmental conditions. Food, however, is not limiting in this system. These beetles are literally oversupplied with food continuously. Instead, intraspecific and interspecific cannibalism by adults and larvae eating eggs and pupae is responsible for the density-dependence (Park 1965, Wade 1979, 1980). At higher densities these deadly encounters happen more frequently. Also, Park (1965) demonstrated that overall interspecific predation rates were greater than intraspecific predation rates.

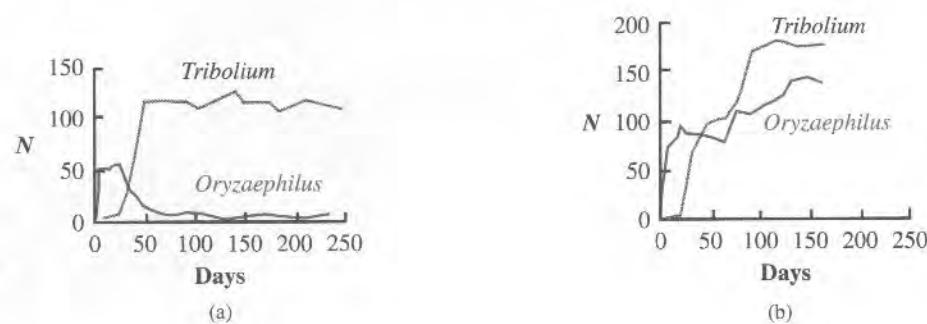
This suggests that if mutual predation could be eliminated in this system, more prolonged coexistence might be possible. Crombie (1946) found just this result. Two beetles, this time a *Tribolium* and a related genus, *Oryzaephilus*, show the same sort of competitive incompatibility found in Park's experiments with two species of *Tribolium*: no coexistence and *Tribolium* was always the winner. Crombie (1946) next added short lengths of capillary tubing to the flour mixture. These provided *Oryzaephilus* safe sites for pupation free from predation by *Tribolium*. Now the two species could coexist, as illustrated in Figure 14.8. *Tribolium* reached higher densities in spite of the now higher numbers of *Oryzaephilus*, suggesting that it was relieved of some cannibalism as well.

In summary, the ultimate outcome of competition depends on environmental conditions and sometimes on initial conditions. Some species can coexist, as with some species of *Paramecium*, but for other species or environmental conditions, they cannot, as with other *Paramecium* species pairs and the *Tribolium*. Those species that can coexist seem to utilize the environment in different ways or have a spatial refuge from the pressures of the other species (mutual cannibalism in the case of *Tribolium* and food and oxygen exploitation in *Paramecium*).

We now search for a conceptual framework for these observations. We'd like to uncover general rules about the assembly of competitors in communities—rules that might let us predict which species combinations will be compatible and which will not.

Figure 14.8

Competition between two flour beetles. After Crombie (1946). (a) Without glass tubing. (b) With glass tubing. Fine glass capillary tubing added to the flour provides safe sites for pupation free from predation, allowing the two species to coexist.



MODELING COMPETITION

As we have already shown with single-species growth models, logistic equations implicitly invoke intraspecific competition in the form of a carrying capacity term for a population. The experimental results discussed earlier show that competition can also occur between individuals of different species. The dynamical effects of interspecific competition may be modeled by using two different approaches, depending on whether resource dynamics are **explicitly** or **implicitly** considered, as depicted in Figure 14.9. The explicit approach considers the dynamics of the consumer–resource interactions. The arrows represent qualitative effects of one species on another's per capita growth rate with the sign indicated. Resources increase consumers' growth rates, so the sign on this arrow is positive. Consumers decrease resource growth rates, so the sign on this arrow is negative. A full explicit model would flesh this out by specifying differential or difference equations for the functions f and g .

Figure 14.9

Two approaches to modeling competition. Implicit versus explicit models for interspecific competition among two consumers, C_1 and C_2 . The plus or minus sign by the arrowhead shows the effect on that species caused by the other species.

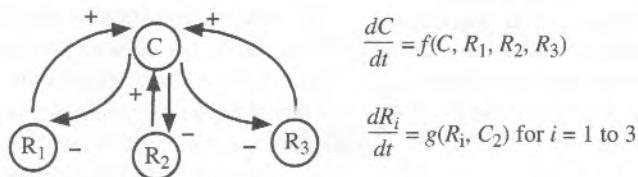
Intraspecific Competition

Implicit intraspecific competition within a consumer species, C .



$$\frac{dC}{dt} = f(C)$$

Explicit intraspecific competition of a consumer species, C , for three resources.



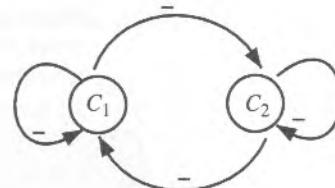
$$\frac{dC}{dt} = f(C, R_1, R_2, R_3)$$

$$\frac{dR_i}{dt} = g(R_i, C_2) \text{ for } i = 1 \text{ to } 3$$

Interspecific Competition

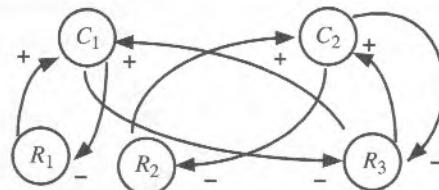
Implicit Models

Exploitation and interference cannot be distinguished, but the model is much simpler.

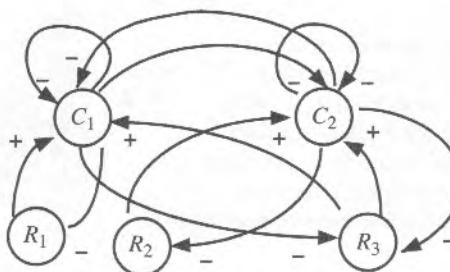


Explicit Models

Exploitation competition between two consumers for three resources. Resources have positive effects on consumer growth, and consumers have negative effects on resource growth.



Exploitation plus interference competition among consumers



The implicit approach buries all these details into an implicit competition equation, just as the logistic equations ignored the mechanisms of intraspecific competition by introducing the notion of a carrying capacity for the population.

By modeling resource dynamics explicitly, we gain a better understanding of how resources influence competitive success and the mechanisms involved (Tilman 1986). In going from an explicit consumer–resource model to an implicit model, we necessarily lose important features of the dynamics of species interactions. The hope, though, is that we will not be seriously misled in our search for simplicity, at least regarding qualitative aspects of competition, such as whether two competitors can or cannot coexist. However, with implicit models we may lose the ability to predict accurately the actual trajectories and to understand the mechanism of competition.

The Lotka–Volterra competition equations, like the logistic equations, treat competition implicitly; they extend the logistic equations by incorporating inter- as well as intraspecific growth limitations. Moreover, in this formulation, the per capita effects of density on per capita growth rate are assumed to be linear for both intra- and interspecific effects, as shown in Figure 14.10. Also interference and exploitative competition are not distinguished. Figure 14.11 takes you through the qualitative dynamics to the development of one competitor’s zero-isocline, just as we did with predator–prey systems in Chapter 12.

As we did with predator–prey systems, we have now developed the zero-isocline for a species in state space and have drawn arrows indicating the qualitative direction of growth for that species in different regions of state space. The zero-isocline for species i defines the set of points in the N_1 – N_2 phase plane where species i ’s population neither increases nor decreases.

We can also overlay information about the magnitude of the growth rates at various points of the species 1–species 2 phase space, just as a topographical map overlays elevations on the two dimensions of latitude and longitude. Figure 14.12 shows a plot of the three-dimensional representation of species 1’s growth, originally plotted in just two dimensions—the N_1 – N_2 plane—with the different isolines representing different “elevations.”

Usually, however, as with predator–prey systems, useful information about the direction of initial trajectories and the stability of equilibrium points can be determined solely from qualitative information depicted in plots that show the zero-isoclines of each species and the regions of state space that yield positive or negative growth for each. These diagrams are also useful for another reason. Analytical mathematical

Figure 14.10

Two species Lotka–Volterra Competition. The red triangular plane shows the per capita growth rate of species 1 declining with increases in density of both species 1 and species 2. At high densities, species 1’s growth rate even becomes negative.

How do the densities of species 1 (N_1) and species 2 (N_2) affect the growth rate of species 1? Plot species 1’s per capita growth rate in the vertical direction as a function of N_1 and N_2 .

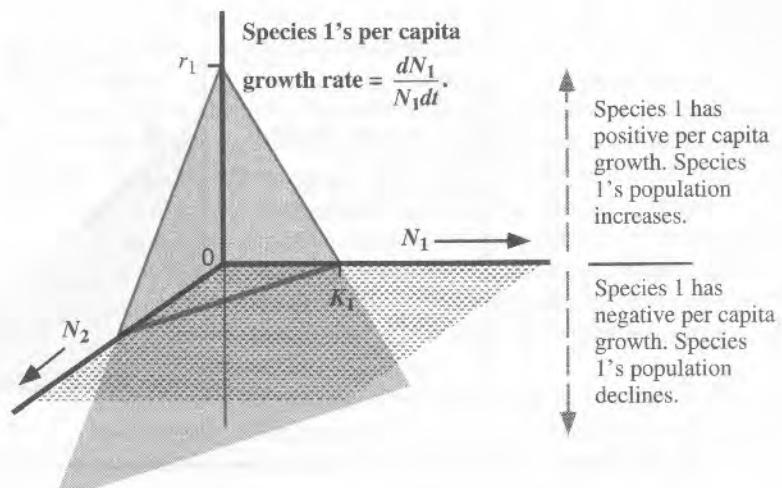
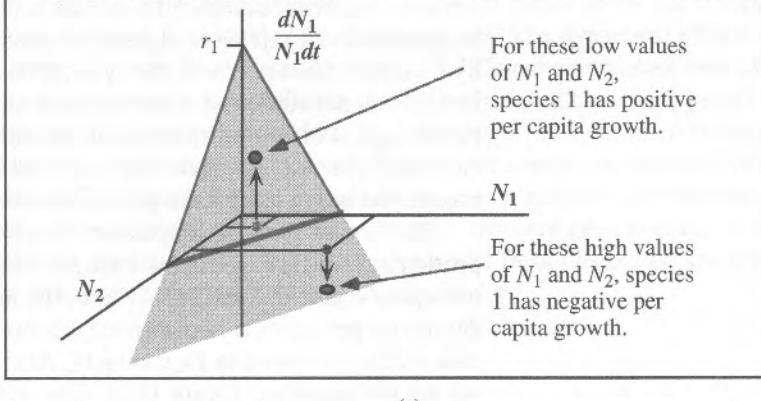


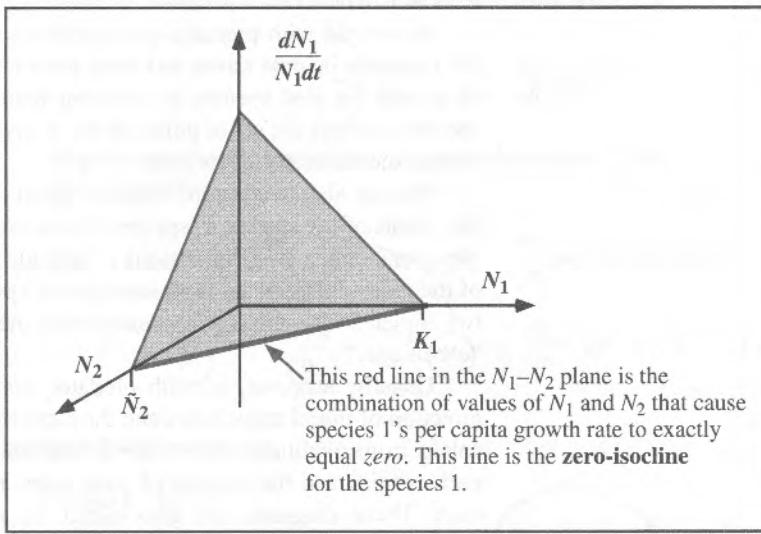
Figure 14.11

These three diagrams develop a zero-isocline for species 1.

Here, for example, are two joint densities of N_1 and N_2 (the gray dots). Each is projected onto the red growth plane for species 1 to show the corresponding per capita growth rate for species 1 at these two points.

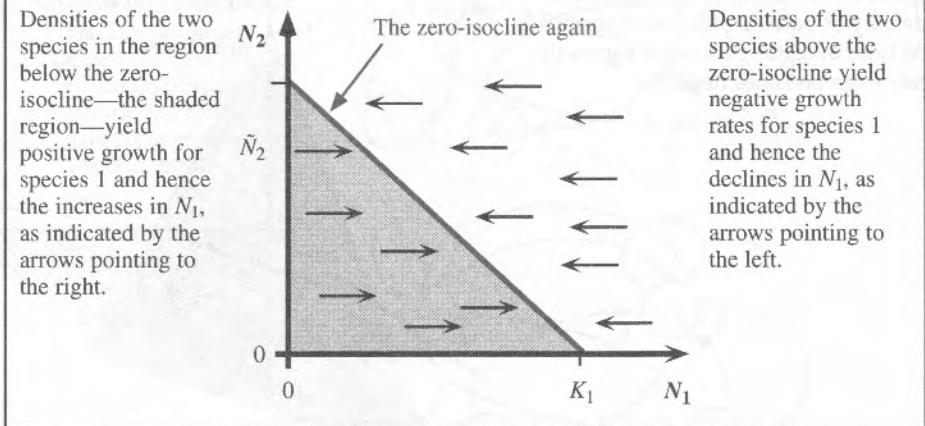


(a)



(b)

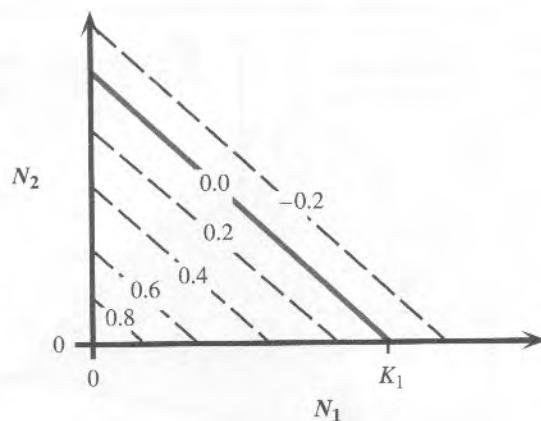
Now flip the bottom plane in (b) on its side and get rid of the per capita growth dimension so that you now look at just the N_1 - N_2 phase plane.



(c)

Figure 14.12

A “topographic map” of species 1’s per capita growth rate as a function of density of both species 1 and 2.



results for coupled differential equations are often impossible to achieve. For example, the predator-prey equations that you studied in Chapter 12 do not have a general closed-form analytical solution for $C(t)$ and $R(t)$ over time (as we found for exponential growth and logistic growth of single species). The best we can do is infer qualitative dynamics from approximate or numerical solutions or instead rely on qualitative information based on these phase-space pictures. Similarly, the Lotka-Volterra competition equations, which we develop next, as simple as they are, have no closed-form analytical solution.

LOTKA-VOLTERRA COMPETITION EQUATIONS

With this graphical exposition behind us, we move on to the equations that match the depictions in Figures 14.10 and 14.11. The assumptions behind these graphs may be encapsulated in a differential equation for species 1’s growth:

$$\frac{dN_1}{dt} = \frac{r_1 N_1}{K_1} (K_1 - N_1 - \alpha_{12} N_2). \quad (14.1)$$

Except for this term, this equation is the continuous logistic equation.

The last term with the α_{12} converts species 2’s numbers into an effect on species 1’s per capita growth rate; α_{12} is the scaling factor that makes the conversion. Read the term α_{12} as the “effect of an individual of species 2 on the per capita growth rate of species 1.” Its magnitude will be relative to species 1’s effect on its own growth rate. Note that there is an implicit constant of 1 in front of the term N_1 (i.e., $\alpha_{11} = 1$). If, for every additional individual of species 2, the per capita growth rate of species 1 declines by half the amount that it would by the addition of an individual of species 1, then $\alpha_{12} = 0.5$. If species 1’s per capita growth rate declines twice as fast with additions of species 2 compared to additions of species 1, then $\alpha_{12} = 2$. The relationship between per capita growth and numbers of both species is presented visually in Figure 14.13.

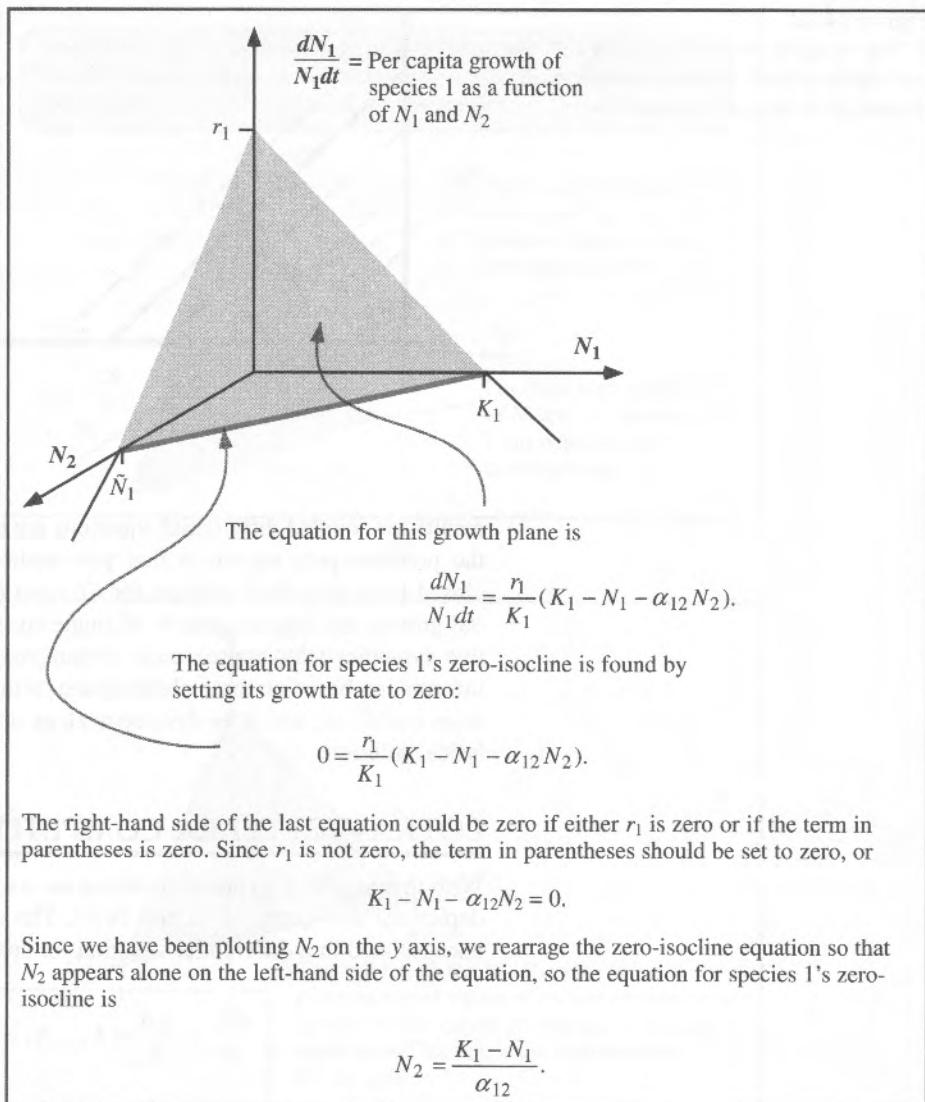
Now, armed with an actual equation for competition, we return to Figure 14.13 and label points of interest to arrive at the diagram shown in Figure 14.14.

Next, we need to add the second competing species to the picture. We do this by drawing its per capita growth rate as it is affected by species 1’s density as well as its own density, as illustrated in Figure 14.15.

We abstract this three dimensional depiction to just the two dimensions of the N_1-N_2 phase plane by eliminating the quantitative information provided by the vertical growth rate axis. This leads us to the zero-isocline depiction shown in Figure 14.16, which is just the bottom plane in Figure 14.15 flipped on its side.

Figure 14.13

Lotka–Volterra competition equations.
Derivation of the equation for species 1's zero-isocline.

**Figure 14.14**

Solving algebraically for the slope and y intercept of species 1's zero-isocline.

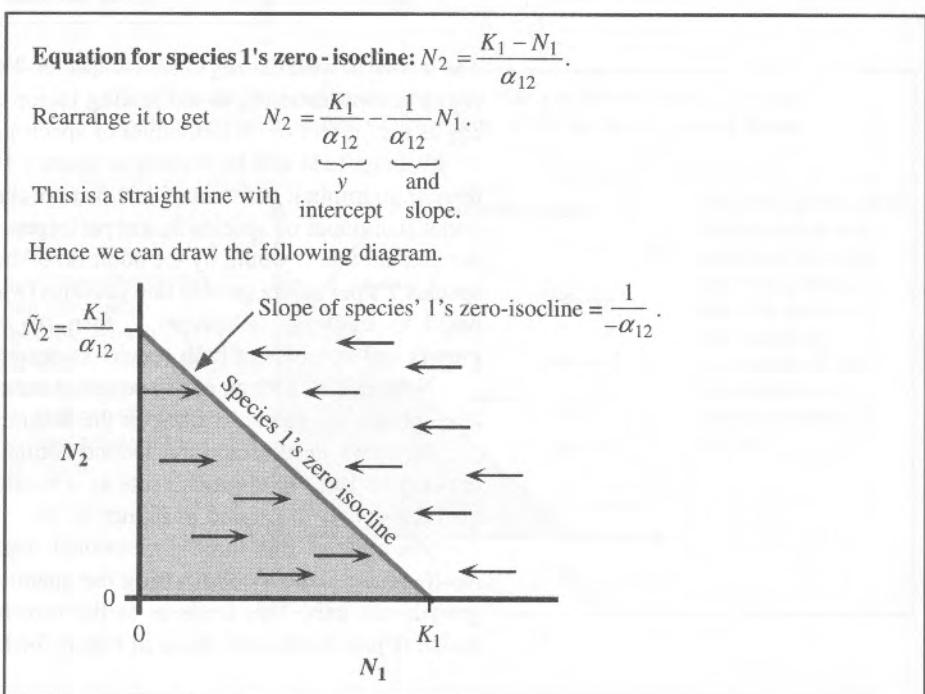
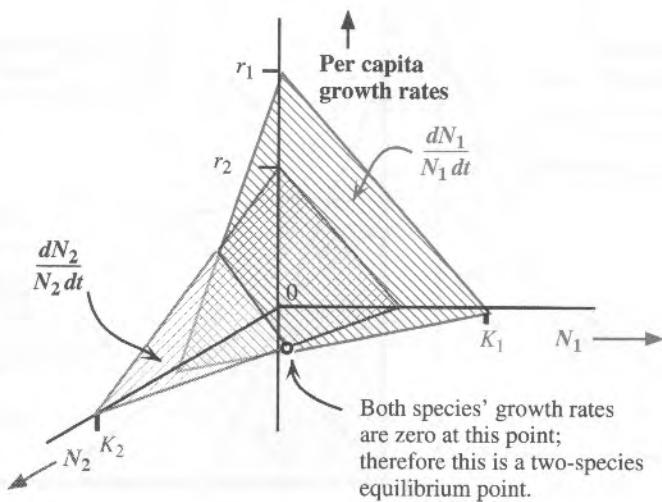


Figure 14.15

The decline in per capita growth rate for species 1 and 2, with increases in density of species 1 and 2. The axis lines meet at the origin $(0, 0, 0)$.

**Figure 14.16**

Zero-isoclines separate regions of positive and negative growth rates for each species. The black arrows in (b) indicate the qualitative direction of growth from a point in state space (i.e., initial values for N_1 and N_2) and are derived from the arrows for each species in (a). Refer to Appendix 1, Part 2 and Figure 5.8 for a review of the concept of stability and the meaning of a saddle point.

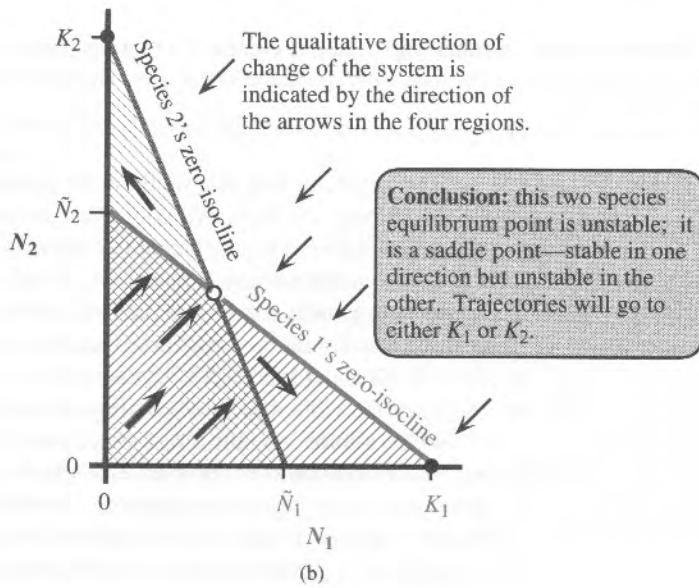
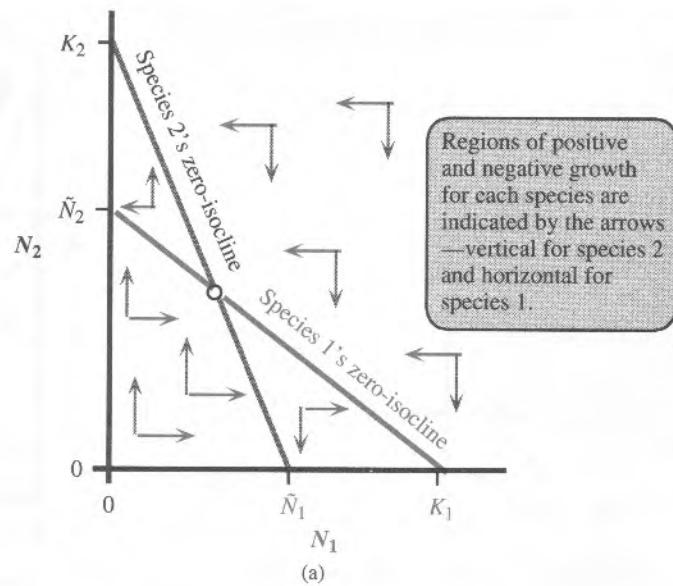
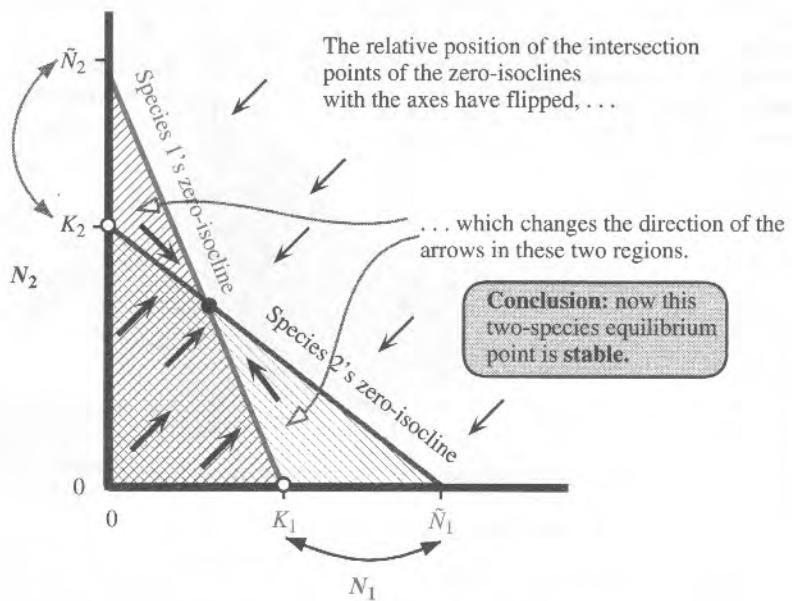
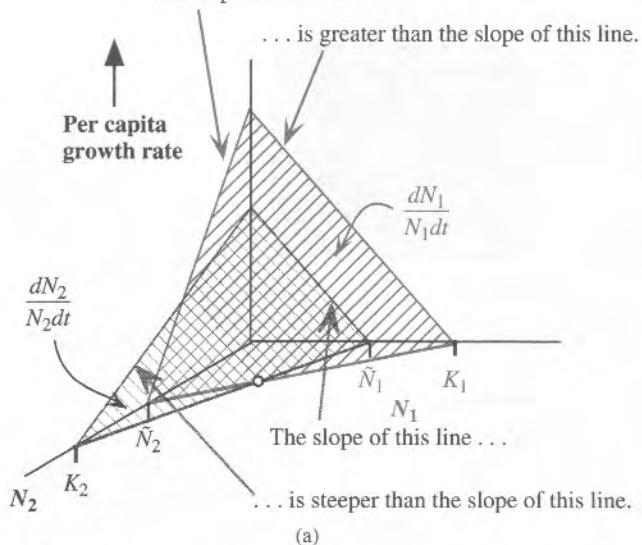


Figure 14.17

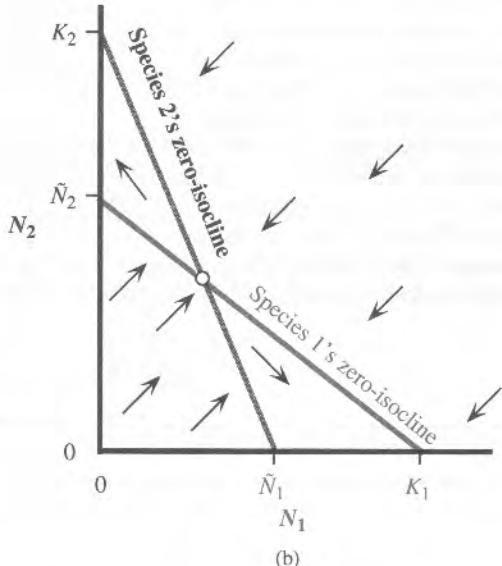
Drawing the zero-isoclines with different slopes and y intercepts makes it possible to construct a phase-space diagram with zero-isoclines that produce a stable interior equilibrium point.



The slope of this line . . .



(a)



(b)

Figure 14.18

An explanation of the difference between stable and unstable competitive interactions in terms of per-capita effects—the unstable case. Intraspecific competition is *less* than interspecific competition. The growth rate declines shown in (a) produce the zero-isoclines shown in (b).

The particular way that we drew the growth rate response of the two species in Figure 14.15 was arbitrary. We could just as easily have drawn the two zero-isoclines somewhat differently as depicted in Figure 14.17.

In the **unstable** case (Figures 14.15 and 14.16), the effect of species 1's numbers on its own growth rate is *less* than the effect of species 2's numbers on species 1's growth rate. Similarly, the effect of species 2's numbers on its own growth rate is *less* than the effect of species 1's numbers on its growth rate. In other words, intraspecific competition is less than interspecific competition, as summarized in Figure 14.18.

In the **stable** case, the effect of species 1's numbers on species 1's own growth rate is *greater* than the effect of species 2's numbers on species 1's growth rate. Similarly, the effect of species 2's numbers on species 2's own growth rate is *greater* than the effect of species 1's numbers on species 2's growth rate. In other words, intraspecific competition is greater than interspecific competition, as summarized in Figure 14.19.

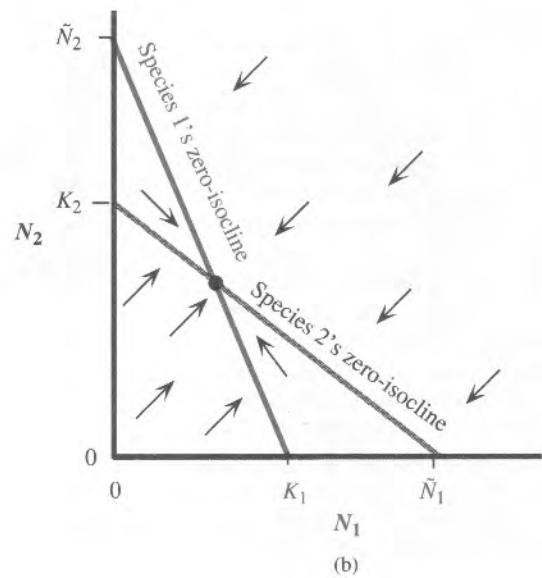
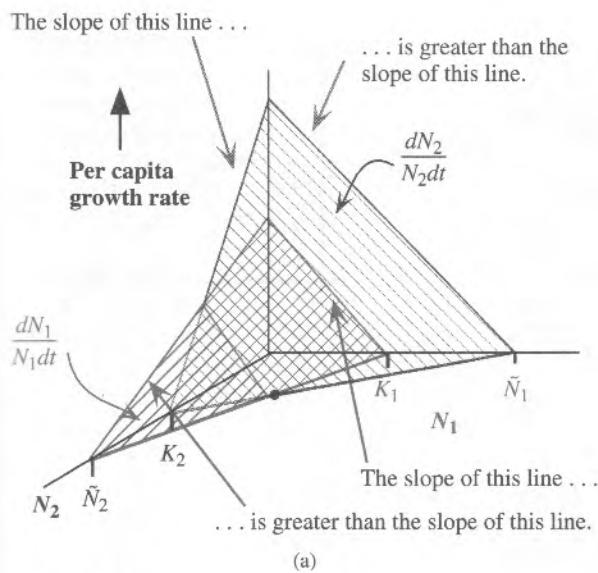


Figure 14.19

An explanation of the difference between stable and unstable competitive interactions in terms of per capita effects—the stable case. Intraspecific competition is greater than interspecific competition. The growth rate declines shown in (a) produce the zero-isoclines shown in (b).

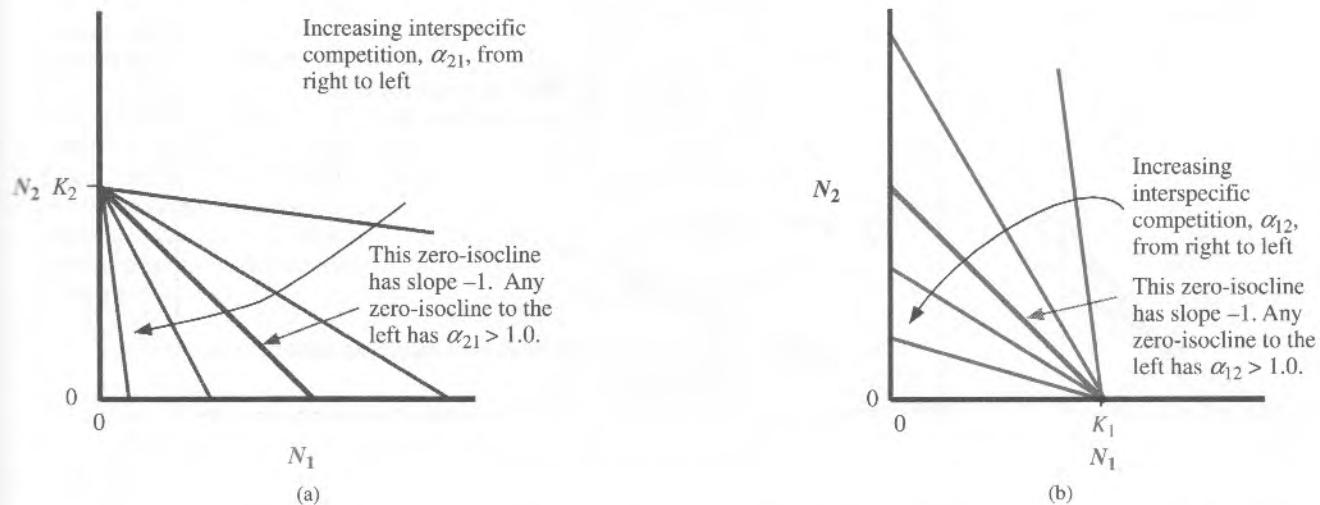


Figure 14.20

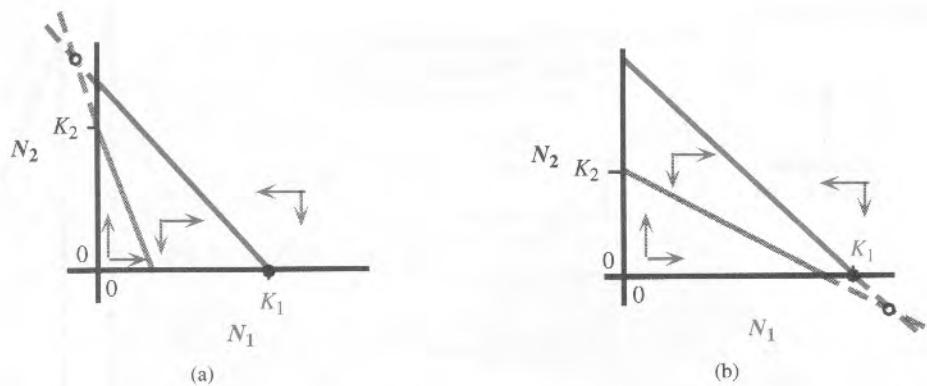
The intensity of interspecific competition affects the slope of the zero-isoclines. (a) Some possible zero-isoclines for species 2. (b) Some possible zero-isoclines for species 1.

In summary, the difference between the stable and unstable cases depends on the relative strengths of interspecific and intraspecific competition. Figure 14.20 illustrates how increasing interspecific competition affects the species' zero-isoclines.

The unstable case in Figure 14.18 corresponds to a situation where both α_{12} and α_{21} are greater than 1. We show later that this is not necessary for instability; instead it is necessary and sufficient that the product $\alpha_{12}\alpha_{21}$ be greater than 1. In addition to stability, we also need information on the feasibility of the equilibrium point: Are the species densities positive? Figure 14.21 explores the meaning of situations where the two zero-isoclines do not intersect in the positive orthant, leading to “negative” equilibrium species abundances.

Figure 14.21

If the zero-isoclines do not intersect in the positive orthant, then the mathematical “equilibrium point” will be negative for one of the species. In both (a) and (b), species 1 outcompetes species 2 because species 1’s zero-isocline completely encloses species 2’s. In (a), species 1 has a negative mathematical “equilibrium density,” while in (b), species 2 has a negative “equilibrium density.” Organism numbers, of course, can’t be negative, so the real equilibrium density is the boundary solution where species 1 is at its carrying capacity K_1 and species 2 is at zero, for both situations. Thus algebraic negativity of N_i^* is not necessarily indicative of extinction.

**Figure 14.22**

The algebraic conditions for stability and feasibility of an equilibrium point for two-species Lotka–Volterra competition.

Stability and Feasibility Conditions for an Equilibrium Point Are Separate Issues

Stability condition:

$$\underbrace{\alpha_{12}\alpha_{21}}_{\text{Strength of interspecific competition}} < \underbrace{1}_{\text{Strength of intraspecific competition; both } \alpha_{11} \text{ and } \alpha_{22} \text{ are 1.}}$$

Feasibility condition:

Both N_1^* and $N_2^* > 0$.

The feasibility condition means that the two zero-isoclines must cross in the positive orthant of phase space.

Figure 14.22 provides a summary of the separate criteria of stability and feasibility. The combination of the possible stability and feasibility outcomes for two-species competition are cataloged in Figure 14.23.

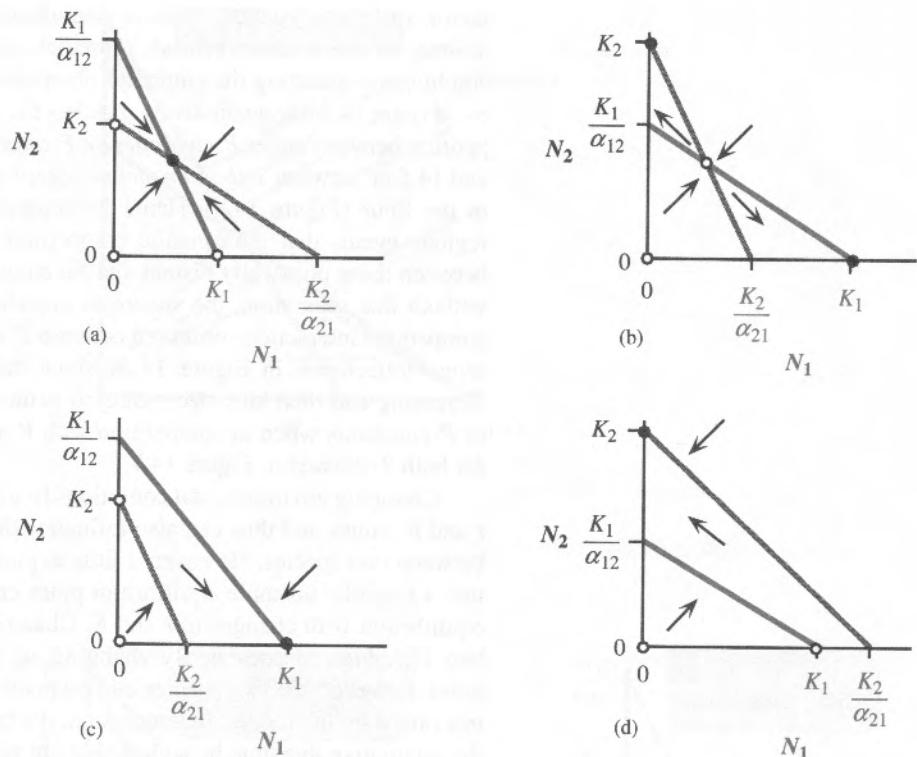
Figure 14.24 shows sample trajectories for these four cases. Look at the trajectories with the open arrows in parts (b), (c), and (d). The loser in the competition can initially increase before it turns around and becomes extinct, as, for example, does species 2 in part (c) and species 1 in part (d).

BACK TO TRIBOLIUM AND PARAMECIUM

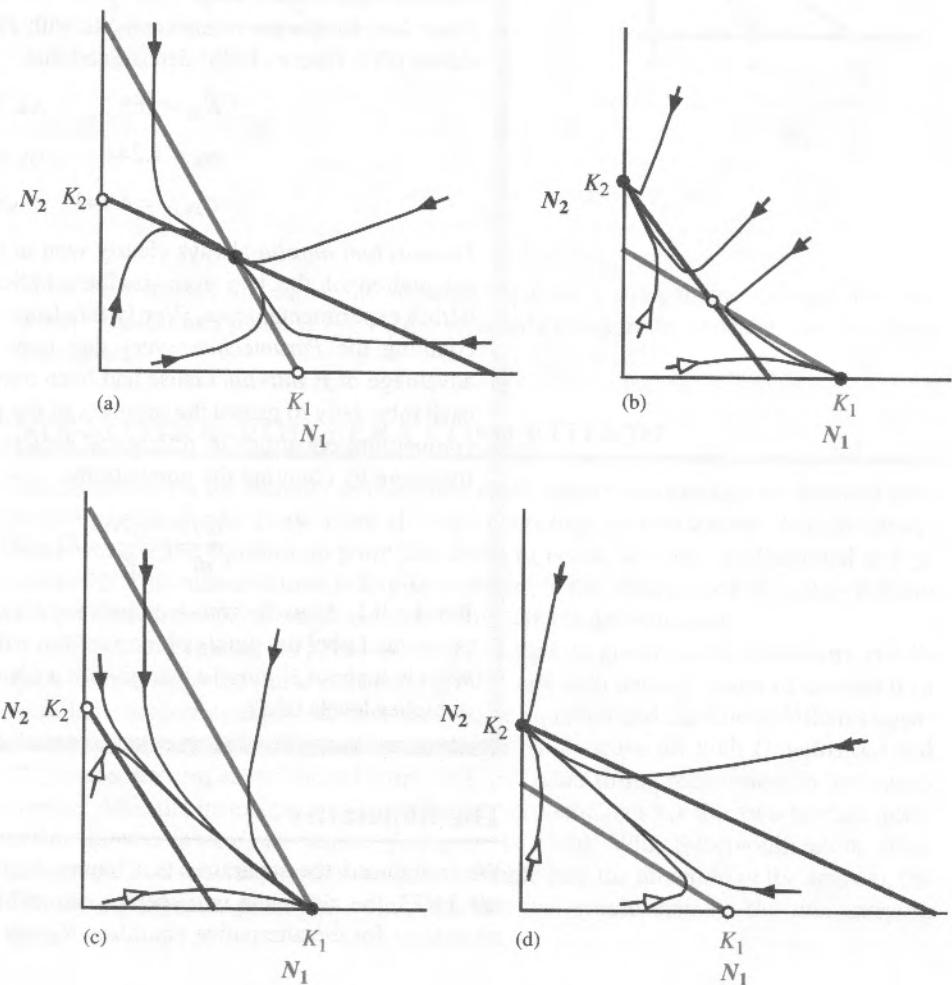
Figure 14.24(b) depicts the case of an unstable interior equilibrium point. Although the interior equilibrium point is unstable, two locally stable (but not globally stable) single-species equilibrium points exist at K_1 and K_2 . This situation corresponds to the features of *Tribolium* competition. It is produced when interspecific competition is greater than intraspecific competition. Recall that this was the case with the main density regulating

Figure 14.23

Possible outcomes for two-species Lotka–Volterra competition. In each case, stable equilibrium points are indicated by dark dots and unstable equilibrium points by white dots.

**Figure 14.24**

Sample trajectories for the four cases of the two-species Lotka–Volterra competition shown in Figure 14.23. Arrowheads show the direction of trajectories over time. Open arrowheads mark trajectories in which the losing species first increases before later becoming extinct ($r_1 = r_2 = 1$).



factor for these beetles—mutual cannibalism. This situation predicts a complete absence of coexistence; instead, it predicts alternative outcomes, depending on initial conditions—matching the empirical observations with *Tribolium*.

Figure 14.24(a) qualitatively matches the empirical pattern and mechanism of competition between either *P. caudatum* or *P. aurelia* and *P. bursaria* shown in Figures 14.3 and 14.5 or between *Tribolium* and *Oryzaephilus* once glass capillary tubing was added to the flour (Figure 14.8). Here, the separation of the species into different spatial regions means that intraspecific competition will be more intense than competition between these physically distant and functionally different competing species. Finally, without this separation, the situations depicted in Figures 14.24(c) or (d) parallel the competitive interactions observed between *P. caudatum* and *P. aurelia*. Indeed, the open arrow trajectories in Figure 14.24 show the competitively inferior competitor first increasing and then later decreasing to extinction; this pattern matches the abundance of *P. caudatum* when in competition with *P. aurelia* in Figure 14.3 and the trajectories for both *Tribolium* in Figure 14.7.

Changing environmental conditions (temperature, humidity, food levels, etc.) alter r and K values and thus can also influence the outcome of the competitive interaction between two species. However, a little exploring with the model should convince you that a feasible, unstable equilibrium point cannot be converted into a stable, feasible equilibrium with changes in r and K . Changing climatic conditions never allowed the two *Tribolium* to coexist. By changing α_{ij} terms by the addition of glass capillary tubes, however, the two species can be made to coexist, again matching the possibilities raised by the model. In conclusion, the model seems to provide a reasonable fit to the qualitative dynamic behaviors that are predicted for different sets of environmental conditions.

Exercise: In one set of experiments with *Paramecium aurelia* (Pa) and *P. caudatum* (Pb), Gause (1935) determined that

$$\begin{aligned} K_{\text{Pa}} &= 265.2 & K_{\text{Pc}} &= 64 \\ r_{\text{Pa}} &= 1.244 & r_{\text{Pc}} &= 0.794 \\ \alpha_{\text{Pa},\text{Pc}} &= 4.141 & \alpha_{\text{Pc},\text{Pa}} &= 0.242 \end{aligned}$$

Paramecium aurelia always clearly won in competition in all replicates, but the calculation of the two zero-isoclines indicated that they were superimposed, within experimental error. (Verify this fact). Gause concluded that his method of counting the *Paramecium* every day may be contributing to the competitive advantage of *P. aurelia*. Gause had been removing one-tenth of the volume from each tube daily to record the progress of the populations. He therefore revised the competition equations to reflect the density independent mortality he had been imposing by counting the populations:

$$\frac{dN_i}{dt} = \frac{r_i N_i}{K_i} (K_i - N_i - \alpha_{ij} N_j) - dN_i.$$

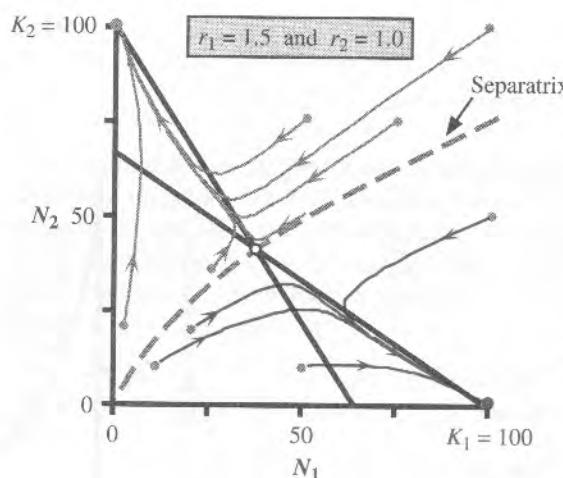
For $d = 0.1$, draw the zero-isoclines for *P. caudatum* and *P. aurelia* based on this equation. Label the points of intersection with the axes. In terms of this equation, what is it about *P. aurelia* that gives it a competitive advantage over *P. caudatum* at higher levels of d ?

The Separatrix

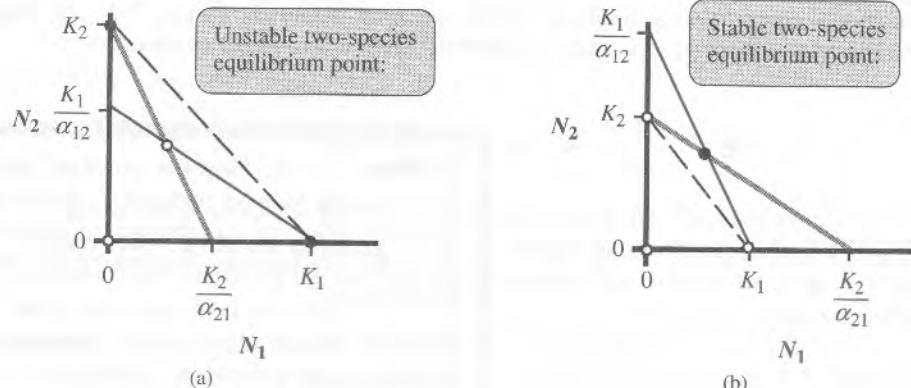
We introduced the separatrix in Chapter 12 (Figure 12.38). In situation (b) of Figure 14.23, the r 's of the two species can influence the relative shape of the basin of attractions for the alternative equilibria K_1 and K_2 , as shown in Figure 14.25. If the r 's

Figure 14.25

The separatrix for an unstable interior equilibrium point. Species 1 or 2 alone at their respective carrying capacities, K_1 and K_2 , are the two locally stable equilibrium points. The value of the growth rates, r , influences the shape and position of the separatrix, which divides the two domains of attraction. Trajectories above the separatrix go to K_2 and trajectories below it go to K_1 . The separatrix goes through the unstable feasible equilibrium point. In this example, $\alpha_{12} = \alpha_{21} = 1.5$ and the K 's are also equal. Only the r 's of the two species differ; $r_1 > r_2$, and the separatrix bows toward the N_1 axis. If r_2 were greater than r_1 , then the separatrix would bow toward the N_2 axis.

**Figure 14.26**

(a) Note that in (b), the stable interior equilibrium point falls above the dashed line connecting the carrying capacities, while the unstable interior equilibrium point in (a) falls below the dashed line. For Lotka–Volterra competition, species that stably coexist produce a combined density at equilibrium that is greater than the density of either species when alone. Species that cannot stably coexist have a combined density at equilibrium less than either species when alone.

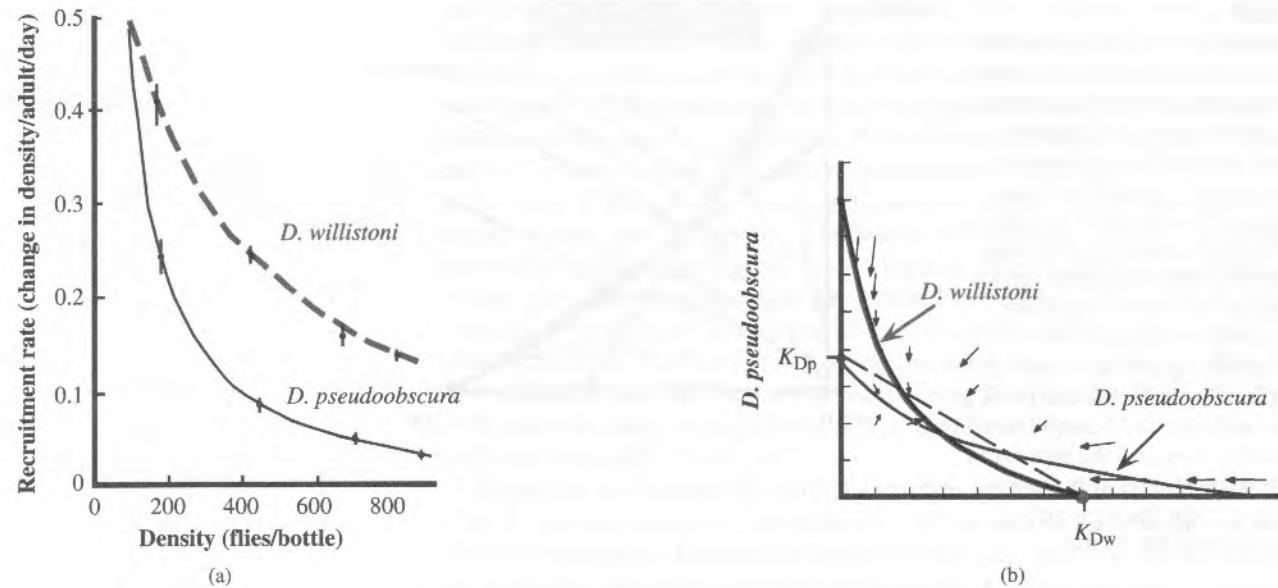


of the two species are equal, the separatrix will be a straight line through the two-species equilibrium point. If $r_2 > r_1$, the separatrix bows in the opposite direction from that shown.

NON-LOTKA-VOLTERRA COMPETITION

The condition for the stability of a feasible equilibrium point can also be assessed by a simple graphical rule: Draw a straight line connecting the two species' K 's, and determine whether the equilibrium point lies above or below this line, as illustrated in Figure 14.26. This rule-of-thumb is fragile, however, to the assumptions of Lotka–Volterra competition. It breaks down if the competitive effects are nonlinear.

Gilpin and Justice (1972) found that *Drosophila* grown under laboratory conditions did not show the linear decline in growth rate with density, either of conspecifics or of heterospecifics expected from the logistic equation and the Lotka–Volterra equations. The intraspecific effects were not linear but concave for both *D. willistoni* and *D. pseudoobscura*, as shown in Figure 14.27(a). After fitting recruitment to the experimental data, the investigators found that the zero-isoclines for this two-species interaction bowed inward, as shown in Figure 14.27(b). With this modification, even though the two-species equilibrium point is stable (see the direction of the arrows), the interior equilibrium point lies below the line that would connect the two carrying capacities.

**Figure 14.27**

Two-species competition in laboratory *Drosophila*. After Gilpin and Justice (1972). (a) Both species display nonlinear per capita recruitment as a function of intraspecific density. (b) The zero-isoclines are concave.

Exercise: Use the θ logistic model of Problem 3 at the end of Chapter 5 to modify the Lotka–Volterra competition equations to produce nonlinear zero-isoclines like those observed for laboratory populations of *Drosophila*. For what values of θ will the zero-isoclines bow inward? For what values of θ will the zero-isoclines bow outward?

Exercise: Vandermeer's (1969) experiments with competition between species of *Paramecium* allowed the calculation of r and K for each species, as well as the α_{ij} terms for their interactions. The Lotka–Volterra equations proved to be a good fit to the data. The results for one species pair were

$$P. aurelia: r_a = 1.05, K_a = 671;$$

$$P. bursaria: r_b = 0.47, K_b = 230;$$

$$\alpha_{ab} = -2.0, \alpha_{ba} = 0.5.$$

(Yes, the competition coefficient for the effect of *P. bursaria* on *P. aurelia* is negative, meaning a positive interaction).

Sketch the zero-isoclines for this system (put *P. aurelia* numbers on the x axis). What do you predict regarding the coexistence of this species pair? What would happen if the carrying capacity of *P. bursaria* were doubled?

ANALYTICAL EXPOSITION OF LOTKA-VOLTERRA COMPETITION (ADVANCED)

We now derive the rule of Figure 14.21: Stable competition demands that $\alpha_{12}\alpha_{21} < 1.0$, which we developed earlier using a graphical argument. We also extend competition theory to more than two species. First we write the two-species Lotka–Volterra competition in algebraic form:

$$\frac{dN_1}{dt} = f_1(N_1, N_2) = \frac{r_1 N_1}{K_1} [K_1 - N_1 - \alpha_{12} N_2] \quad (14.2a)$$

and

$$\frac{dN_2}{dt} = f_2(N_1, N_2) = \frac{r_2 N_2}{K_2} [K_2 - N_2 - \alpha_{21} N_1]. \quad (14.2b)$$

At an equilibrium point, the population growth rates for both species must be zero, by definition. Equations (14.2) indicate that this can happen in two ways: either the abundance of the species is zero ($N_i = 0$) so that the term in front of the bracket is zero, or $N_i \neq 0$, but the term in the brackets—and hence the *per capita* growth rate—is zero. The latter condition for both species specifies the solution of the **interior equilibrium point**:

$$K_1 - N_1^* - \alpha_{12} N_2^* = 0 \quad (14.3a)$$

and

$$K_2 - N_2^* - \alpha_{21} N_1^* = 0 \quad (14.3b)$$

The asterisk on N_i indicates that this is a nonzero equilibrium value of N . Equations (14.3) are simply two linear equations in two unknowns, N_1^* and N_2^* , and so are easy to solve. However, because we later want to expand this analysis to include more than two interacting species, it is useful now to write Eq. (14.3) in more general matrix form. (As usual, matrices and vectors are set in boldface type.)

$$\mathbf{K} = \boldsymbol{\alpha} \mathbf{N}^*, \quad (14.4)$$

where

$$\mathbf{K} = \begin{bmatrix} K_1 \\ K_2 \end{bmatrix}, \mathbf{N}^* = \begin{bmatrix} N_1^* \\ N_2^* \end{bmatrix}, \text{ and } \boldsymbol{\alpha} = \begin{bmatrix} 1 & \alpha_{12} \\ \alpha_{21} & 1 \end{bmatrix}.$$

The alpha matrix gives the per capita interaction strengths. The intraspecific effects, which are all 1, are on the diagonal, while the interspecific effects are in the off-diagonal positions. Also, recall that the notation rule is **to subscript rows first and then to subscript columns**. Thus α_{12} means the element in the first row and second column of the $\boldsymbol{\alpha}$ matrix, and this represents the effect of species 2 *on* species 1.

To solve Eq. (14.4), we'd like to find the values of the unknowns, N_i^* , that fulfill the identity of Eq. (14.4), given the parameters in the $\boldsymbol{\alpha}$ matrix and the \mathbf{K} vector. Two techniques for solving matrix equations like these are presented in Appendices 2 and 3; one method involves taking the inverse of the matrix such that

$$\mathbf{N}^* = \boldsymbol{\alpha}^{-1} \mathbf{K}. \quad (14.5)$$

The other method (and this really amounts to the same thing) is to apply **Cramer's rule** (see Appendix 3). To solve for the equilibrium level of N_1^* , we take the ratio of the determinants of two different matrices. In the numerator, we form the matrix $\boldsymbol{\alpha}(1)$, which is simply the matrix $\boldsymbol{\alpha}$ with the first column replaced by the \mathbf{K} vector, and, in the denominator, we have the matrix of $\boldsymbol{\alpha}$:

$$N_1^* = \frac{\det \begin{vmatrix} K_1 & \alpha_{12} \\ K_2 & 1 \end{vmatrix}}{\det \begin{vmatrix} 1 & \alpha_{12} \\ \alpha_{21} & 1 \end{vmatrix}} = \frac{K_1 - K_2 \alpha_{12}}{1 - \alpha_{21} \alpha_{12}}. \quad (14.6a)$$

The equilibrium density of species 2, $N_2^* = \det |\boldsymbol{\alpha}(2)| / \det |\boldsymbol{\alpha}|$, gives

$$N_2^* = \frac{\det \begin{vmatrix} 1 & K_1 \\ \alpha_{21} & K_2 \end{vmatrix}}{\det \begin{vmatrix} 1 & \alpha_{12} \\ \alpha_{21} & 1 \end{vmatrix}} = \frac{K_2 - K_1 \alpha_{21}}{1 - \alpha_{21} \alpha_{12}}. \quad (14.6b)$$

The denominator of Eqs. (14.6a and b) is the determinant of $\boldsymbol{\alpha}$. Unless the determinant of $\boldsymbol{\alpha}$ is > 0 (i.e., $\alpha_{12} \alpha_{21} < 1$), the interior equilibrium will be unstable. To show

how this falls out analytically, we perform a local stability analysis like that developed in Chapter 13. You should review Chapter 13 to refresh your memory about Jacobian matrices and how they relate to the stability of an equilibrium point. For two-species Lotka–Volterra competition, the dynamics of small deviations (n_1 and n_2) away from equilibrium points N_1^* and N_2^* can be described by the linear matrix differential equation,

$$\begin{bmatrix} \frac{dn_1}{dt} \\ \frac{dn_2}{dt} \end{bmatrix} = \begin{bmatrix} \frac{\partial f_1}{\partial N_1} & \frac{\partial f_1}{\partial N_2} \\ \frac{\partial f_2}{\partial N_1} & \frac{\partial f_2}{\partial N_2} \end{bmatrix} \begin{bmatrix} n_1 \\ n_2 \end{bmatrix},$$

which can also be written as

$$\frac{d\mathbf{n}}{dt} = \mathbf{J} \mathbf{n},$$

where \mathbf{J} is the Jacobian matrix and all the partial derivatives in \mathbf{J} are evaluated at the equilibrium point. The local stability of the equilibrium point can be determined from the eigenvalues of the Jacobian matrix. We now calculate the Jacobian matrix for the interior equilibrium point for two-species Lotka–Volterra competition. Let's begin with the term in the upper left-hand corner:

$$f_1(N_1, N_2) = r_1 N_1 - \frac{r_1}{K_1} N_1^2 - \frac{r_1}{K_1} \alpha_{12} N_1 N_2.$$

Taking the partial derivative of f_1 with respect to N_1 (keeping N_2 fixed) gives

$$\frac{\partial f_1}{\partial N_1} = r_1 - \frac{2r_1 N_1}{K_1} - \frac{r_1}{K_1} \alpha_{12} N_2. \quad (14.7)$$

We want to evaluate this partial derivative at the equilibrium point \mathbf{N}^* , so

$$\frac{\partial f_1}{\partial N_1} = \frac{r_1}{K_1} (K_1 - 2N_1^* - \alpha_{12} N_2^*). \quad (14.8)$$

Note that the term in parentheses is identical to Eq. (14.3a), except for the 2 in front of N_1^* . Thus we may also write Eq. (14.8) as

$$\frac{\partial f_1}{\partial N_1} = \frac{r_1}{K_1} (K_1 - N_1^* - \alpha_{12} N_2^* - N_1^*),$$

and, since $K_1 - N_1^* - \alpha_{12} N_2^* = 0$ at the interior equilibrium, we reach

$$\frac{\partial f_1}{\partial N_1} = \frac{-r_1 N_1^*}{K_1}. \quad (14.9)$$

The text term in the first row of \mathbf{J} is

$$\frac{\partial f_1}{\partial N_2} = -\frac{r_1}{K_1} \alpha_{12} N_1^*. \quad (14.10)$$

The second row of \mathbf{J} will have the same form as the first row so that, finally, we arrive at

$$\mathbf{J}(\text{interior}) = \begin{bmatrix} -\frac{r_1 N_1^*}{K_1} & -\frac{r_1}{K_1} \alpha_{12} N_1^* \\ -\frac{r_2}{K_2} \alpha_{21} N_2^* & -\frac{r_2 N_2^*}{K_2} \end{bmatrix}.$$

The next step is to realize that, for simplicity, $\mathbf{J}(\text{interior})$ may also be written as the product of two matrices:

$$\mathbf{J}(\text{interior}) = \begin{bmatrix} -\frac{r_1 N_1^*}{K_1} & 0 \\ 0 & -\frac{r_2 N_2^*}{K_2} \end{bmatrix} \begin{bmatrix} 1 & \alpha_{12} \\ \alpha_{21} & 1 \end{bmatrix}. \quad (14.11)$$

The first matrix in Eq. (14.11) is a diagonal matrix, and each element is a negative constant if the equilibrium point is feasible, or $N_i^* > 0$. The second matrix is simply the original α matrix. One useful aspect of Eq. (14.11) is that it simplifies the determination of the eigenvalues of \mathbf{J} . It can be shown that for any two \times two matrix like $\mathbf{J}(\text{interior})$ —which is the product of an all-negative diagonal matrix times another matrix α —all the eigenvalues of \mathbf{J} will have negative real parts if, and only if, the eigenvalues of α are all positive. Thus, if the eigenvalues of α are all positive, the eigenvalues of \mathbf{J} are all negative, and the interior equilibrium point is locally stable. Let's now evaluate the eigenvalues of α . We set up the characteristic equation:

$$\det \begin{vmatrix} 1-\lambda & \alpha_{12} \\ \alpha_{21} & 1-\lambda \end{vmatrix} = 0$$

or

$$\lambda^2 - 2\lambda + (1 - \alpha_{21}\alpha_{12}) = 0. \quad (14.12)$$

At this point, we could go ahead and solve for the two λ 's, but simply by the sign structure of Eq. (14.12) we can see that it can be factored to have the form

$$(\lambda - \text{something})(\lambda - \text{something else}) = 0.$$

and therefore the two eigenvalues are positive if, and only if, the determinant of α is positive.

Applying the quadratic formula (see Appendix 4),

$$x = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a},$$

where $a = 1$, $b = -2$, and $c = 1 - \alpha_{12}\alpha_{21}$, we reach

$$\begin{aligned} \lambda_i &= \frac{2 \pm \sqrt{4 - 4 + 4\alpha_{21}\alpha_{12}}}{2} \\ &= 1 \pm \sqrt{\alpha_{21}\alpha_{12}}, \end{aligned}$$

which can also be written as

$$\lambda_i = \sqrt{1 \pm \sqrt{\alpha_{21}\alpha_{12}}}.$$

From this expression we may again infer that both λ 's of α will be positive if, and only if, $\sqrt{1 - \sqrt{\alpha_{21}\alpha_{12}}} > 0$. This, of course, means that $1 - \alpha_{21}\alpha_{12}$ must be positive. Thus stability demands that **intraspecific competition ($\alpha_{11}\alpha_{22} = 1$) be greater than interspecific competition ($\alpha_{12}\alpha_{21}$)**.

The Stability of a Boundary Equilibrium Point

We next evaluate the stability of one of the boundary equilibria. As an example, consider the boundary point where species 1 is at its carrying capacity, K_1 , and species 2 is at zero. This is an equilibrium point, but is it stable? We have already evaluated the form of the partial derivatives for \mathbf{J} , but now we need to substitute the boundary equilibrium point $(K_1, 0)$ instead of the interior equilibrium point (N_1^*, N_2^*) . We rewrite Eq. (14.7) with this substitution to get

$$\frac{\partial f_1}{\partial N_1} = \frac{r_1}{K_1}(K_1 - 2K_1 - 0) = -r_1,$$

and, from Eq. (14.10),

$$\frac{\partial f_1}{\partial N_2} = -\frac{r_1}{K_1} \alpha_{12} N_1.$$

This last partial derivative evaluated at $N_1 = K_1$ is simply $-r_1 \alpha_{12}$.

Continuing with the second row of \mathbf{J} , we have

$$\frac{\partial f_2}{\partial N_1} = \frac{-r_2 \alpha_{21} N_2}{K_1} = 0 \quad (\text{since } N_2 = 0),$$

and, finally,

$$\begin{aligned} \frac{\partial f_2}{\partial N_2} &= \frac{r_2}{K_2} (K_2 - 2N_2 - \alpha_{21} N_1) \\ &= \frac{r_2}{K_2} (K_2 - \alpha_{21} K_1). \end{aligned}$$

Putting this all together, we get for the Jacobian matrix \mathbf{J} ,

$$\mathbf{J}(N_1 = K_1, N_2 = 0) = \begin{bmatrix} -r_1 & -r_1 \alpha_{12} \\ 0 & \frac{r_2 (K_2 - \alpha_{12} K_1)}{K_2} \end{bmatrix}. \quad (14.13)$$

The eigenvalues of \mathbf{J} (boundary) are easy to find since \mathbf{J} is a *triangular* matrix; that is, all the elements below the diagonal are zero. The eigenvalues of a triangular matrix are simply given by the elements on the diagonal

$$\lambda_1 = -r_1$$

and

$$\lambda_2 = \frac{r_2 (K_2 - \alpha_{12} K_1)}{K_2}. \quad (14.14)$$

Compare this second eigenvalue to the Lotka–Volterra per capita growth rate equation for the missing species 2:

$$\frac{dN_2}{N_2 dt} = \frac{r_2}{K_2} (K_2 - N_2 - \alpha_{21} N_1).$$

If N_2 is negligible, as it would be if species 2 were invading at low density, and if N_1 were at its carrying capacity, then the growth rate of species 2, when rare, is identical to this eigenvalue. Since r is always positive, the sign of 2 from Eq. (14.14) is given simply by the term in parentheses, which we call g_2 for convenience:

$$g_2 = K_2 - \alpha_{12} K_1. \quad (14.15)$$

Hence this boundary equilibrium is stable (the eigenvalue λ_2 has a negative real part) if species 2 cannot invade species 1 at its carrying capacity. This will be true as long as $g_2 < 0$, which is pretty intuitive. After all, how could the boundary equilibrium lacking species 2 be stable if species 2 can invade species 1 and increase?

Finally, just for notational completeness, the Jacobian matrix $\mathbf{J}(N_1 = K_1, N_2 = 0)$ can be written as the product of a diagonal matrix and the original α matrix, as we did for the Jacobian matrix of the interior equilibrium point, Eq. (14.11), but now we must add a third matrix:

$$\mathbf{J}(N_1 = K_1, N_2 = 0) = \begin{bmatrix} -r_1 N_1 & 0 \\ \frac{K_1}{K_1} & -r_2 N_2 \\ 0 & \frac{K_2}{K_2} \end{bmatrix} \begin{bmatrix} 1 & \alpha_{12} \\ \alpha_{21} & 1 \end{bmatrix} + \begin{bmatrix} 0 & 0 \\ 0 & \frac{r_2 g_2}{K_2} \end{bmatrix}. \quad (14.16)$$

Comparing Eq. (14.16) for this boundary equilibrium to Eq. (14.11) for the interior equilibrium point, we see that the Jacobian matrices are formed identically from the

same three matrices (with suitable interpretation for the N_i values) in the first matrix. However, the last matrix—when the interior equilibrium point is zero—drops out of consideration. As we show in the next section, this feature generalizes to the structure of the Jacobian matrix for any boundary equilibrium involving subsets of arbitrary size from n competing species.

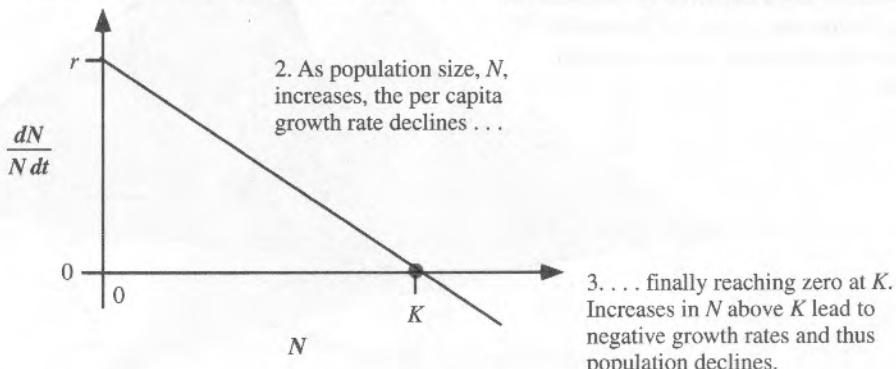
Problem: Verify that the matrix multiplication specified by Eq. (14.16) with $N_1 = K_1$ and $N_2 = 0$, does yield \mathbf{J} , as given in Eq. (14.13).

MORE THAN TWO COMPETING SPECIES

We can generalize the concept of zero-isoclines to more or less than two interacting species. Figure 14.28 makes the comparison, and Figure 14.29 summarizes this development.

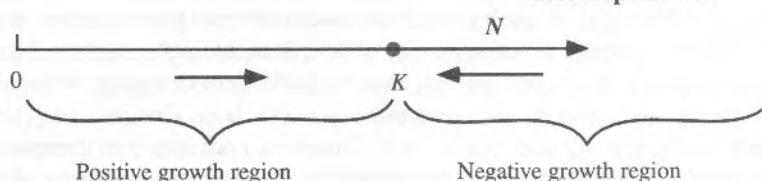
Figure 14.28
Isopoints and isosurfaces.

1. When it comes to defining isoclines, there is nothing special about two-species systems. We have already discussed the concept in the logistic equations for single species population growth.



4. Removing the y dimension and just looking at numbers of N , . . .

. . . now the state space is one-dimensional, and we have a **zero-isopoint** at K .



6. Similarly for three species, we could define a **zero-isosurface** as in . . .

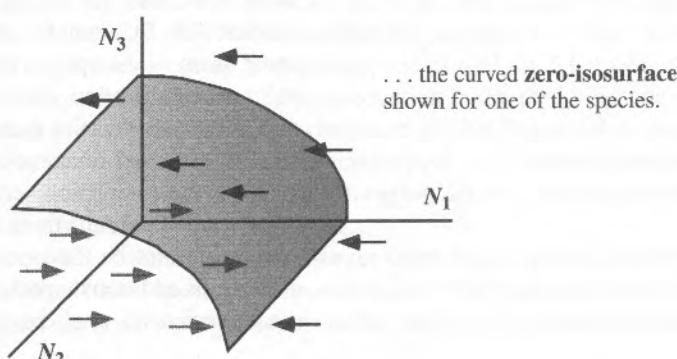


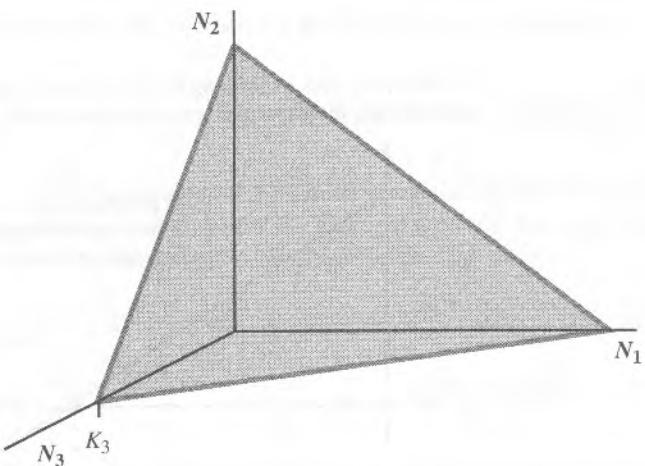
Figure 14.29

The isospace is one dimension less than the state space represented by the number of species, n , because it is an intersection of two n -space shapes.

Number of species, n	Isospace
One	Zero: a point
Two	One: a line or curve
Three	Two: a plane or surface
\vdots	\vdots
X	$X - 1$: a hypersurface

Figure 14.30

A zero-isoplane for species 3 in a three-species Lotka–Volterra competition system. Above the plane species 3 has a negative growth rate, and below the plane (i.e., towards the origin) it has a positive growth rate.



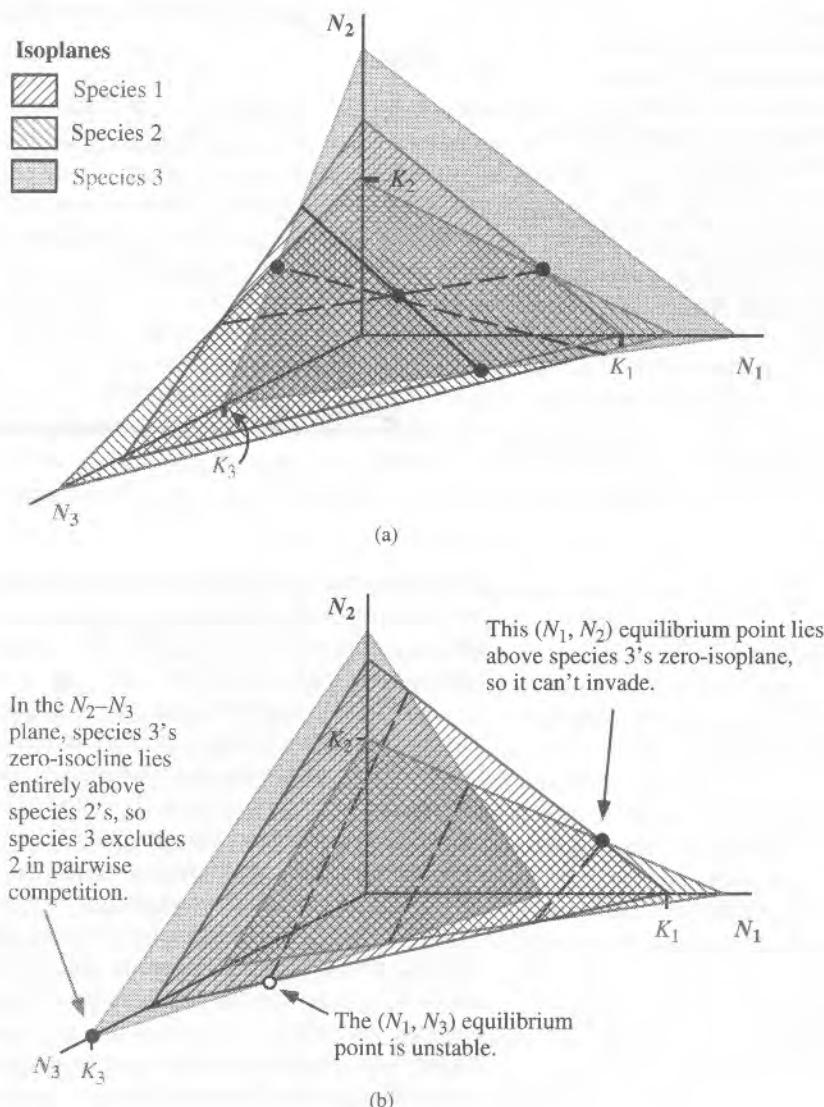
For three species of Lotka–Volterra competitors the state space will be a cube and the zero-isosurface of each species is a plane, as depicted in Figure 14.30.

By superimposing isoplanes, one for each species, we can examine graphically the nature of the various equilibria, as illustrated in Figure 14.31. However, it is difficult to draw and to interpret these cluttered diagrams, so an analytical approach is preferred and, of course, is absolutely necessary for more than three species. The needed mathematics is a straightforward extension of that already examined for two-species competition; we develop it a bit later. First, however, let's examine a more fundamental question.

Imagine a community of three fish species, A, B, and C, existing together in a large aquarium. By raising populations of each of these species alone, we could find their respective intrinsic growth rates, r , and carrying capacities, K . However, this would not tell us anything about their relative competitive abilities, the α_{ij} terms. To determine these, we could put the species together in each possible pairwise combination of species: AB, BC, and AC. From the resulting dynamics and previous knowledge of r and K from single-species populations, we would then be able to calculate α_{ij} for each pairwise combination. We could now put these α_{ij} terms into a 3×3 matrix. An open question is whether this α matrix, along with the \mathbf{K} and \mathbf{r} vectors, enables us to predict the behavior and outcome of the full three-species system. The answer depends on whether the interaction terms, α_{ij} , which we estimated in pairwise contests, fully express all the interactions between the species in the full three-species community. This would not be the case if the pairwise α_{ij} terms were altered by the presence or absence of additional species. If some species combinations formed coalitions against other species, the total competitive effect could be greater than or less than the sum of

Figure 14.31

Two examples of three-species Lotka–Volterra competition systems. The pairwise equilibrium points are indicated by dots—solid for stable and open for unstable. The intersections of the zero-isoplanes are shown as dashed lines. (a) All pairwise species sets are locally stable, and all three species coexist at a stable equilibrium point—where the dashed lines for the intersection of each pair of isoplanes cross. It is stable because it falls above the plane connecting the species K's (not shown). (b) The three-species equilibrium point falls outside the positive orthant, so it is unfeasible. There are two locally stable equilibrium points: species 3 alone at its carrying capacity and species 1 and 2 together.

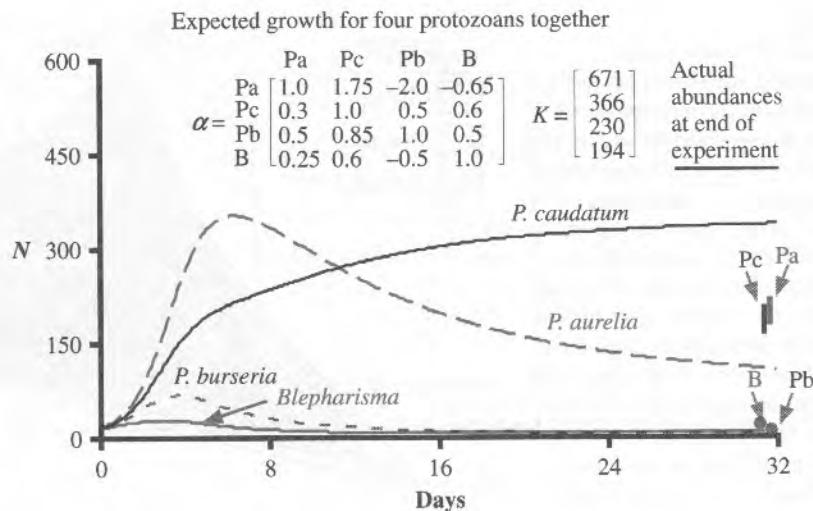


each species' interaction when competition occurs only in pairs. In ecology, such “non-additive” behavior is called **higher-order interactions** or **interaction modifications** (Billick and Case 1994, Wootton 1994). The presence of species C might increase or moderate the competitive impact of A on B (also see Chapter 6). One particularly interesting type of interaction modification is where one species’ mere presence “intimidates” others, such that they alter their behavior and thus the strength of their interaction (Beckerman et al. 1997). **Trait mediated indirect effects** are these more rapid changes in the interactions between species. They are those *not* mediated by numerical changes in population size of intervening species in the food chain but simply by changes in the behavioral reaction of a species due to another species (Abrams 1993). For example, Peacor and Werner (1997) found that the presence of predacious dragonfly larvae, even if caged and restricted from eating prey, caused small tadpoles to reduce their foraging efforts and this, in turn, led to a reduction in the predation rate of these tadpoles by another predator. Similarly, Beckerman et al. (1997) glued shut the jaws of spiders so that they could not kill or consume grasshopper prey. Nevertheless, the mere presence of such spiders reduced grasshopper foraging activity, leading to decreased rates of exploitation of grass by the grasshoppers.

Vandermeer (1969) searched for higher-order interactions in competition among four species of ciliates (three species of *Paramecium* and *Blephararia*). He found that the extrapolation of the r , K , and α_{ij} terms from the one- and two-species experiments

Figure 14.32

A simulation of Lotka–Volterra competition for four interacting protozoan species, using the parameter values calculated from the one- and two-species competition experiments. The actual range of densities for each species at the end of the four-species competition experiments is also shown for day 32. After Vandermeer (1969).



fit the dynamics of the four-species community qualitatively. The four-species community experimentally collapsed to just two species: *P. aurelia* coexisting with *P. caudatum*, as predicted. However, as shown in Figure 14.32, the abundances of the surviving species were off by about 40%.

Additional simulations from an assortment of different initial densities reveal that this boundary equilibrium is globally stable. In summary, based on an assumption of no higher-order interactions, this four-species system is predicted to collapse to a particular two-species boundary solution (Pc with Pa), which is globally stable. This behavior is, in fact, what is observed experimentally with these four species. In surely one of the most exhaustive searches yet for higher-order interactions, Fryar (1998) compared the growth rates of seven species of wood-rotting fungi, with the convenient property that they can be grown readily in the laboratory in petri dishes. Fryar conducted all possible single-species, pairwise, and three-species sets and compared their growth rates. In 18 out of a possible 35 three-species combinations, she found a nonadditive interaction, based on pairwise performance. In 13 of the 18 nonadditive interactions the direction of the higher-order interaction was to increase coexistence, that is, to allow the three species to coexist when extrapolations of two-species interactions predicted just the opposite.

Boundary Equilibria

Is there an analytical way to determine the stability of the various boundary equilibria? If we assume that higher-order interactions are absent, a first step in attempting to do so is to enumerate the locations of all the various equilibrium points and next determine which, if any, are stable. Let's consider a system with three species, like those in Figure 14.31, and the following equilibria.

Number of species	Number of equilibrium points
Zero species	1 (the (0, 0, 0) point)
Single species	3 (each K)
Two-species	3 (each pairwise combination of the three species)
Three-species	1 (the interior equilibrium point)

To obtain the local stability of each of these points by calculating eigenvalues for each of the relevant Jacobian matrices J is straightforward but tedious and not intuitive. We can, however, make use of some theorems dealing with the stability properties of matrices.

One appealing aspect of Eqs. (14.5) and (14.11) is that they generalize to n species. The interior equilibrium point is given by

$$\mathbf{N}^* = \alpha^{-1} \mathbf{K},$$

and the stability matrix for this interior equilibrium point is

$$\mathbf{J}(\text{interior}) = \mathbf{D} \alpha, \quad (14.17)$$

where \mathbf{D} is an $n \times n$ matrix of diagonal elements $-r_i N_i^*/K_i$, and α is the $n \times n$ interaction matrix with 1's along the diagonal (the α_{ii} terms) and α_{ij} elsewhere. By evaluating the sign of the real parts of the eigenvalues of $\mathbf{J}(\text{interior})$, we will know whether this equilibrium point is stable. Recall that for two species we could short-circuit this by simply evaluating the eigenvalues of α . When n is greater than 2, for reasons that are a little too complicated to explain here, we lose this ability. Instead, the eigenvalues of the Jacobian matrix $\mathbf{J}(\text{interior})$ must be determined. The sign of the eigenvalues of α are not necessarily indicative of the sign of the eigenvalues of \mathbf{J} as they were for two species; even changes in r can alter the stability of an equilibrium point in three space (Strobeck 1973). We present an example of this in the last section of this chapter. However, for one class of a matrix there is the same correspondence as for the two-species case; namely, symmetric α matrices. Moreover, even if α itself is not symmetric, but is formed as the product of a symmetric matrix and some diagonal matrix,

$$\alpha = \mathbf{D} \mathbf{S}, \quad (14.18)$$

where \mathbf{S} is a symmetric matrix and \mathbf{D} is a diagonal matrix, then the sign of the eigenvalues of α will again be fully indicative of the sign of the eigenvalues of \mathbf{J} . (The proof of this is far beyond the scope of this book but may be found in Case and Casten 1978). You may think that this is a pretty worthless shortcut: Why should nature contrive species interactions that happen to follow the rather strict formula in Eq. (14.18)? In Chapter 15, on niche theory, we show that, under some broad assumptions, this could be the case if competitive interactions are based on niche overlap.

The use of the Jacobian matrix to evaluate various boundary equilibria can be extended in a simple way for any number of competing species because the Jacobian of a boundary solution has a special simple form for Lotka–Volterra competition. To illustrate, let's imagine a four-species system, with species 1 and 2 at equilibrium with each other but in isolation from species 3 and 4. We denote the equilibrium abundance of species 1 and 2 in the absence of species 3 and 4 as $N_1^*(3, 4)$ and $N_2^*(3, 4)$. Importantly, these values are not the same as N_1^* and N_2^* , the equilibrium abundances of species 1 and 2 in the full four-species community. The equilibrium values for the two-species system (1, 2) are given by Eq. (14.6a). The structure of the Jacobian matrix for the boundary equilibrium with species 3 and 4 absent is

$$\mathbf{J}(3, 4) = \mathbf{R} \alpha + \mathbf{G},$$

where \mathbf{R} is a 4×4 diagonal matrix with terms $-r_i N_i/K_i$ (as in Eq. 14.16), α is the original α matrix, and \mathbf{G} contains zeros everywhere except for the growth-when-rare terms on the diagonal for the missing species ($i = 3$ and 4):

$$\mathbf{G} = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & \frac{r_3 g_3}{K_3} & 0 \\ 0 & 0 & 0 & \frac{r_4 g_4}{K_4} \end{bmatrix}. \quad (14.19)$$

By a simple extension of Eq. (14.15), we get the condition for positive growth of the invader, i , g_i , as

$$g_i = \left[K_i - \sum_{j=1}^2 \alpha_{ij} N_j^*(3, 4) \right] \text{ for } i = 3 \text{ to } 4.$$

Since $N_i^* = 0$ at the boundary for each missing species $i = (3, 4)$, the matrix $\mathbf{R} \alpha$ becomes

$$\mathbf{R}\alpha = \begin{bmatrix} -\frac{N_1^*(3,4)r_1}{K_1} & -\alpha_{12}\frac{N_1^*(3,4)r_1}{K_1} & -\alpha_{13}\frac{N_1^*(3,4)r_1}{K_1} & -\alpha_{14}\frac{N_1^*(3,4)r_1}{K_1} \\ -\alpha_{21}\frac{N_2^*(3,4)r_2}{K_2} & -\frac{N_2^*(3,4)r_2}{K_2} & -\alpha_{23}\frac{N_2^*(3,4)r_2}{K_2} & -\alpha_{24}\frac{N_2^*(3,4)r_2}{K_2} \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix},$$

and the full Jacobian matrix $\mathbf{J}(3, 4)$ is

$$\mathbf{J}(3, 4) = \mathbf{R}\alpha + \mathbf{G} = \begin{bmatrix} -\frac{N_1^*(3,4)r_1}{K_1} & -\alpha_{12}\frac{N_1^*(3,4)r_1}{K_1} & -\alpha_{13}\frac{N_1^*(3,4)r_1}{K_1} & -\alpha_{14}\frac{N_1^*(3,4)r_1}{K_1} \\ -\alpha_{21}\frac{N_2^*(3,4)r_2}{K_2} & -\frac{N_2^*(3,4)r_2}{K_2} & -\alpha_{23}\frac{N_2^*(3,4)r_2}{K_2} & -\alpha_{24}\frac{N_1^*(3,4)r_2}{K_2} \\ 0 & 0 & \frac{r_3g_3}{K_3} & 0 \\ 0 & 0 & 0 & \frac{r_4g_4}{K_4} \end{bmatrix}.$$

The boundary equilibrium is locally stable if (a) the two-species equilibrium point for species 1 and 2 together is stable in the N_1 - N_2 orthant and (b) if species 3 and 4 cannot invade this boundary equilibrium (g_3 and g_4 are then negative). This will ensure that all the eigenvalues of $\mathbf{J}(3, 4)$ have negative real parts. Condition (a) ensures that the first two eigenvalues of \mathbf{J} have negative real parts, and condition (b) ensures that the second two eigenvalues have negative real parts, as demonstrated in Box 14.1.

In a similar vein, we can determine the structure of the Jacobian matrix for any boundary solution and for any number of species present or absent from some larger species pool. The ordering of the species in the interaction matrix is immaterial. You can always rearrange the order of the species by rearranging the rows and columns of the interaction matrix. If the full species pool is n and you wish to evaluate the boundary solution involving, say, m particular missing species, you can place all the missing species at the end of the rows and columns of the interaction matrix (the ordering of the rows and columns must be the same). Then the bottom m rows of the Jacobian matrix $\mathbf{J}(\text{boundary})$ will be zero, except for the diagonal elements, which are $r_i g_i / K_i$ (for $i = n-m$ to n species). Finally, note that the calculation of the Jacobian matrix as $\mathbf{R} \alpha + \mathbf{G}$, also applies to the interior equilibrium point. In this case \mathbf{G} simply contains all zeros, and the \mathbf{R} matrix contains the N_i^* terms for the interior equilibrium point in its diagonal elements.

Invasions

What happens when one species invades a community? Will the invasion be resisted or will the invader increase? If it increases, what happens to the resident species? Will they persist or become extinct? Answers to these questions can be easily visualized with two resident species and one invader. Let's call the invader species 3 and the resident species 1 and 2. In the absence of the invader, the two resident species are at their equilibrium densities, $N_1^*(3)$ and $N_2^*(3)$. The condition for the growth rate of the invader to be positive is

$$g_3 = [K_3 - \alpha_{31}N_1^*(3) - \alpha_{32}N_2^*(3)] \geq 0.$$

Box 14.1 The Determinant and Eigenvalues of a Block Matrix

Consider a matrix \mathbf{A} as being composed of four blocks:

$$\mathbf{A} = \begin{bmatrix} \mathbf{A}_{11} & \mathbf{A}_{12} \\ \mathbf{A}_{21} & \mathbf{A}_{22} \end{bmatrix}.$$

The only restriction on the dimensions of the blocks is that blocks \mathbf{A}_{11} and \mathbf{A}_{22} must be square (since we're going to take their determinants). A theorem in linear algebra provides a convenient expression for the determinant of \mathbf{A} in terms of the blocks. The determinant of \mathbf{A} , denoted $|\mathbf{A}|$, is given by

$$|\mathbf{A}| = |\mathbf{A}_{22}| |\mathbf{A}_{11} - \mathbf{A}_{12} \mathbf{A}_{22}^{-1} \mathbf{A}_{21}|. \quad (14.20)$$

In our case the Jacobian matrix, \mathbf{J} , is 4×4 and each block is a 2×2 submatrix. Moreover, the \mathbf{A}_{21} block contains only zeros, so we have

$$\mathbf{J} = \begin{bmatrix} \mathbf{A}_{11} & \mathbf{A}_{12} \\ 0 & \mathbf{A}_{22} \end{bmatrix}.$$

Hence the determinant of $\mathbf{J}(3, 4)$ is

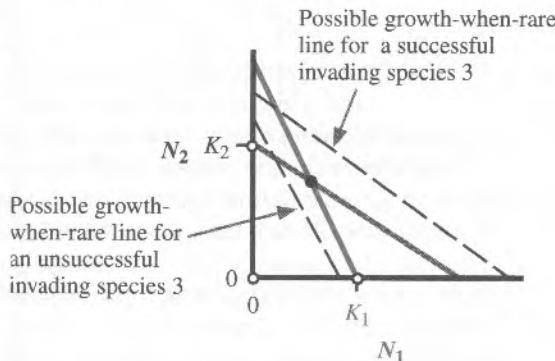
$$|\mathbf{J}| = |\mathbf{A}_{22}| |\mathbf{A}_{11}|.$$

Now, to get the characteristic equation of \mathbf{J} , we must take the determinant of the matrix \mathbf{J} , with λ_i subtracted from each diagonal term, and then set this determinant to zero, or

$$|\mathbf{J} - \lambda \mathbf{I}| = |\mathbf{A}_{22} - \lambda \mathbf{I}| |\mathbf{A}_{11} - \lambda \mathbf{I}| = 0. \quad (14.21)$$

Here \mathbf{I} is the identity matrix, which is 4×4 on the left-hand side but only 2×2 in each term on the right-hand side. The solutions for λ are the eigenvalues of \mathbf{J} . Because of the special form of Eq. (14.21), the four eigenvalues of \mathbf{J} will be equal to the two eigenvalues \mathbf{A}_{22} plus the two eigenvalues of \mathbf{A}_{11} . Since \mathbf{A}_{22} is a diagonal matrix, its eigenvalues are simply the terms on the diagonal, which in our case are $r_i g_i / K_i$. The eigenvalues of \mathbf{A}_{11} will have negative real parts as long as that community subset coexists at a stable and feasible equilibrium point.

Figure 14.33
Invasion criterion for a third competitor, species 3, invading species 1 (red) and species 2 (gray) at their two-species equilibrium point (the solid dot). The dashed lines are given by Eq. (14.23).



The growth rate of the invading species 3 for any combination of densities of species 1 and 2 is

$$K_3 - \alpha_{31}N_1 - \alpha_{32}N_2 = 0. \quad (14.22)$$

Equation (14.22) can be rearranged and then plotted as a line in $N_1 - N_2$ space, or

$$N_2 = \frac{K_3}{\alpha_{32}} - \frac{\alpha_{31}}{\alpha_{32}} N_1, \quad (14.23)$$

and compared to point $[N_1^*(3), N_2^*(3)]$ on the $N_1 - N_2$ plane.

Figure 14.33 shows two cases: an unsuccessful invader and a successful invader. An unsuccessful invader is represented by a line given by Eq. (14.23) that falls below the $[N_1^*(3), N_2^*(3)]$ equilibrium point. The line for a successful invader falls above this

equilibrium point. However, we cannot determine from Figure 14.33 alone whether the invader will supplant one or more of the resident species or coexist with them at a three-species equilibrium point. This would require a full three-species depiction like those shown in Figure 14.31. For more than two resident species, the resulting community composition after the invasion must usually be determined by simulation since general analytical techniques are lacking (Case 1990).

Problem: Show that the growth-when-rare line for species 3 as given by Eq. (14.23) is just the projection of species 3's zero-isoplane onto the N_1-N_2 plane. (**Hint:** Write the equation for species 3's zero-isoplane and then set species 3 to zero to get the line in just the N_1-N_2 plane.) Examine species 3's zero-isoplane in Figure 14.31 as it hits the N_1-N_2 plane. In Figure 14.31(a), species 3 can invade, but in Figure 14.31(b), it cannot.

Competitive Limit Cycles

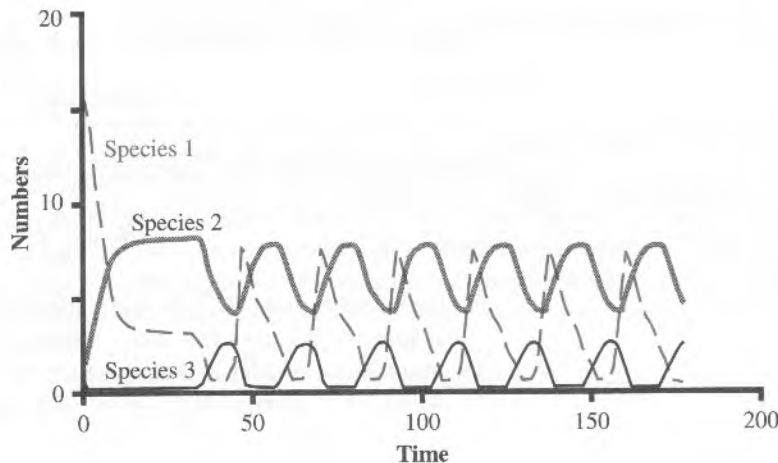
With three or more Lotka–Volterra competitors the interior equilibrium point may be unstable, but all species still indefinitely coexist because they follow a limit cycle. An example of such a limit cycle for three Lotka–Volterra competitors is shown in Figure 14.34. This limit cycle is stable and results from differential equations (not difference equations). The parameters that lead to the particular cycle shown in Figure 14.34 (from Strobeck 1973) are

$$\alpha = \begin{bmatrix} 1 & 2 & 4 \\ 1/3 & 1 & 2 \\ 1/3 & 1/3 & 1 \end{bmatrix}, \quad K = \begin{bmatrix} 19 \\ 9 \\ 4 \end{bmatrix}, \quad \text{and} \quad r = \begin{bmatrix} 19 \\ 3/2 \\ 12 \end{bmatrix}. \quad (14.24)$$

Note how asymmetric the competition is here (e.g., $\alpha_{13} = 4$, but $\alpha_{31} = 1/3$). Also note that r_1 and r_3 are relatively huge compared to r_2 . In fact, it is quite difficult to find situations that yield a limit cycle for three Lotka–Volterra competitors (Gilpin 1975). With a little work, it is possible to show that species 2 and 3 can coexist stably in the absence of species 1, that species 1 and 3 cannot coexist with each other since species 3 ousts species 1, and that species 1 and 2 can coexist at a stable equilibrium point in the absence of species 3. Thus the limit cycle shown here is an emergent property of all three competitors' interactions. None of the three species pairs cycle alone; the cycle emerges only when all three competitors are present. Box 14.2 summarizes some observations about limit cycles in ecological models.

Figure 14.34

The time course for three competitors following a limit cycle specified by the parameters of Eq. (14.24).



Box 14.2 A Few More Words about Limit Cycles

- For a single-species model, limit cycles can emerge with differential equations that contain time lags or with discrete time models.
- For two interacting species, limit cycles may also occur in continuous time models (i.e., without time lags) but only if the zero-isoclines are nonlinear.

The existence of a two-species limit cycle requires an unstable interior equilibrium point inside the cycle. Also, neither species can increase without bounds in the presence of the other.

- For more than two interacting species, limit cycles may emerge in differential equations even when zero-

isosurfaces are linear. For example, limit cycles can occur with three Lotka–Volterra competitors and with two prey and one predator with a type 1 functional response (see Chapter 15).

When the zero-isoclines are linear, the time average of the abundance of each species over the period of the limit cycle is equal to the abundance of that species at the unstable interior equilibrium point (*Note:* This average is not the same as the geometric center of the limit cycle since the trajectory moves at an uneven speed.) When the zero-isoclines are nonlinear, as in some two-species predatory-prey systems, the time average does not necessarily equal the equilibrium abundance.

Exercise: For the system described by Eq. (14.24), what is the interior equilibrium density for the three species? Next, write the Jacobian matrix to evaluate the stability of the interior equilibrium point. Use Eq. (14.11). Verify that the answer is

$$N^* = \begin{bmatrix} 3 \\ 6 \\ 1 \end{bmatrix} \quad \text{and} \quad \mathbf{J} = \mathbf{D}\alpha = \begin{bmatrix} -3 & 0 & 0 \\ 0 & -1 & 0 \\ 0 & 0 & -3 \end{bmatrix} \begin{bmatrix} 1 & 2 & 4 \\ 1/3 & 1 & 2 \\ 1/3 & 1/3 & 1 \end{bmatrix}.$$

How can you show that this interior equilibrium point is unstable?

With three or more competitors, it is possible to alter the local stability of the interior equilibrium point by simply altering the r 's (Strobeck 1973). Show what happens to the stability of the interior equilibrium point if the \mathbf{r} vector is changed to

$$\mathbf{r} = \begin{bmatrix} 19/3 \\ 3/2 \\ 4 \end{bmatrix}.$$

PROBLEMS

1. Assume that the population dynamics of rabbits (r) and hares (h) on a 100-acre plot follows the Lotka–Volterra competition equations. Suppose that you have determined that a 100-acre plot can support either 70 rabbits alone or 90 hares alone or 46 rabbits and 49 hares together.

- What are α_{hr} and α_{rh} ?
- Is $(\alpha_{hr})(\alpha_{rh}) < 1.0$?

Plot the zero-isoclines. Label your axes and points of intersection with each axis. Indicate whether the joint densities form a stable equilibrium point.

2. The competition equations for two species are

$$\frac{dN_1}{dt} = \frac{0.5N_1}{90}(90 - N_1 - 0.5N_2)$$

and

$$\frac{dN_2}{dt} = \frac{N_2}{200}(200 - N_2 - N_1).$$

- What are the equations for the N_1 and N_2 zero-isoclines?
- With N_2 plotted on the y axis and N_1 on the x axis, what is the y intercept for species 1's zero-isocline? _____ for species 2's? _____

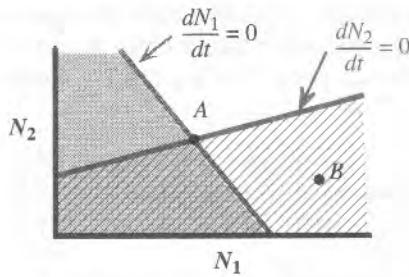
- c. What is the slope of the zero-isocline for species 1? _____
 For species 2? _____
- d. Plot the zero-isocline for species 1 and shade the regions of positive growth.
- e. Plot the zero-isocline for species 2 and shade its region of positive growth.
- f. Draw the approximate trajectory from point (25, 25).
- g. What will be the ultimate outcome of this competition?

Now suppose that K_1 is increased to 150.

- h. Write the zero-isocline equations for both species and plot them again.
- i. Hatch the areas of positive growth; draw the arrows for growth in each different area.
- j. Draw the approximate trajectory from point (25, 25).
- k. What will be the ultimate outcome of this competition?

3. In the Lotka–Volterra equations for two species, what is the biological meaning of
- a situation in which $\alpha_{12} = \alpha_{21}$? In which $\alpha_{12} = \alpha_{21} = 1$?
 - What outcome is predicted when $\alpha_{12} = \alpha_{21} = 1$ and $K_1 = K_2$?
 - What ecological reasons might cause α_{12} to be greater than 1.0?

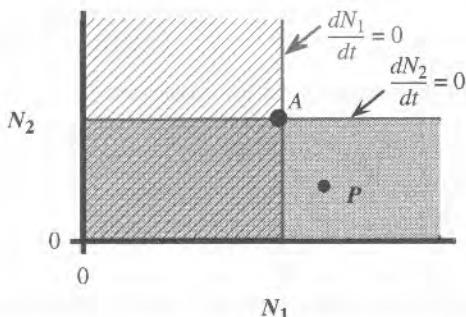
4. Consider the 2-species system described by the following isocline representation.



The hatched regions indicate positive growth.

- Is the qualitative effect (i.e., the sign) of species 1 on its own per capita growth rate positive or negative? _____
- Is the qualitative effect of species 1 on 2's per capita growth rate positive or negative? _____
- Is the equilibrium point labeled A stable? _____
- If initial densities were at point B, sketch the resulting trajectory describing the dynamical behavior of the two species.

5. Given a 2-species system described by the zero-isocline shown—in which the hatched regions indicate positive population growth—circle the single correct answer in each of (a)–(c).



- The qualitative effect (i.e., the sign) of species 1 on its own per capita growth rate is (i) positive, (ii) negative, (iii) neutral, (iv) variable in sign.

- b. The qualitative effect of species 1 on species 2's per capita growth is (i) positive, (ii) negative, (iii) neutral, (iv) variable in sign.

- c. The qualitative effect of species 2 on species 1's per capita growth is (i) positive, (ii) negative, (iii) neutral, (iv) variable in sign.

- d. Is the equilibrium point labeled A stable? _____

- e. Is the equilibrium point (0, 0) stable? _____

- f. If the initial densities of the two species were at point P, draw the resulting trajectory in phase space describing the dynamic changes in N_1 and N_2 .

6. Consider Lotka–Volterra two-species competition with $\alpha_{12} = 1.5$ and $\alpha_{21} = 1.5$; both species have equal carrying capacities, but species 1's r is larger than species 2's. How will the competitive outcome depend on initial abundances?

7. For the equation

$$\frac{dN_1}{dt} = \frac{0.5N_1}{100}(100 - N_1 - 0.5N_2 - 1.2N_3)$$

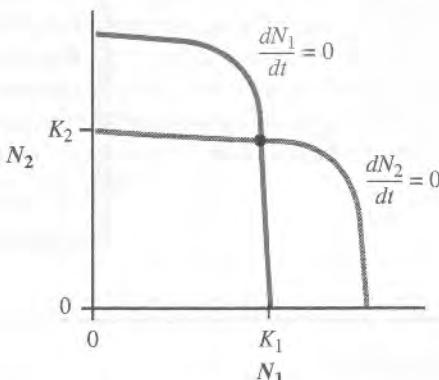
solve for the zero-isosurface and plot it in the state space of N_1 , N_2 , and N_3 . (Let N_3 be the vertical axis).

8. Construct a three-species Lotka–Volterra competition system that has three locally stable boundary equilibria, one for each of the species at its carrying capacity. Give the α matrix and \mathbf{K} vector.

9. Write the discrete-time analog of the two-species Lotka–Volterra competition equations. What will be the effect of R on the stability of the system? Do you expect limit cycles under some conditions?

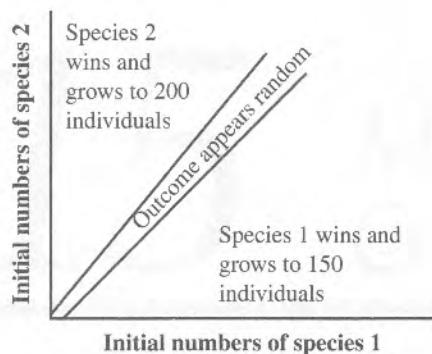
10. Do you agree with the following statement? “The relative magnitude of the r 's in Lotka–Volterra competition can influence which species will beat the other in competition in some situations.” If you agree, give an example of the circumstances under which this statement is true.

11. Consider the following zero-isoclines for two-species competition.



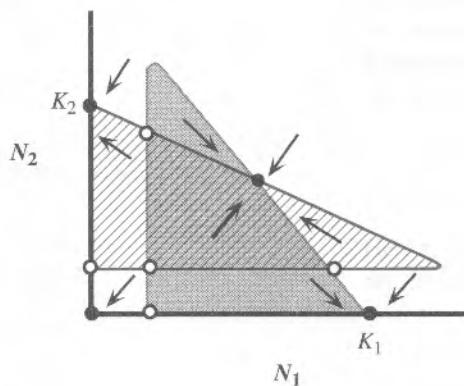
Suppose that these two species have the densities of the interior equilibrium point. You do a field experiment to see if these two species compete. You remove species 1 and wait until species 2 reaches a new equilibrium. You also do the reciprocal experiment in some other plots by removing species 2. What results would you find? What would you conclude about the extent of competition between these two species? How would these results compare to a second set of experiments wherein you doubled the size of species 2's population in some plots while in others you doubled the size of species 1's population?

12. Experimentally, you obtain the following result for the outcome of competition between two species based on many different initial abundances of the two.



In the region labeled “outcome appears random”, only one species persists, but sometimes it’s species 1 and sometimes it’s species 2 in an unpredictable fashion. Draw a plausible scheme for the zero-isoclines for this system and label all points of intersection with each axis. Also, draw small circles around each equilibrium point and indicate which are stable and which are unstable.

13. The following zero-isocline diagram incorporates an Allee effect into two-species competition for the case where the interior equilibrium point is stable (see Figure 14.23a).



Note how many new equilibrium points this adds. Stable equilibria are indicated by a black dot and unstable equilibria by a white dot. Construct depictions of the other three cases previously shown in Figure 14.23 by incorporating this type of Allee effect.

14. Consider three Lotka–Volterra competitors. All have the same K , and the α matrix is

$$\alpha = \begin{bmatrix} 1 & 1.5 & 0 \\ 0 & 1 & 1.5 \\ 1.5 & 0 & 1 \end{bmatrix},$$

and the determinant of α is positive.

a. Assuming any initial numbers where all species have positive density, how many domains of attraction are there for this three-species system? What are they?

b. In the absence of species 3, can species 1 and 2 coexist? If not, who wins?

c. In the absence of species 2, can species 1 and 3 coexist? If not, who wins?

d. If species 1 is at its carrying capacity, can species 2 invade? Can species 3 invade?

e. Interpret the symbolism in the following diagram.

