

Lecture notes for Monday 16th March 2020 class

MSc (IV) semester: Paper-19 System Analysis and Modelling

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Topic that was to be covered in the lecture was:

Mathematical Model of Lotka and Volterra for competition

Subtopics:

- 1) The Lotka–Volterra model of interspecific Competition
- 2) Five cases of competition
- 3) Cases 1 and 2: Competitive dominance, and elimination of one species by another
- 4) Case 3: Either species can eliminate the other when grown in the same conditions
- 5) Case 4: Coexistence of the two species at a stable equilibrium density
- 6) Case 5: Coexistence at a range of equilibrium densities
- 7) Competition in Experimental Laboratory Populations

I have attached relevant study material for the above topics from the references mainly:

- 1) Krebs, C. J. The experimental analysis of distribution and abundance. *Ecology*. New York: Harper and Row, 1-14.
Chapter 10: Species Interactions I: Competition (pages 175-182)
- 2) Neal, D. *Introduction to population biology*. Cambridge University Press.
Chapter 17: Interspecific competition and amensalism (pages 270-277)

resources for plants, but plants may also compete for pollinators or for space. Water, food, and mates are possible sources of competition for animals. In some animals, competition for space may involve many types of specific requirements, such as nesting sites, wintering sites, or resting sites that are safe from predators. Species must share a common interest in one or more resources before they can be potential competitors.

Several aspects of the process of competition must be kept clear. First, animals need not see or hear their competitors. A species that feeds by day on a plant may compete with a species that feeds at night on the same plant if the plant is in short supply. Second, many or most of the organisms that an animal sees or hears will not be its competitors. This is true even if resources are shared by the organisms. Thus, even though oxygen is a resource shared by most terrestrial organisms, there is no competition for it among these organisms because this resource is superabundant. Third, competition in plants usually occurs among individuals rooted in position and therefore differs from competition among mobile animals. The spacing of individuals is thus more important in plant competition.

Theories on Competition for Resources

Mathematical models have been used extensively to build hypotheses about what happens when two species live together, either sharing the same food, occupying the same space, or preying on or parasitizing the other. The classical models of these phenomena are the **Lotka-Volterra equations**, which were derived independently by Lotka (1925b) in the United States and Volterra (1926) in Italy. More mechanistic models by

Tilman (1982, 1990) have provided another important perspective on competition theory.

Mathematical Model of Lotka and Volterra

Lotka and Volterra each derived two different sets of equations: One set applies to predator-prey interactions, the other set to nonpredatory situations involving competition for food or space. We are concerned here only with their second set of equations for nonpredatory competition.

The Lotka-Volterra equations, which describe competition between organisms for food or space, are based on the logistic curve. We have seen that the logistic curve is described by the following simple logistic equations: for species 1,

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1}{K_1} \right) \quad (1)$$

and for species 2,

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2}{K_2} \right) \quad (2)$$

where N_1 = population size of species 1

t = time

r_1 = intrinsic capacity for increase of species 1

K_1 = asymptotic density or "carrying capacity" for species 1

and these variables are similarly defined for species 2.

We can visualize two species interacting—that is, affecting the population growth of each other—with the following simple analogy illustrated in **Figure 1**.

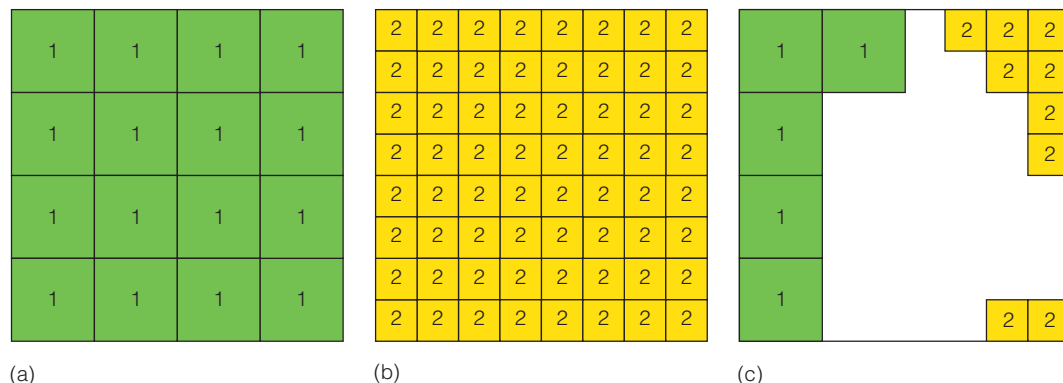


Figure 1 Schematic illustration of the resources two species utilize in competition.

(a) Species 1 has a high utilization rate, and only 16 individuals can be supported in this habitat. (b) Species 2 uses much less of this resource per individual, and 64 individuals can be supported. (c) In competition these two species vie for the common resource. The resource might be nitrogen in the soil for two competing plant species, or a particular food source for two animal species. The size of the box represents the amount of the resource that is available for both species.

Species Interactions I: Competition

Consider the environment to contain a certain amount of a limiting resource, such as nitrogen in the soil. Species 1 uses this resource, and the environment will hold K_1 individuals of this species (shown in green) when all the resource is being monopolized. But some of this resource can also be used by a competitor, species 2 (shown in yellow), which in this example needs much less of the resource to support one individual.

In most cases, the amount of resource used by one individual of species 2 is not exactly the same as that used by one individual of species 1, as illustrated in Figure 1. For example, species 2 may be smaller and require less of the critical resource that is contained in the environment. For this reason, we need a factor to convert species 2 individuals into an equivalent number of species 1 individuals. For this competitive situation, we define

$$\alpha N_2 = \text{equivalent number of species 1 individuals} \quad (3)$$

where α is the conversion factor for expressing species 2 in units of species 1. This is a very simple assumption, which states that under all conditions of density there is a constant conversion factor between the competitors. We can now write the competition equation for species 1 as

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha N_2}{K_1} \right) \quad (4)$$

This equation is mathematically equivalent to the simple analogy we just developed. **Figure 2** shows this graphically for the equilibrium conditions, when dN_1/dt is zero.

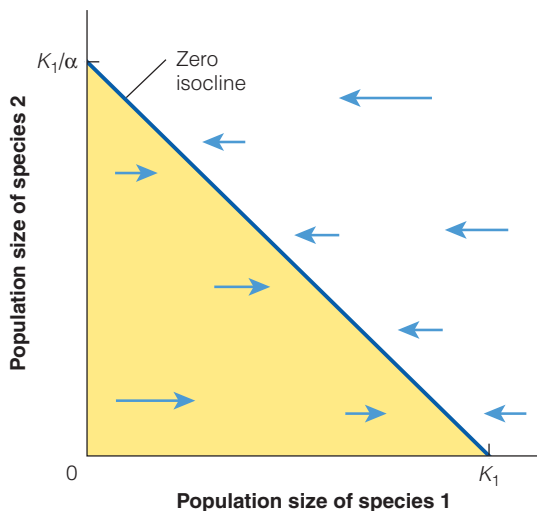


Figure 2 Changes in population size of species 1 when competing with species 2. Populations in the yellow area will increase in size and will come to equilibrium at some point on the blue diagonal line. The sizes of the arrows indicate the approximate rate at which the population will move toward the blue diagonal line. The blue diagonal line represents the zero growth isocline, all those points at which $dN_1/dt = 0$.

The two extreme cases are shown at the ends of the diagonal line in Figure 2. All the “space” for species 1 is used (1) when there are K_1 individuals of species 1, or (2) when there are K_1/α individuals of species 2. Populations of species 1 below this line will increase in size until they reach the diagonal line, which represents all points of equilibrium and is called the isocline. Note that we do not yet know where along this diagonal we will finish, but it must be somewhere at or between the points $N_1 = K_1$ and $N_1 = 0$.

Now we can retrace our steps and apply the same line of argument to species 2. We now have a volume of K_2 spaces to be filled by N_2 individuals but also by N_1 individuals. Again we must convert N_1 into equivalent numbers of N_2 , and we define

$$\beta N_1 = \text{equivalent number of species 2 individuals} \quad (5)$$

where β is the conversion factor for expressing species 1 in species 2 units.¹ We can now write the competition equations for the second species, as follows:

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - \beta N_1}{K_2} \right) \quad (6)$$

Figure 3 shows this equation graphically for the equilibrium conditions when dN_2/dt is zero.

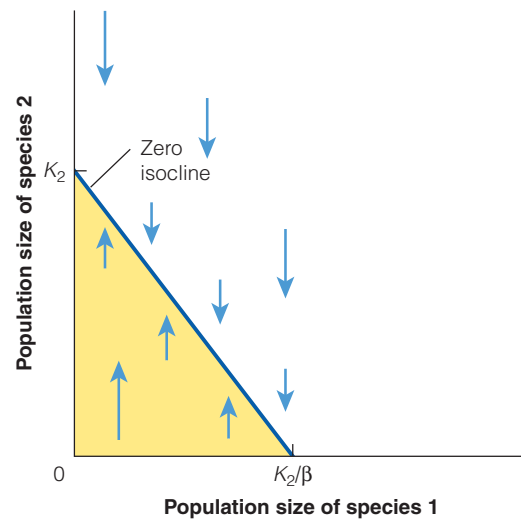


Figure 3 Changes in population size of species 2 when competing with species 1. Populations in the yellow area will increase in size and will come to equilibrium at some point on the blue zero growth isocline, all those points at which $dN_2/dt = 0$. The sizes of the arrows indicate the approximate rates at which the population will move toward the isocline.

¹ α and β can be written more generally as a_{ij} , the effect of species j on species i . Thus $\alpha = a_{12}$ and $\beta = a_{21}$.

Species Interactions I: Competition

Now if we put these two species together, what might be the outcome of this competition? Only three outcomes are possible: (1) Both species coexist, (2) species 1 becomes extinct, or (3) species 2 becomes extinct. Intuitively, we would expect that species 1, if it had a very strong depressing effect on species 2, would win out and force species 2 to become extinct. The converse would apply for the situation in which species 2 strongly affected species 1. In a situation in which neither species has a very strong effect on the other, we

might expect them to coexist. These intuitive ideas can be evaluated mathematically in the following way.

Solve the following simultaneous equations at equilibrium:

$$\frac{dN_1}{dt} = 0 = \frac{dN_2}{dt} \quad (7)$$

This can be done by superimposing figures (such as Figures 2 and Figure 3) and adding the arrows by vector addition. **Figure 4** shows the four possible

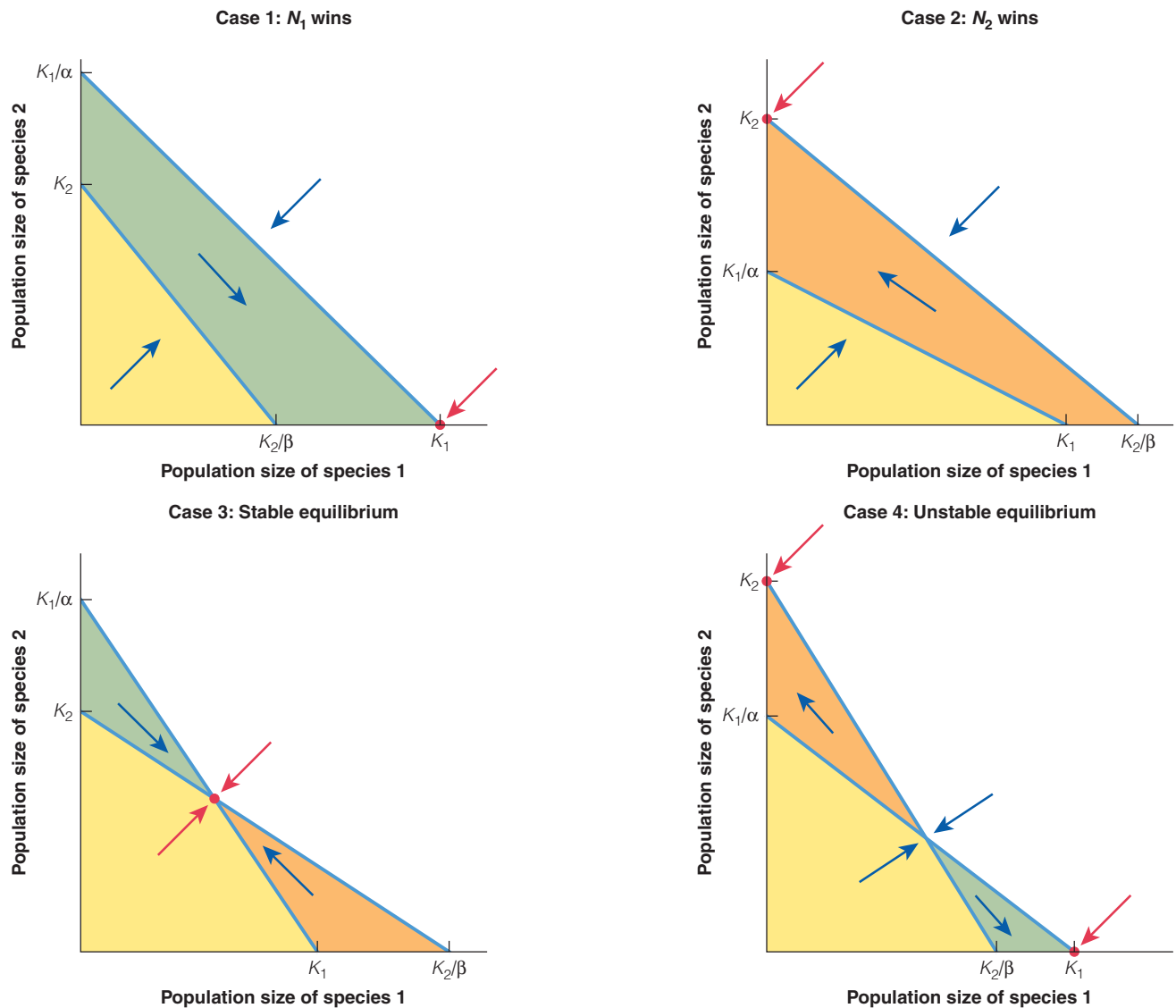


Figure 4 Four possible outcomes of competition between two species. Blue arrows indicate direction of change in populations, and red dots and red arrows indicate the final equilibrium points. In the yellow zone, both species can increase; in the green zone, only species 1 can increase; in the orange zone, only species 2 can increase; and in the white zone both species must decrease.

geometric configurations. In each of these, the vector arrows have been abstracted, and the results can be traced by following the arrows. Species 1 will increase in yellow and green areas, and species 2 will increase in yellow and orange areas. There are a number of principles to keep in mind in viewing these kinds of curves. First, there can be no equilibrium of the two species unless the diagonal curves cross each other. Thus, in cases 1 and 2, there can be no equilibrium, because one species is able to increase in a zone in which the second species must decrease. These cases lead to the extinction of one competitor. Second, if the diagonal lines cross, the equilibrium point represented by their crossing may be either a stable point or an unstable point. It is stable if the vectors about the point are directed toward the point, and unstable if the vectors are directed away from it. In case 4, the point where the two lines cross is unstable because if in response to some small disturbance the populations move slightly downward, they reach a zone in which N_1 can increase but N_2 can only decrease, which results in species 1 coming to an equilibrium by itself at K_1 . Similarly, slight movement upward will lead to an equilibrium of only species 2 at K_2 .

Tilman's Model

The Lotka-Volterra equations describe competition only by its results—that is, according to changes in the population sizes of the two competing species. In the Lotka-Volterra models, no mechanisms are specified by which the effects of competition are produced. Tilman (1987) criticized this approach to competition and emphasized that we need to study the mechanisms by which competition occurs.

Tilman (1977, 1982) presented a mathematical model of competition based on resource use. We begin our examination of the essential features of Tilman's model by considering **Figure 5**, which illustrates the response of an organism to two essential resources; for terrestrial plants these might be nitrogen and light, for example, or for a freshwater fish these might be zooplankton concentration and oxygen level. If the level of abundance of either resource 1 or resource 2 is too low, the population declines; conversely, if both resources are abundant, the population increases. The boundary between population growth and decline is the zero growth isocline of this species. A second key parameter for Tilman's model is the rate of consumption of the two essential resources. Each species will consume resources at different rates. For example, a plant might utilize water more rapidly than it utilizes nitrogen. These rates of

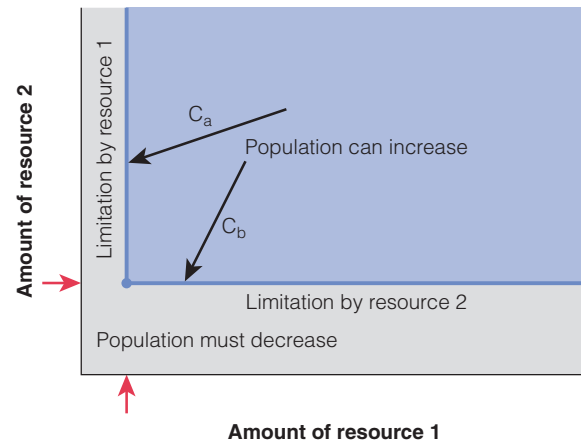


Figure 5 The response of a single species population to variations in two essential resources (such as nitrogen and water, for plants). The blue lines represent the zero growth isoclines, the lower one set by resource 2 and the left one set by resource 1 (red arrows). Above these isoclines in the blue shaded area, the population can increase in size; below these isoclines in the gray area, the population will decline. In the left side of the gray area, resource 1 is limiting; in the bottom side of the gray area, resource 2 is limiting. Only at the intersection point (blue dot) are both resources simultaneously limiting. At the hypothetical consumption vectors C_a the organism uses resource 1 more rapidly and resource 2 more slowly; C_b represents the opposite case. (Modified from Tilman 1982.)

consumption will determine the slope of the consumption vectors illustrated in Figure 5.

If we repeat this analysis for a second species, we can superimpose the two zero growth isoclines. **Figure 6** shows the possible outcomes of competition for the two competing species. In the first case (Figure 6a), species *B* needs more of both resources than species *A*. Thus species *A* will win out in competition, and species *B* will go extinct. The second case (Figure 6b) is the mirror image of the first case, and species *A* goes extinct. In the remaining case (Figure 6c) the zero growth isoclines cross, so there is an equilibrium point. To determine whether this equilibrium is stable or unstable, we need additional information on the consumption curves for each species. At the equilibrium point in Figure 6c, species *A* is limited by resource 2, and species *B* is limited by resource 1. If species *A* consumes relatively more of resource 1 than does species *B*, the equilibrium point is unstable, and one species or the other will go extinct. To apply Tilman's model to a

Species Interactions I: Competition



Figure 6 Tilman's model of competition for two essential resources. The zero isoclines for species A (blue) and species B (red, dashed line) are shown, along with the consumption rate vectors for each species (C_a and C_b). For all three cases the regions are labeled and colored as follows: 1 (gray) = neither species can live; 2 (yellow) = only species A can live; 3 (blue) = species A wins out in competition; 4 (white) = stable coexistence; 5 (orange) = species B wins out in competition; 6 (green) = only species B can live. • = stable equilibrium point. (From Tilman 1982.)

particular environment, we must know the rate of supply of the limiting resources to the populations (a function of the habitat) and the rates of consumption of these resources by each species (represented by the vectors in Figure 5).

Tilman's model provides the same final predictions as the Lotka-Volterra model (compare Figure 6 with Figure 4), but Tilman's model can be extended to make community-level predictions about species diversity and succession (Tilman 1986, 1990). The strength of Tilman's model is in its emphasis on mechanism, and because of this it can help us understand more precisely how species interact over limited resources.

Three important ideas have come from these mathematical models of two competing species:

1. Competition can lead to one species winning and the second species going extinct.
2. Some competitive interactions can lead to coexistence.
3. We can understand competitive interactions only by knowing the resources involved and the mechanisms by which species compete.

Now that we have these mathematical formulations and some simple hypotheses of competitive interactions, we must see if they are an adequate representation of what happens in actual biological systems.

Competition in Experimental Laboratory Populations

One of the first and most important investigations of competitive systems was conducted by a Russian microbiologist named Georgyi Frantsevich Gause working at Moscow University. Gause (1932) studied in detail the mechanism of competition between two species of yeast, *Saccharomyces cerevisiae* and *Schizosaccharomyces kephir*.² In the first aspect of his investigations, concerning the growth of these two species in isolation, he found that the population growth of both species of yeast was sigmoid and could reasonably be fitted by the logistic curve.

Gause then asked: What are the factors in the environment that depress and stop the growth of the yeast population? Richards (1928) had previously shown that when the growth of yeast stops under anaerobic conditions, a considerable amount of sugar and other necessary growth substances remain in the cultures. Because growth ceases before the reserves of food and energy are exhausted, something else in the environment must be responsible for the restriction of population increase. The decisive factor seems to be the accumulation of ethyl alcohol, which is produced by the breakdown of sugar for energy under anaerobic conditions

²These organisms' scientific names have changed since Gause's studies.

Species Interactions I: Competition

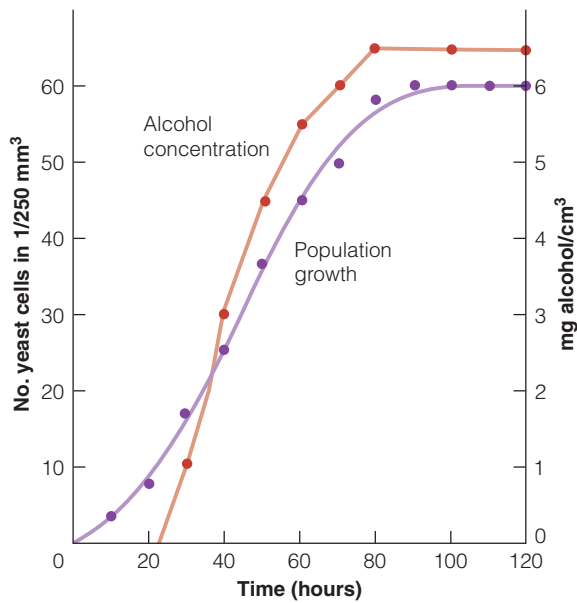


Figure 7 Population growth (purple) and ethyl alcohol accumulation (red) in a population of yeast (*Saccharomyces*). (After Richards 1928.)

(Figure 7). High concentrations of alcohol kill the new yeast buds just after they separate from the mother cell. Richards showed that the yeast growth could be reduced by artificially adding alcohol to cultures, and changes in the pH of the medium were of secondary importance. Thus with yeast we apparently have a quite simple relationship, with the population in test tube cultures being limited principally by one factor: ethyl alcohol concentration.

When grown separately, the two yeast species reacted as shown in Figure 8. From these curves, Gause calculated logistic curves (calculated in units of volume):

	<i>Saccharomyces</i>	<i>Schizosaccharomyces</i>
K	13.00	5.80
r	0.22	0.06

Gause then investigated what would happen when the two yeast species were grown together, and he obtained the results shown in Figure 9 and Figure 10. Gause assumed that these data fit the Lotka-Volterra equations, and using

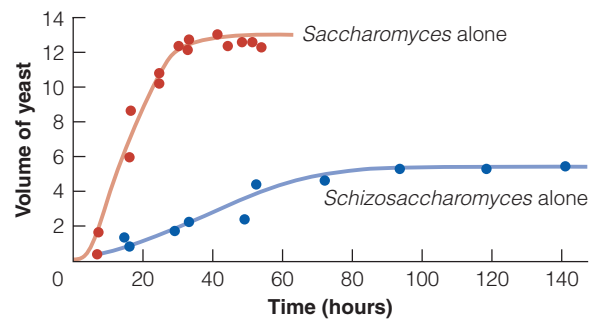


Figure 8 Population growth of pure cultures of two yeasts, *Saccharomyces* and *Schizosaccharomyces*. (After Gause 1932.)

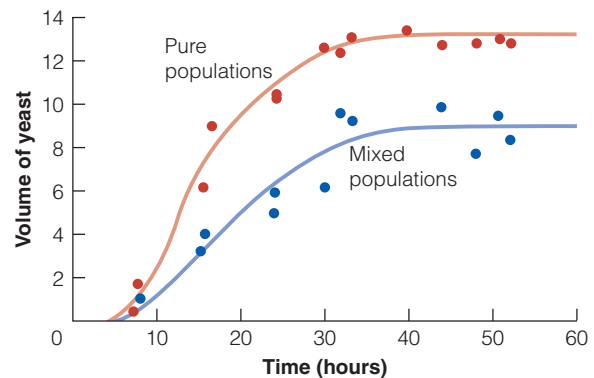


Figure 9 Growth of populations of the yeast *Saccharomyces* in pure cultures and in mixed cultures with *Schizosaccharomyces*. (After Gause 1932.)

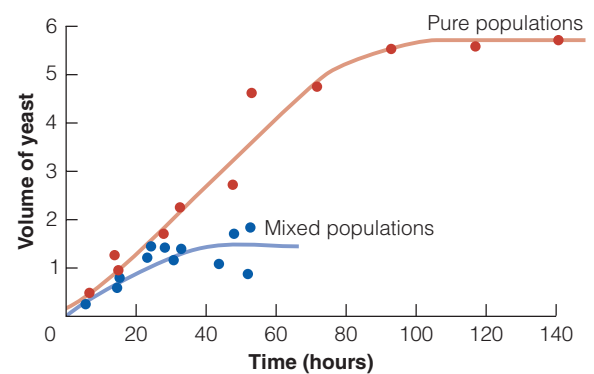


Figure 10 Growth of populations of the yeast *Schizosaccharomyces* in pure cultures and in mixed cultures with *Saccharomyces*. (After Gause 1932.)

Species Interactions I: Competition

the equations on the data from the mixed cultures, he obtained the following data:

Age of Culture (hr)	Competition coefficients	
	α <i>Saccharomyces</i>	β <i>Schizosaccharomyces</i>
20	4.79	0.501
30	2.81	0.349
40	1.85	0.467
Mean value	3.15	0.439

The influence of *Schizosaccharomyces* on *Saccharomyces* is measured by α , and this means that, in terms of competition, *Saccharomyces* can fill its K_1 spaces according to the equivalence

1 volume of *Schizosaccharomyces* = 3.15 volumes of *Saccharomyces*

Note that the α and β values tend to change with the age of the culture, but as a first approximation we can assume α and β to be constants.

If alcohol concentration is the critical limiting factor in these anaerobic yeast populations, Gause argued, then we should be able to determine the competition coefficients α and β by measuring the alcohol production rate of the two yeasts. He found:

	Alcohol production (% EtOH/mL yeast)
<i>Saccharomyces</i>	0.113
<i>Schizosaccharomyces</i>	0.247

Gause then argued that since alcohol was the limiting factor of population growth, the competition coefficients, α and β , should be determined by a direct ratio of these alcohol production figures:

$$\alpha = \frac{0.247}{0.113} = 2.18$$

$$\beta = \frac{0.113}{0.247} = 0.46$$

These independent physiological measurements agree in general with those obtained from the population data given previously. Gause attributed the differences in the α values to the presence of other waste products affecting *Saccharomyces*. Gause assumed that the competition coefficients would be the reciprocals of each

other, but this assumption need not apply to all cases of competition.

In many laboratory experiments, a species can do well when raised alone but can be driven to extinction when raised in competition with another species. When Birch (1953b) raised the grain beetles *Calandra oryzae* and *Rhizopertha dominica* at several different temperatures, he found that *Calandra* would invariably eliminate *Rhizopertha* at 29°C (Figure 11) and that *Rhizopertha* would always eliminate *Calandra* at 32°C (Figure 12). Birch found that he could predict these results from the intrinsic capacity for increase; for example,

	r	Temperature	Winner
<i>Calandra</i>	0.77	29.1°C	<i>Calandra</i>
<i>Rhizopertha</i>	0.58		
<i>Rhizopertha</i>	0.69	32.3°C	<i>Rhizopertha</i>
<i>Calandra</i>	0.50		

Thus we could change the outcome of competition by changing only one component of the environment, temperature, by only 3°C.

In all the grain beetle experiments just discussed, one species or the other died out completely. All these situations fall under cases 1 or 2 in our treatment of the Lotka-Volterra equations. What about case 3, in which the species coexist? Yeasts coexisted in Gause's experiments; does coexistence ever occur in grain beetles?

Under the conditions of extreme crowding in laboratory experiments, it is possible for two species to live together indefinitely if they differ even slightly in their

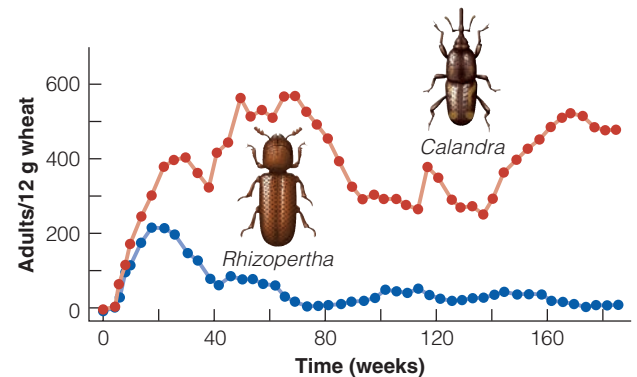


Figure 11 Population trends of adult grain beetles (*Calandra oryzae* and *Rhizopertha dominica*) living together in wheat of 14% moisture content at 29.1°C.

Calandra eliminates *Rhizopertha* in competition at this temperature. (After Birch 1953b.)

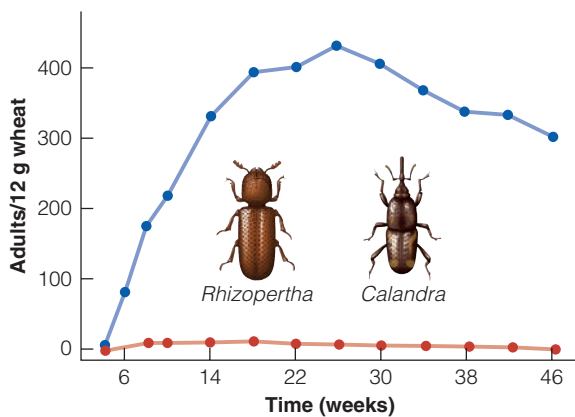


Figure 12 Population trends of adult grain beetles (*Calandra oryzae* and *Rhizopertha dominica*) living together in wheat of 14% moisture content at 32.3°C. *Calandra* goes extinct and *Rhizopertha* wins in competition at this temperature. (After Birch 1953b.)

requirements. For example, Crombie (1945) reared the grain beetles *Rhizopertha* and *Oryzaephilus* in wheat and found that they would coexist indefinitely. The larvae of *Rhizopertha* live and feed inside the grain of wheat; the larvae of *Oryzaephilus* live and feed outside the grain. (The adults of both species have the same feeding behavior, feeding outside the wheat grain.) Apparently these larval differences were sufficient to allow coexistence.

Gause (1934) found that *Paramecium aurelia* and *P. bursaria* would coexist in a tube containing yeast. *P. aurelia* would feed on the yeast suspension in the upper layers of the fluid, whereas *P. bursaria* would feed on the bottom layers. This difference in feeding behavior allowed these species to coexist.

Thus by introducing only very slight differences in the environment, or given very slight differences in species habits, coexistence can occur between competing animal species under laboratory conditions.

Competition in Natural Populations

We now come to the question of how these theoretical and laboratory results apply to nature. In asking this question, we come up against a controversy of modern ecology, the problem of Gause's hypothesis.

Gause (1934) wrote: "As a result of competition two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain peculiar kinds of food and modes of life in which it has an advantage over its competitor" (p. 19). Gause referred to Elton (1927), who had defined **niche** as follows: "The niche of an animal

means its place in the biotic environment, its relations to food and enemies" (p. 64). Thus Elton used the term niche to describe the role of an animal in its community, so one could speak (for example) of a broad herbivore niche, which could be further subdivided.

Gause went on to say that the Lotka-Volterra equations do "not permit any equilibrium between the competing species occupying the same 'niche,' and [lead] to the entire displacing of one of them by another. . . . Both species survive indefinitely only when they occupy different niches in the microcosm in which they have an advantage over their competitors" (p. 48). Gause identifies case 3 (stable coexistence) with the situation of "different niches" and cases 1, 2, and 4 with the situation of "same niche."

Gause himself never formally defined what is called **Gause's hypothesis**. In 1944 the British Ecological Society held a symposium on the ecology of closely related species. An anonymous reporter (who turned out to be David Lack) wrote that year in the *Journal of Animal Ecology* that "the symposium centered about Gause's contention (1934) that two species with similar ecology cannot live together in the same place . . ." (p. 176).

As is usual, several workers immediately searched out and found earlier statements of "Gause's hypothesis." Monard, a French freshwater biologist, had expressed the same idea in 1920, and Grinnell, a California biologist, had written much the same thing in 1904. Darwin apparently had the same idea but never clearly expressed it. The solution to this has been to drop the use of names and call this idea the competitive exclusion principle, which Hardin (1960) states succinctly: "Complete competitors cannot coexist." The competitive exclusion principle encapsulates the conclusions of the Lotka-Volterra models for competition.

The concept of the niche is intimately involved with the competitive exclusion principle, and so we must clarify this concept first. The term niche was almost simultaneously defined to mean two different things. Joseph Grinnell, who in 1917 was one of the first to use the term niche, viewed it as a subdivision of the habitat: Each niche was occupied by only one species. Elton in 1927 independently defined the niche as the "role" of a species in the community. These vague concepts were incorporated into Hutchinson's redefinition of the niche in 1958. If we consider just two environmental variables, such as temperature and precipitation, and determine for each species the range of values that allow the species to persist, we can produce an analysis like that in **Figure 13**. This ecological space in which the species can survive is defined as the realized niche of that species. We could measure other environmental variables, such as pH or soil nutrients for plants, until all the ecological factors relative to the species have been measured. In an ideal world we could measure the ecological

slow the regeneration and growth of chamise by their utilization of light, water and soil nutrients, but I suspect that the effects would be relatively small and difficult to show.

17.3 The Lotka–Volterra model of interspecific competition

In the mid-1920s, a simple mathematical model of interspecific competition was independently derived by Alfred James Lotka, a physical chemist in the United States who was interested in modelling biological processes, and Vito Volterra, an Italian mathematician. Volterra had been asked to model the process by his daughter, Luisa, an ecologist, and her fiancé, Umberto d’Ancona, who was a marine biologist. The model is now called the Lotka–Volterra competition model. The model is a simple extension of the logistic growth model (Chapter 5) for a pair of species, which are designated as N_1 and N_2 . When the two species are growing independently, their population growth is reduced by intraspecific competition as follows:

$$\frac{\delta N_1}{\delta t} = r_1 N_1 \left(\frac{K_1 - N_1}{K_1} \right) \quad (\text{Exp. 17.1})$$

$$\frac{\delta N_2}{\delta t} = r_2 N_2 \left(\frac{K_2 - N_2}{K_2} \right) \quad (\text{Exp. 17.2})$$

These equations are simple modifications of Eqn 5.2a. When the two species grow together the growth rate of each species is further reduced by the presence of the other, i.e. by interspecific competition. Lotka and Volterra modified the above two expressions as follows:

$$\frac{\delta N_1}{\delta t} = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha N_2}{K_1} \right) \quad (\text{Eqn 17.1})$$

$$\frac{\delta N_2}{\delta t} = r_2 N_2 \left(\frac{K_2 - N_2 - \beta N_1}{K_2} \right) \quad (\text{Eqn 17.2})$$

We are familiar with most of the terms in this pair of equations. The carrying capacities of the two species are denoted by K_1 and K_2 , the rates of population increases are denoted by r_1 and r_2 , and the densities of the two species are denoted by N_1 and N_2 . The coefficients α and β (called *competition coefficients*) are new to us, and as they are a key feature of the model we need to understand what they represent. In simple terms, α is a coefficient to make the individuals of species 2 equivalent to individuals of species 1, in terms of their effect on the population growth of species 1. For example, if each individual of species 2 had the same effect as 2.5 individuals of species 1 on the growth of species 1, α would equal 2.5. Similar reasoning shows that β is a coefficient to make the individuals of species 1 equivalent to individuals of species 2, in terms of their effect on the

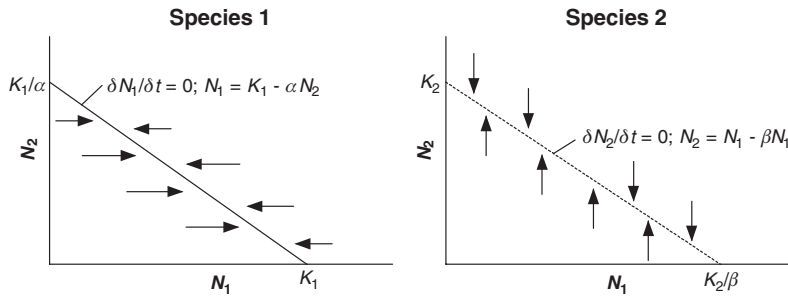


Fig. 17.2 Graphical representation of the zero isoclines of two species in the Lotka-Volterra competition model. The arrows show the direction of population growth for each species at various combination densities of the two species.

population growth of species 2. We can express these relationships as follows:

$$\alpha = \frac{\text{effect of one unit of sp. 2 on the growth of sp. 1}}{\text{effect of one unit of sp. 1 on the growth of sp. 1}} \quad (\text{Exp. 17.3})$$

$$\beta = \frac{\text{effect of one unit of sp. 1 on the growth of sp. 2}}{\text{effect of one unit of sp. 2 on the growth of sp. 2}} \quad (\text{Exp. 17.4})$$

Normally the units are individuals, in which case the competition coefficients are a measure of the relative importance *per individual* of interspecific and intraspecific competition. However, in some cases the species are measured by biomass or volume, and we would use these measures to compare the effects of competition.

To determine the outcome of competition between the two species, Eqns 17.1 and 17.2 must be solved simultaneously. We do this by determining the equilibrium population densities when the two species reach their combined saturation densities and there is no further growth, i.e. when $\delta N_1/\delta t$ and $\delta N_2/\delta t = 0$. This occurs when the numerator of the terms in parentheses in Eqns 17.1 and 17.2 equal zero.

Thus, when $\delta N_1/\delta t = 0$, $K_1 - N_1 - \alpha N_2 = 0$, and this may be rearranged to show us that at equilibrium:

$$N_1 = K_1 - \alpha N_2 \quad (\text{Eqn 17.3})$$

Similarly,

$$N_2 = K_2 - \beta N_1 \quad (\text{Eqn 17.4})$$

Equations 17.3 and 17.4 can be represented graphically (Fig. 17.2) as zero isoclines,² which represent the densities of the two species when there is no further population growth. The graphs and equations make intuitive sense. If species 2 is not present, species 1 will grow to its carrying capacity, K_1 , but its equilibrium density is reduced as species 2 (N_2) increases in density. We can see from Eqn 17.3 that N_1 will decline to zero when $\alpha N_2 = K_1$, and so this occurs when $N_2 = K_1/\alpha$. Similar reasoning shows us that species 2 will grow to K_2 in the absence of species 1 (i.e. $N_1 = 0$), and will decline to zero when

² A zero isocline represents a set of conditions where there is no growth, i.e. $r = 0$, which in the case of interspecific competition occurs when a species is at its saturation density.

Table 17.1 Growth parameters for *Saccharomyces cerevisiae* and *Schizosaccharomyces kephir* when cultured under aerobic and anaerobic conditions

	K	r	Competition coefficient	Relative alcohol production
Aerobic conditions				
<i>Saccharomyces</i> (sp. 1)	9.80	0.287 69	$\alpha = 1.25$	1.25
<i>Schizosaccharomyces</i> (sp. 2)	6.9	0.189 39	$\beta = 0.85$	0.80
Anaerobic conditions				
<i>Saccharomyces</i> (sp. 1)	6.25	0.215 29	$\alpha = 3.05$	2.08
<i>Schizosaccharomyces</i> (sp. 2)	3.0	0.043 75	$\beta = 0.40$	0.48

Source: 1932 data from Gause (1934).

$N_1 = K_2/\beta$. In addition, each species can increase in density when the combined densities of the two species occur to the left of its zero isocline, but will decline in density when the combined densities of the two species occur to the right of its zero isocline (Fig. 17.2).

17.3.1 Five cases of competition

The equilibrium densities have been determined separately for each species, but the equilibrium density of species 1 depends on the equilibrium density of species 2, and vice versa. To understand the combined dynamics of the two species we combine the two graphs, and discover that there are five possible combinations of the two isoclines, which represent five possible outcomes of competition as predicted by the Lotka–Volterra equations.

Cases 1 and 2: Competitive dominance, and elimination of one species by another

The great Russian biologist Gause used the approach of Lotka and Volterra to investigate competition between two species of yeasts, *Saccharomyces cerevisiae* and *Schizosaccharomyces kephir* (= *S. pombe*), in the early 1930s. First, he grew the two species separately and fitted a logistic growth curve to estimate the r and K values for each species (see Chapter 5). Then the two species were grown together, and he estimated the competition coefficients, α and β , by the way in which the growth curves were modified. He did this for cultures grown in anaerobic and aerobic conditions and obtained the following results given in Table 17.1.

If we use these data to predict the outcome of competition (Fig. 17.3), under aerobic conditions the model predicts that *Saccharomyces* will eliminate *Schizosaccharomyces*, because it has the higher growth characteristics (r and K values) and the competition coefficients of the two species are similar. Under anaerobic conditions, however, it is predicted that *Schizosaccharomyces* will eliminate *Saccharomyces*, because its increased competitive ability (α is much greater than β) more than compensates for its inferior growth characteristics (r and K values). In each case, the zero isocline of one species lies to

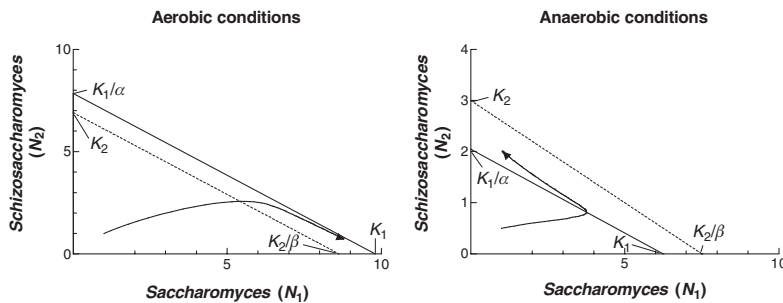


Fig. 17.3 The outcome of competition between *Saccharomyces cerevisiae* (solid line) and *Schizosaccharomyces kephir* (dotted line) grown under aerobic and anaerobic conditions, as predicted by the Lotka–Volterra model. Arrows show the predicted growth of the two species. (Data from Gause 1934.)

the right of the other (Fig. 17.3) and so it can continue to increase in density at the expense of the other species and should eventually eliminate it. In fact, however, neither species was eliminated because the two species went into a resting stage as they approached their combined saturation densities.

Now my objective is not to show that the Lotka–Volterra model is useless. I could have selected an example that supports the prediction of the model. We can make, however, the following observations from Gause’s work. First, if you tried to predict the outcome of competition from the data in Table 17.1, without drawing the zero isoclines, I suspect that you would guess incorrectly. Most people expect *Saccharomyces* to win under both sets of conditions because it consistently has the higher r and K values, although others expect *Schizosaccharomyces* to win because it always has the higher competition coefficient. The model predictions, therefore, are not always very obvious. Second, a change in conditions can alter the outcome of competition, and so one species may be a superior competitor to another under some conditions but be an inferior competitor under other conditions. Finally, Gause’s work on yeast is interesting because it is one of the few cases where the process of competition has been quantified. Gause grew his yeast with an excess of sugar, and so this should not have been limiting to growth. However, growth was inhibited by the increasing concentration of alcohol, and Gause showed that under aerobic conditions both species were inhibited to the same degree by alcohol. He calculated the relative production of alcohol per unit volume of the two species and showed that they corresponded to the competition coefficients of the two species when grown under aerobic conditions (Table 17.1). Gause concluded that competition between the two species grown in aerobic conditions is entirely regulated by their relative alcohol production. The competitive interaction appears to be more complex under anaerobic conditions. *Saccharomyces* appears to inhibit *Schizosaccharomyces* purely by the production of alcohol (the competition coefficient of 0.4 is approximately equal to its relative alcohol production of 0.48 – see Table 17.1), but *Schizosaccharomyces* produces 2.08 times as much alcohol per unit volume than *Saccharomyces* but inhibits the growth of the latter species 3.05 times as much. Gause postulated that other products, such as carbon dioxide, were also involved in the competitive process.

Table 17.2 Percentage of cultures where *Tribolium confusum* eliminated *T. castaneum* when cultured at different temperatures and relative humidity

Temperature	Relative humidity	
	30%	70%
24 °C	100%	71%
29 °C	87%	14%
34 °C	90%	0%

Source: Data from Park (1962).

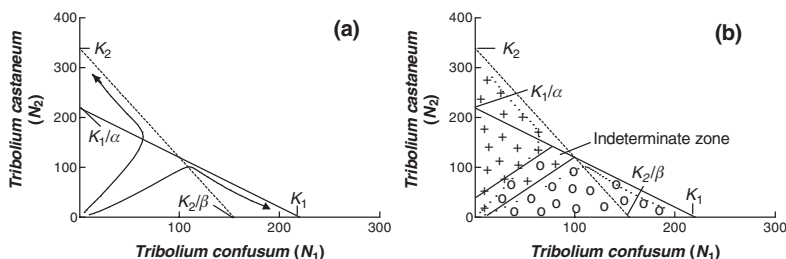


Fig. 17.4 (a) The outcome of competition between *Tribolium confusum* (solid line) and *T. castaneum* (dotted line) when grown at 24 °C and 70% relative humidity, as predicted by the Lotka-Volterra model. Two growth trajectories are shown by arrows. (b) The observed outcome of competition between the two species when started at different densities. Starting densities of cultures won by *T. confusum* are indicated by circles, and those won by *T. castaneum* are indicated by crosses. (Data from Park 1962.)

Case 3: Either species can eliminate the other when grown in the same conditions

Competition between different species of flour beetles has been extensively studied by Park, Mertz, Dawson, and others. They are ideal experimental animals, because they are small, about 4–5 mm in length as adults, and can complete their entire life cycle in small containers of flour. They can be counted by sieving the flour, and it is possible to do well-replicated experiments by keeping several containers in controlled environment chambers. In one such series of experiments, Park (1962) studied the growth of single and mixed species populations of *Tribolium confusum* and *T. castaneum* at different temperatures and humidity (Table 17.2). *Tribolium confusum* always eliminated *T. castaneum* at 24 °C and 30% relative humidity (Case 1), whereas at 34 °C and 70% relative humidity *T. castaneum* always eliminated *T. confusum* (Case 2). However, at intermediate temperatures and humidity either species can eliminate the other, although *T. confusum* wins more frequently at lower humidity and temperatures and *T. castaneum* wins more frequently at higher humidity and temperatures (Table 17.2).

If we consider the interaction at 24 °C and 70% relative humidity, the carrying capacity of *T. confusum* (K_1) was 220 and of *T. castaneum* (K_2) was 340, and the competition coefficients were $\alpha = 1$ and $\beta = 2.2$,

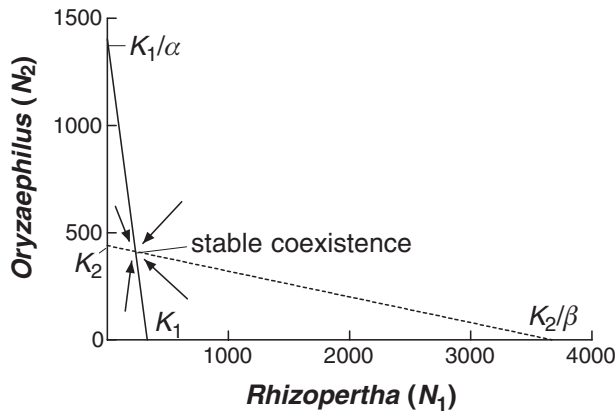


Fig. 17.5 Outcome of competition between *Rhizopertha* (solid line) and *Oryzaephilus* (dotted line), as predicted by the Lotka–Volterra model. Arrows show the predicted growth of the two species from different combinations of their densities. (Data from Crombie 1945.)

enabling us to draw the zero isoclines for this interaction (Fig. 17.4a). It may be seen that the model predicts that either species can win depending on their initial densities and relative rates of increase.

Park grew cultures starting with different combinations of densities of the two species (Fig. 17.5) and showed that a species would always eliminate the other if the starting densities were weighted in its favour. However, there was a region of intermediate densities, which he called an indeterminate zone, where it was not possible to predict with certainty the winning species. In this region, stochastic (chance) events probably determined which species increased faster than the other, so that it would overwhelm and eventually eliminate the other species.

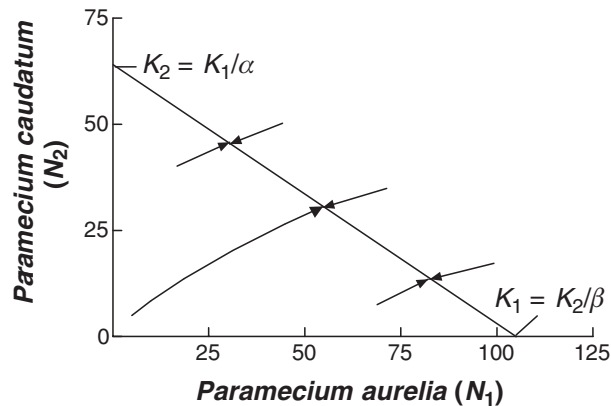
The process of competition between these two species is complex. There is the exploitation of the flour by the two species, but this is affected by the production of growth inhibitors by each species, which is difficult to quantify. There are also predation and cannibalism of eggs and pupae by the larvae and adults. Each species prefers to eat the eggs and pupae of the other species, and it is likely that this mutual predation dominates the competitive interaction. Park considered that this mutual predation was a type of interference competition.

The Lotka–Volterra model correctly predicts the outcome of competition between these two species. Noting the conditions for Case 3 from the intercepts of the two isoclines (Fig. 17.6), we see that $K_1 > K_2/\beta$ and so $\beta > K_2/K_1$, and that $K_2 > K_1/\alpha$ and so $\alpha > K_1/K_2$. Interspecific competition is usually stronger than intraspecific competition in Case 3.

Case 4: Coexistence of the two species at a stable equilibrium density

Two species will coexist in stable equilibrium when each species inhibits its own growth more than it inhibits the growth of the other species, i.e. intraspecific competition is stronger than interspecific competition in both species. An example of this type of competition is provided by the flour beetles *Oryzaephilus* and *Rhizopertha*, when they are grown in cracked wheat (Crombie 1945).

Fig. 17.6 Predicted outcome of competition between *Paramecium aurelia* and *P. caudatum* according to the Lotka–Volterra model. (Data from Gause 1934.)



In one set of experiments, the carrying capacities were 330 for *Rhizopertha* (K_1) and 440 for *Oryzaephilus* (K_2), and the competition coefficients were $\alpha = 0.235$ and $\beta = 0.12$. The predicted outcome of competition between these two species is shown in Fig. 17.6, and this reflects what is observed. Apparently, the larvae of *Rhizopertha* live, feed and pupate inside the cracks in the grains of wheat, whereas the larvae of *Oryzaephilus* live and feed on the surface of the grain. The adults of both species live and feed on the surface of the grain. The difference in feeding habits of the larvae, and probably a reduced level of predation by *Oryzaephilus* on the eggs and pupae of *Rhizopertha*, allows the two species to coexist in stable equilibrium. The importance of reducing pupal predation has been demonstrated in competition between *Tribolium confusum* and *Oryzaephilus*. *Tribolium* always eliminated *Oryzaephilus* in flour cultures, but when the flour was ‘seeded’ with capillary tubes there was stable coexistence of the two species. The smaller species, *Oryzaephilus*, could pupate in the capillary tubes and so was protected from predation.

The conditions for Case 4 may be inferred from the intercepts of the zero isoclines. We see that $K_1 < K_2/\beta$ and so $\beta < K_2/K_1$, and $K_2 < K_1/\alpha$ and so $\alpha < K_1/K_2$. Normally, the effects of intraspecific competition are greater than those of interspecific competition.

Case 5: Coexistence at a range of equilibrium densities

When $\alpha = K_1/K_2$ and $\beta = K_2/K_1$ the zero isoclines of the two species are coincidental (Fig. 17.6), and the model predicts that the two species can coexist at a range of densities, depending on their initial densities and relative growth rates. Many consider that this case is impossible, but we will consider one example because it reveals a fundamental flaw in the basic Lotka–Volterra model.

Gause (1934) examined competition between *Paramecium aurelia* and *P. caudatum* which appears to conform to this situation (Table 17.3). Although the Lotka–Volterra model predicts that the two species will coexist, *P. caudatum* was eliminated from the mixed species cultures by about day 16. The main reason for the displacement of *P. caudatum*

Table 17.3 Growth parameters for *Paramecium aurelia* and *P. caudatum* cultivated separately and together in buffered medium with a ‘half-loop’ concentration of bacteria

Parameter	<i>Paramecium aurelia</i>	<i>Paramecium caudatum</i>
Carrying capacity	$K_1 = 105$	$K_2 = 64$
Intrinsic rate of increase	$r_1 = 1.1244$	$r_2 = 0.7944$
Competition coefficient	$\alpha = 1.64$	$\beta = 0.61$

Source: Data from Gause (1934).

by *P. aurelia* is related to the daily sampling of the cultures to estimate their densities. To quote from Gause (1934):

The biomass of every species was decreased by 1/10 daily. Were the species similar in their properties, each one of them would again increase by 1/10, and there would not be any alteration in the relative quantities of the two species. However, as one species grows quicker than another, it succeeds not only in regaining what it has lost but also in seizing part of the food resources of the other species. Therefore, every elementary movement of the population leads to a diminution in the biomass of the slowly growing species, and produces its entire disappearance after a certain time.

Gause’s observation makes a great deal of sense. Populations are reduced by predation and various forms of disturbance, and their ability to recover from these reductions undoubtedly influences the outcome of competition between species. However, the Lotka–Volterra model only uses the carrying capacities (K) and the competition coefficients (α and β) to predict the outcome of competition, so it would be useful to modify the model so that the growth rates (r) can also influence the outcome.

17.3.2 Complicating the model: introducing a removal factor

Slobodkin (1961) modified the basic Lotka–Volterra model by including a non-selective removal factor (m), and showed that the relative growth rates of the two species may be important in determining the outcome of competition. He modified Eqns 17.1 and 17.2 by removing a proportion (m) of each population at each time step, and obtained following pair of equations:

$$\frac{\delta N_1}{\delta t} = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha N_2}{K_1} \right) - m N_1 \quad (\text{Eqn 17.5})$$

$$\frac{\delta N_2}{\delta t} = r_2 N_2 \left(\frac{K_2 - N_2 - \beta N_1}{K_2} \right) - m N_2 \quad (\text{Eqn 17.6})$$

If the removal factor is selective, such as a predator eating more of one species than the other, we can still make it conform to our model by making the appropriate reduction to the growth rate, r ,