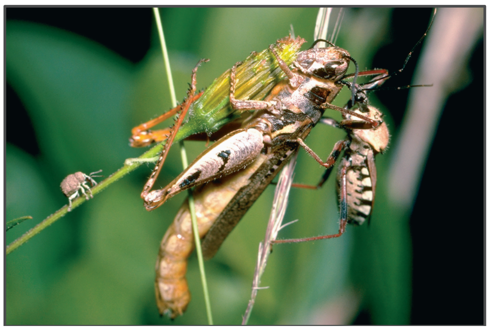
PART FOUR

ECOLOGY OF INTERACTING SPECIES



Species interact in a variety of ways. Some compete for common resources, some species may be food for other species, and some species may benefit one or many other species. In this part, we examine some basic types of interactions between species.

When Darwin wrote about a struggle for existence, the image he conjured up is one of a competition for resources essential to life. Species that have similar ecological requirements will be forced to compete for scarce resources like food, space, or light. In Chapter 12, we review some adaptations used by plants and animals to compete and the impact of competition on population dynamics.

Interactions between species are not always indirect. Some animals eat other animals or plants. These types of interactions are not subtle or inconsequential. A spider that quickly subdues an insect caught in its web makes the struggle for existence obvious. It should not be surprising that predators have evolved elaborate means for successfully capturing prey and that prey have likewise found ways of trying to avoid being eaten. In Chapter 13 we introduce such predators and prey.

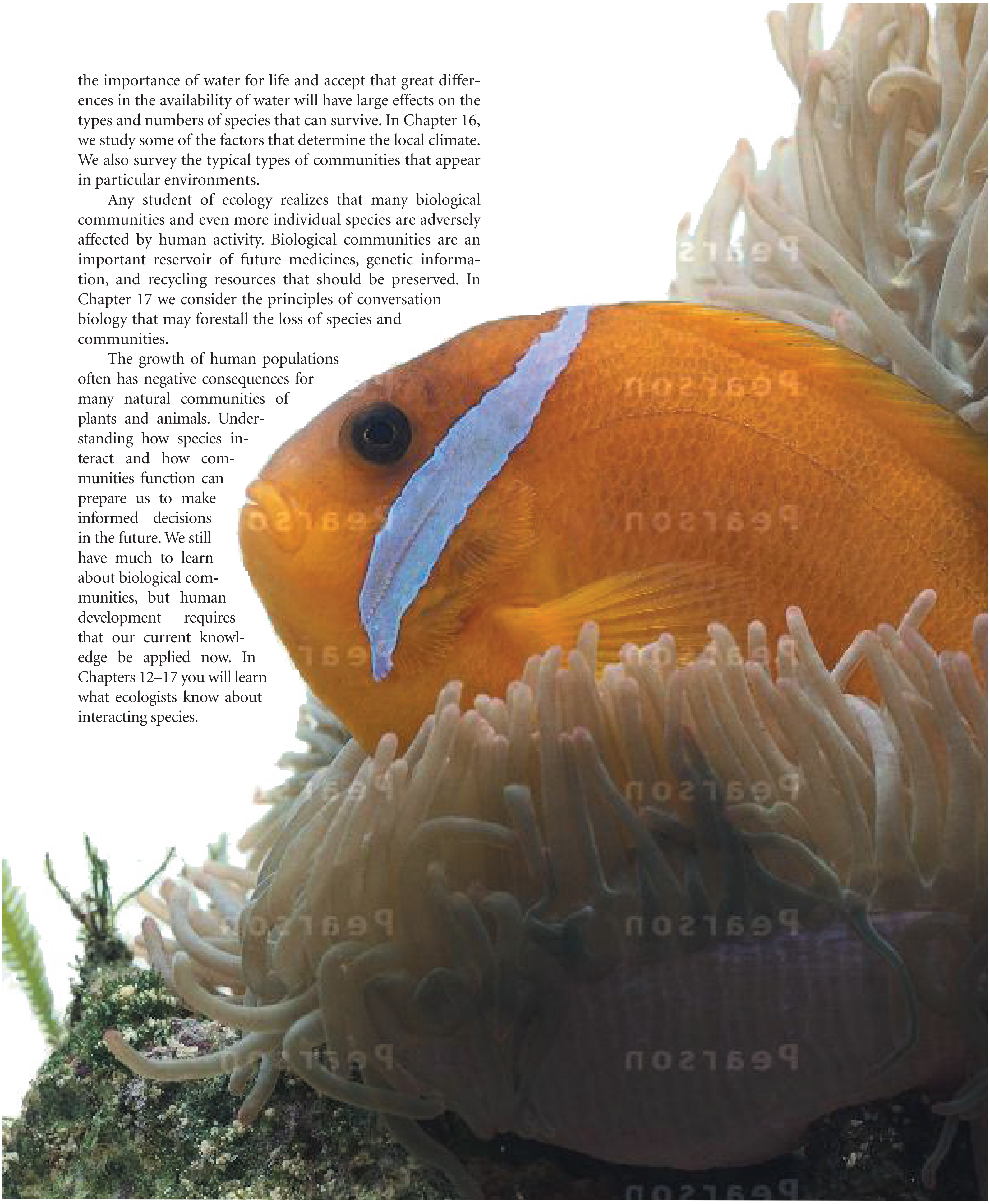
Parasites and hosts represent another important feeding relationship. These interactions are determined both by the adaptations of parasites that overcome host defenses and by the adaptations of the host to resist parasites. In Chapter 14 we consider the coevolution of host-parasite systems. Chapter 14 also introduces the notion that species can interact in a way that mutually benefits each species. Because different species by definition have independent evolutionary histories, understanding the development of mutualistic interactions is a major challenge for evolutionary biology.

When you walk through a forest or field, you see many plants and animals, not just pairs of predators and prey. This ensemble of organisms is called a community. Its members interact in many overt and subtle ways. In Chapter 15, we consider the relationship of community members from several different perspectives. One common thread is energy. Through the feeding relationships of community members, energy flows from plants that fix energy from the sun, up through multiple levels of animals that either feed on plants or feed on other animals. In addition to energy, organisms require nitrogen, water, and carbon. The complex interactions between the environment and the biological community that cycle these nutrients are also examined in Chapter 15.

The local physical environment affects many characteristics of biological communities. We are not surprised by the very different appearance of the flora and fauna in the desert compared with those in a tropical rain forest. We recognize the importance of water for life and accept that great differences in the availability of water will have large effects on the types and numbers of species that can survive. In Chapter 16, we study some of the factors that determine the local climate. We also survey the typical types of communities that appear in particular environments.

Any student of ecology realizes that many biological communities and even more individual species are adversely affected by human activity. Biological communities are an important reservoir of future medicines, genetic information, and recycling resources that should be preserved. In Chapter 17 we consider the principles of conversation biology that may forestall the loss of species and communities.

The growth of human populations often has negative consequences for many natural communities of plants and animals. Understanding how species interact and how communities function can prepare us to make informed decisions in the future. We still have much to learn about biological communities, but human development requires that our current knowledge be applied now. In Chapters 12–17 you will learn what ecologists know about interacting species.



Sea gulls competing for food

12

Competition

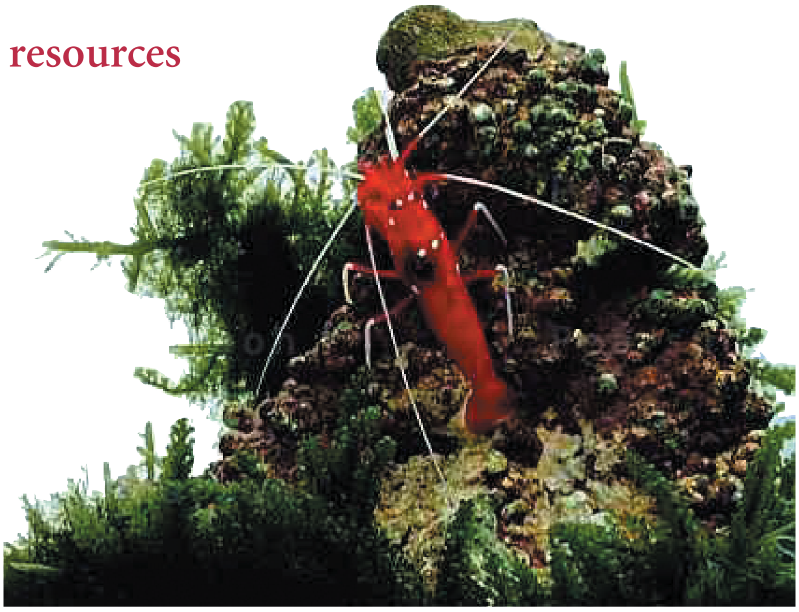
The recognition of competition as an important biological process dates back to Darwin. In his *Origin of Species*, Darwin emphasized a struggle for existence that hinges on the presumption that not all individuals can be supported by the existing resources. For Darwin the competition between individuals was the mechanism that led to adaptive traits increasing within a species. Much of the early work on competition was in fact motivated by Darwin's ideas.

In 1934 the great Russian ecologist G. F. Gause presented much of his experimental work on competition between species of protozoans in a book entitled *The Struggle for Existence*. It is clear from reading Gause that he believed research into the mechanisms of competition was critical for an understanding of Darwin's theory of evolution. As our understanding of natural selection and ecology has progressed, our ideas about competition have changed, but competition remains an important process in ecology.

Although the role of competition in natural selection is still considered vital, ecologists recognize that competition between species may be an important factor affecting the abundance and distribution of a species. In this chapter we will review some of the ways that plants and animals compete for essential resources. We will also see that competition may be a mechanism that explains how some species are able to coexist while others are not. Natural selection is also important in this chapter. We find that some circumstances favor the increase in competitive ability, and others favor the evolution of traits that will reduce the levels of competition. ❖

THE ECOLOGICAL AND EVOLUTIONARY PROCESS OF COMPETITION

12.1 Plants and animals compete for resources



Competition between individuals is an inevitable consequence of increasing population size and limited resources. **Competition** is an interaction between individuals of the same species—or two or more species—that reduces survival, fertility, or both. Discussions of competition typically distinguish competition between individuals of the same species, known as **intraspecific competition**, and competition between individuals of different species, known as **interspecific competition**. For closely related species, the limiting resources and mechanisms that give rise to interspecific competition may be quite similar to those involved with intraspecific competition.

There is one important difference between these two types of competition. Interspecific competition may be reduced or completely eliminated when one species evolves traits that effectively prevent the two species from competing for common resources. But this does not happen in intraspecific competition. For sexually reproducing species, at least, different individuals tend to require the same resources and utilize the environment in a similar fashion, so ultimately they are unable to avoid competing with members of their own species. Asexual organisms, such as bacteria, may produce clones that become genetically differentiated to the point where their resource utilization results in little competition. It is not uncommon, however, for such differentiated clones to be classified as different species.

While it is impossible to classify all mechanisms of competition into two categories, the ecological literature refers to two major categories of competition. **Contest competition** (Figure 12.1A) refers to the ability of some individuals to monopolize a particular resource in short supply. For many animals, competition for space or territories would be considered a type of contest competition. Animals may go through ritualized behavior that determines a dominance hierarchy and ultimately who will posses certain important resources. An important outcome of contest competition is that the distribution of resources is very uneven. Some individuals may get sufficient resources while others get none.

Scramble competition (Figure 12.1A) occurs when all individuals have access to the limiting resource and their acquisition is like a free-for-all. Some individuals may still get more resources than others because they differ in behaviors or morphologies that are important for resource acquisition. However, individuals are not able to sequester or monopolize resources when competition occurs by a scramble process. To use a concrete analogy, imagine the dinner meal at a prestigious but anonymous private boys' school in England.

The competition for water and nutrients between these trees is an example of scramble competition. No one tree can monopolize the resource, rather the amount of resource obtained by each tree will depend on the surface area of its roots and other factors. This picture also illustrates the local neighbor concept of plant competition.

Both the spotted hyenas and vultures are interested in the dead zebra. This leads to a direct conflict or contest for the resource. The hyena will most likely be able to monopolize this resource.

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Male red-winged blackbirds also engage in a contest competition for space. A male defends a particular piece of territory that will be used for foraging and will be important for attracting mates. Males with especially good territories may have several females nest there and thus will father many more offspring than will males with inferior or no territory.

FIGURE 12.1A **Different Types of Competition**

The rules of the school are that no second helpings are permitted until the boy has finished his first helping. The catch is that there is never enough food for all to have second helpings. In this competition, the winners are those that get a solid grasp on the fork during grace and chew as little as possible. An important lesson here is that success in competition comes with a price—indigestion.

Basic biological differences between plants and animals result in differences in the process of competition. Following are some important basic differences between plants and animals:

1. *Plants are sedentary.* Consequently, the distance over which competitive interactions occur is fixed and usually smaller than for a similarly sized animal. An important factor in plant competition is an individual plant's immediate neighbors, rather than the size of the total population.
2. *Tremendous size variation in plants.* The size and growth of plants can vary dramatically, depending on levels of nutrition, sun, and water. Thus, when assessing the competitive interactions of plants, the number and size of competitors will be important. Animals also vary in size, although the range of variation is typically not as great as in plants.
3. *Competition for common resources.* Most species of plants require the same essential resources for growth: light, water, and nutrients. These common requirements imply that competition ought to be more common among a wider variety of plant species. While there are some important differences between some plant species (for instance, certain plants that can fix nitrogen from the atmosphere as opposed to absorbing it from soil nutrients), we expect that plants will often compete for the same essential nutrients.

Our examples of competition and the definitions of scramble and contest competition suggest that in general, competing species exert a negative effect on the growth and reproduction of another species. However, theoretical ecologists Robert Holt and John Lawton described situations in which two species might have a negative effect on each other, even though they do not compete in a direct sense as we have defined it. Holt and Lawton called these situations **apparent competition**.

As an example, consider two animal species that are prey for a common predator. Or consider two plant species eaten by a common herbivore. Suppose one of the prey species increases significantly in number. This may ultimately increase the numbers of predators. Now the predators may increase their rate of attack on the second prey species, obviously having a negative impact on them. In this way, the increase of the first prey species indirectly has a negative impact on the second prey species.

Although apparent competition is an interesting phenomenon, in this chapter we will focus on examples of direct competitive interactions.

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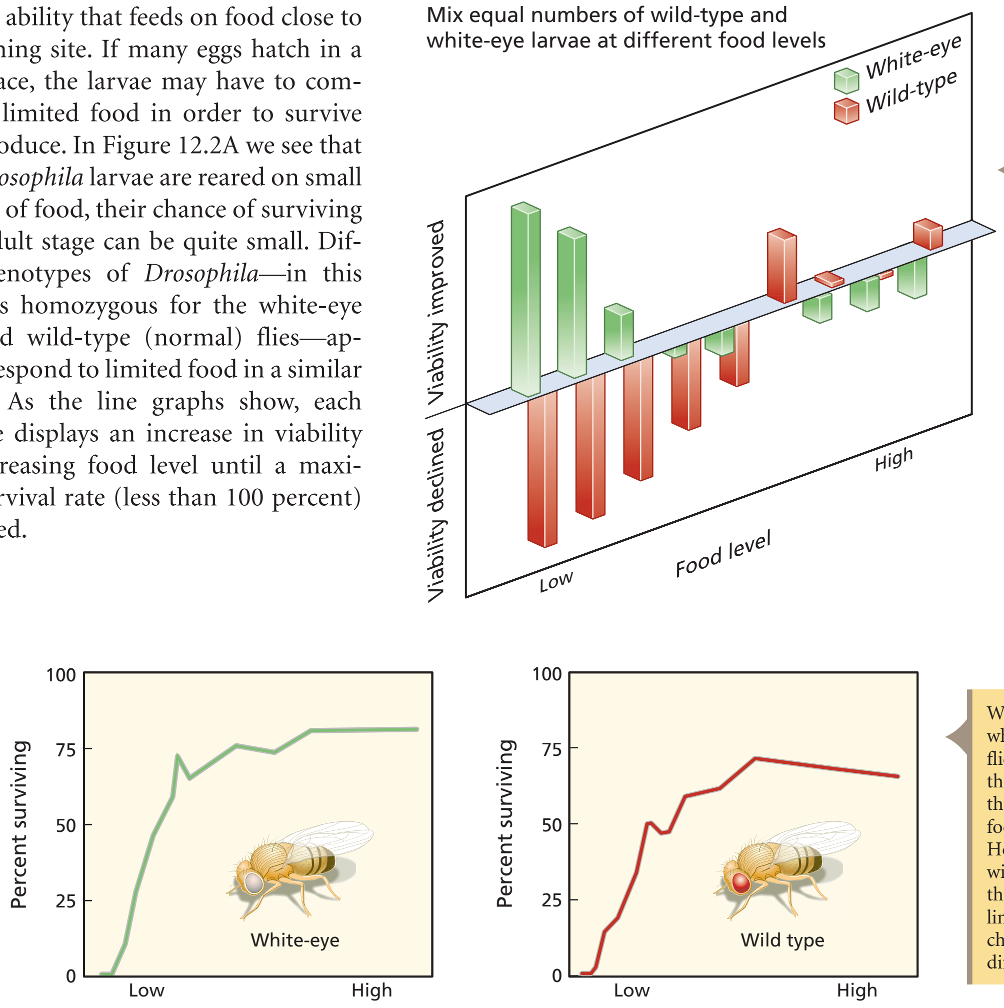
12.2 Competition for resources between individuals affects fitness

Competition is ecologically important because it is caused by resource limitation. Competition is important to evolution because the ability to obtain adequate resources affects fitness. Fitness may be affected due to changes in survival, fertility, or both. As we will see, the connection between competitive ability and fitness means that genetically based differences in competitive ability can result in the evolution of increased competitive ability.

The exact nature of the competitive process often depends on the details of how a particular organism makes its living. For example, many insects, such as fruit flies, have a larval stage with limited dispersal ability that feeds on food close to the hatching site. If many eggs hatch in a small space, the larvae may have to compete for limited food in order to survive and reproduce. In Figure 12.2A we see that when *Drosophila* larvae are reared on small amounts of food, their chance of surviving to the adult stage can be quite small. Different genotypes of *Drosophila*—in this case, flies homozygous for the white-eye allele and wild-type (normal) flies—appear to respond to limited food in a similar manner. As the line graphs show, each genotype displays an increase in viability with increasing food level until a maximum survival rate (less than 100 percent) is achieved.

What happens when white-eye larvae and wild-type larvae are put together so they compete with each other, at least when food levels are limited? At low food levels, the chance that a white-eye larvae will survive is much greater when it is competing with wild-type larvae than when it competes with other white-eye larvae, as the bar graph at the bottom of Figure 12.2A reveals. This is a direct consequence of the fact that the white-eye larvae are better competitors and somehow manage to get a disproportionate amount of the food. Conversely, at low food levels the wild-type larvae suffer a



At low food levels, the white-eye larvae shows a pronounced increase in survival, while the wild-type larvae show a pronounced decline in survival.

When larvae from either the white-eye or the wild-type flies are raised separately, their chances of surviving to the adult stage at different food levels are similar. However, if white-eye and wild-type are raised together, they will compete for the limited food and their chances of surviving will be different.

FIGURE 12.2A **Food levels affect egg-to-adult viability in *Drosophila***

reduction in their chances of surviving when they compete against the white-eye larvae. These wild-type larvae are poor competitors. In these competitive circumstances, the white-eye larvae have greater fitness relative to the wild type due to their relative increase in viability.

How do *Drosophila* larvae compete? In fact, the competitive process here is a simple case of scramble competition. *Drosophila* larvae cannot monopolize resources; but they simply eat the food as fast as possible, before it is all gone. In Figure 12.2B we see that when raised in isolation from each other, the wild-type and white-eye larvae can produce about the same number of surviving larvae as they consume their food. The only difference is that the white-eye larvae consume the food much faster. When the larvae are placed together, the elevated feeding rate of the white-eye larvae gives them an advantage, and they are able to consume a disproportionate amount of the food and thus enjoy an increase in viability.

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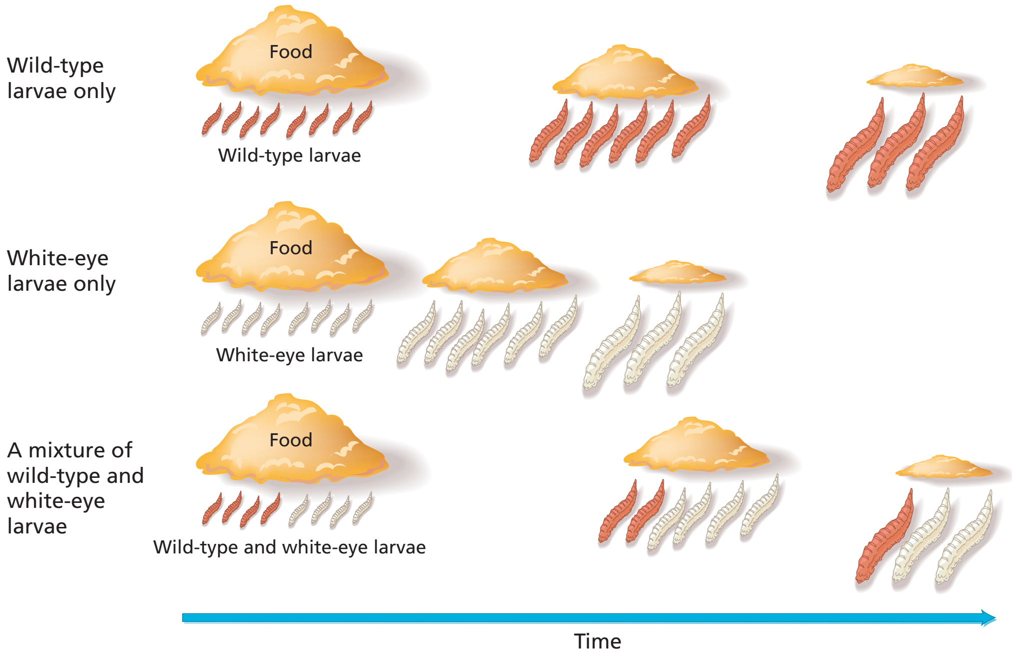

FIGURE 12.2B **The Mechanism of Competition in *Drosophila***

12.3 Plant competition for limited resources may lead to stable coexistence

We have considered one example of how animals compete for food, but how do plants compete for resources? Many resources may limit plant growth in different environments. Some of these resources include water, light, and nutrients such as nitrogen and phosphorus. Some resources, like water and nutrients, are in a constant state of flux. Natural processes such as rainfall and decomposition add these resources back to the local plant environment. As plants grow, they remove these resources, and the level available to all plants is decreased. One way to understand plant competition is by focusing on the dynamics of resource utilization and production. Let's look at plant competition by using graphs to visualize these dynamics.

What happens when two plant species compete in the same environment?

In Figure 12.3A, we consider how plant growth is regulated by the available nutrients. Growth rates increase as nutrient levels increase. At the same time, individual plants lose biomass due to herbivores and other factors. This rate of loss must at least be equaled by growth if the plant is to survive. This leads to the first conclusion: A minimum level of resource is required to sustain a viable population. In Figure 12.3B we show that in fact, more than one essential resource may determine a plant's fate.

Next, we suppose that in an environment with sufficient resources to maintain growth, plants will grow until they drive the resource levels down to a point where plant growth just balances loss of biomass. In Figure 12.3C this

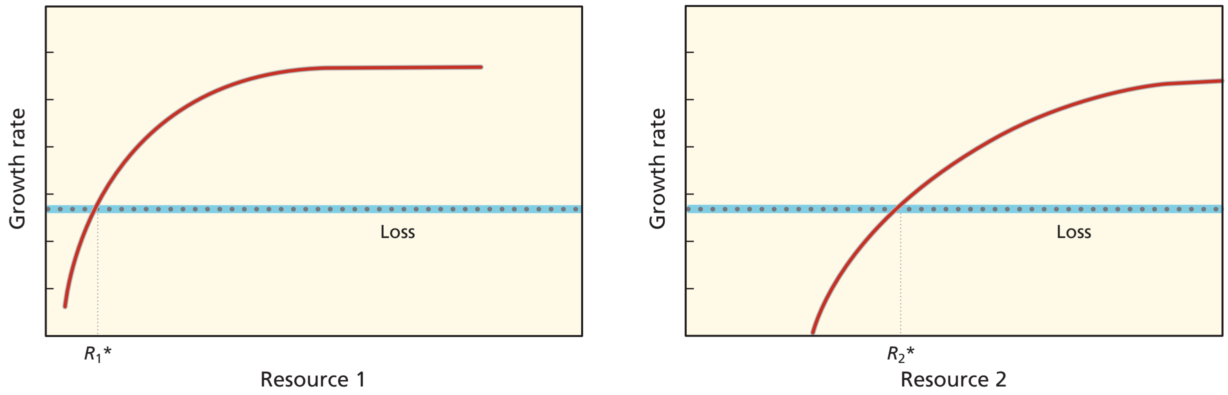

FIGURE 12.3A Plant Competition for Limited Resources An individual plant's growth rate increases with increasing resource level. Loss of biomass is due to herbivores, seed predators, and environmental disturbance. An equilibrium plant biomass is reached when the growth rate equals the loss rate. For resource 1 and resource 2, this occurs at the starred values, R_1^* and R_2^*.

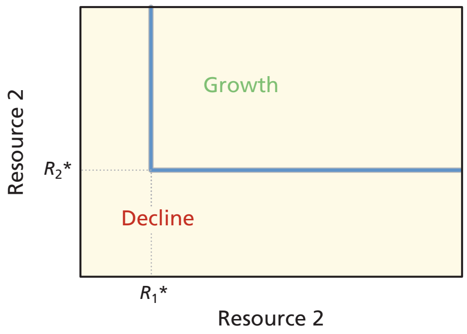

FIGURE 12.3B Plant Competition for Limited Resources We can illustrate the combinations of resource 1 and resource 2 that result in sustained growth (green), sustained decline (red), or no net growth (blue lines).

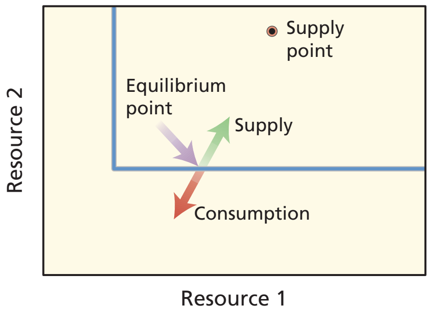

FIGURE 12.3C Plant Competition for Limited Resources Resources are continually added to the environment. The supply point represents the level of resources 1 and 2 in the absence of plants. Renewal of resources is indicated by the green vector and will always point toward the supply point. The point on the blue line where the plant's rates of consumption (red vector) are exactly opposite the green vector represents the equilibrium level of resources.

equilibrium is represented by the point on the blue line where the two vectors (arrows)—plant resource consumption (red arrow) and environmental resource supply (green arrow)—point in opposite directions.

Finally, different environments can be represented by different rates of resource renewal. In Figure 12.3D, environment A results in relatively high levels of resource 2 and low levels of resource 1 at equilibrium, as compared with the resources for environment C.

What happens when two plant species compete in the same environment? Two different species will never have exactly the same resource requirements. Figure 12.3E shows the equilibrium resource curves for two different species of plants, called S_1 and S_2. We see that S_1 requires more of resource 2 and less of resource 1 to maintain a viable population compared with S_2. We also see that the consumption vector of S_1 is close to a vertical line, indicating a high rate of consuming resource 2. Since S_1 requires more of resource 2 to live than S_2 does, we conclude that S_1's high rate of consumption of resource 2 has a greater impact on its own species than it does on species S_2. In a similar fashion, we see that the consumption vector of S_2 is close to a horizontal line, indicating a high rate of resource-1 consumption. Again, this should have a greater impact on other members of S_2 than on members of species S_1. These relationships imply that both species exhibit higher levels of intraspecific competition than interspecific competition, and this ultimately permits both species to coexist if the supply point is in the wedge-shaped region indicated in Figure 12.3E.

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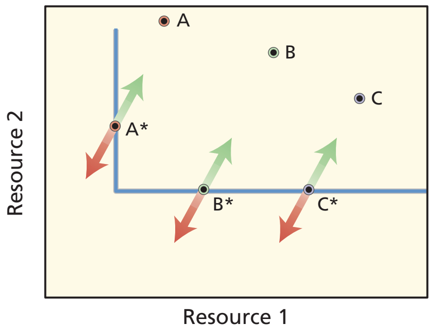


FIGURE 12.3D Plant Competition for Limited Resources Three different environments are represented by three different supply points (A, B, C). The consumption by plants is assumed to be the same. The result is that three different equilibrium levels of resources are reached (A^*, B^*, C^*) in each environment.

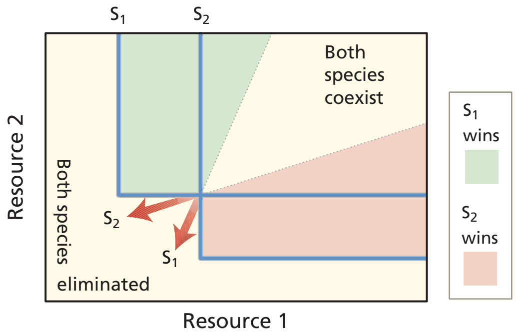
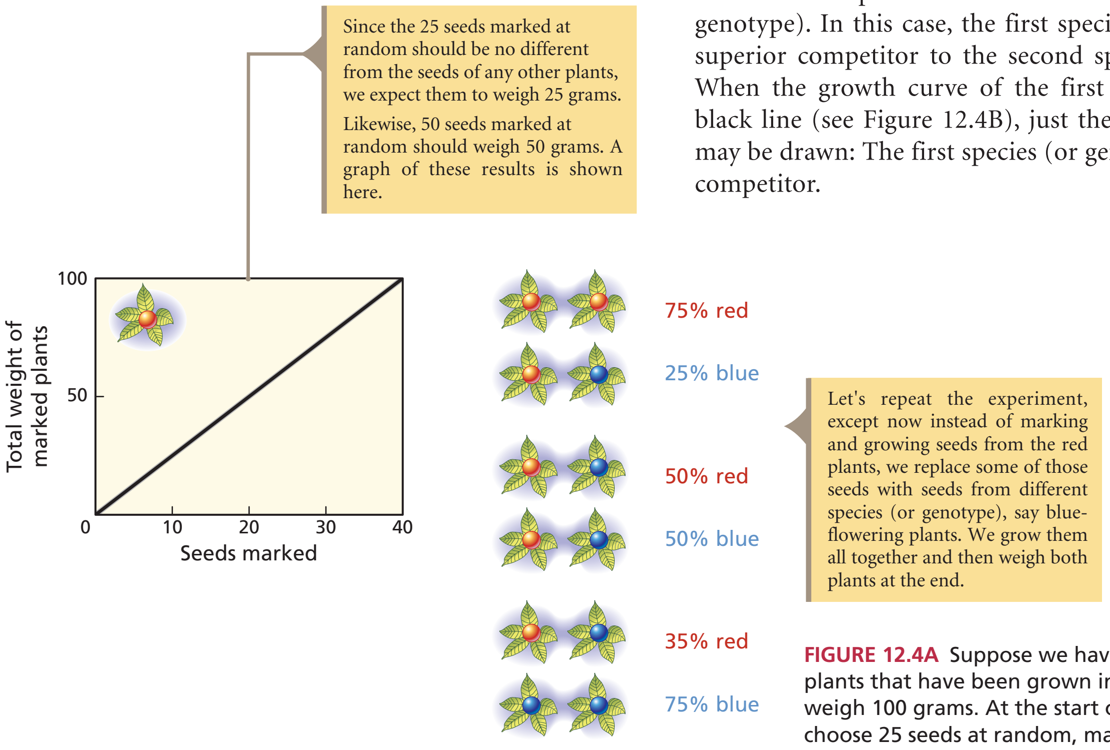


FIGURE 12.3E Two-Species Competition In this figure the equilibrium growth lines for two species, S_1 and S_2, are shown as blue lines. The consumption rates for each species are also shown as red vectors. If the supply point of the environment falls in the green region, S_1 reduces resource 1 to a level where S_2 cannot exist. Just the reverse happens if the supply point is in the dotted region. The wedge-shaped blank area indicates the range of environments where the two species can coexist.

12.4 Belowground plant structures compete for microorganisms, water, and essential nutrients

In some ways it is easier to study competition by observing plants rather than animals. Because plants do not move, they can be placed in close proximity to each other, and nutrients and water they need to grow can be carefully distributed. One technique for estimating competitive ability in plants was developed by de Wit and is illustrated in Figures 12.4A and 12.4B. The technique is based on measuring some characteristic that should indicate the severity of competition, such as plant weight. The total number of plants placed in competition determines the overall level of competition. If we keep the total number constant but vary the relative proportions of competing species (or genotypes), then relative competitive ability can be inferred.

If total weight of one species changes in direct proportion to its relative frequency (black lines on the graphs in Figures 12.4A and 12.4B), then there is no difference between the presence of the alternative species (or genotype), and the two species (or genotypes) are competitively equivalent. When the growth curve (red line) is above the black line (see Figure 12.4B), it indicates that the first species (or genotype) gains weight faster in the presence of a competitor than in the presence of members of the same species (or genotype). In this case, the first species (or genotype) is a superior competitor to the second species (or genotype). When the growth curve of the first species is below the black line (see Figure 12.4B), just the opposite conclusion may be drawn: The first species (or genotype) is an inferior competitor.



Since the 25 seeds marked at random should be no different from the seeds of any other plants, we expect them to weigh 25 grams.

Likewise, 50 seeds marked at random should weigh 50 grams. A graph of these results is shown here.

Let's repeat the experiment, except now instead of marking and growing seeds from the red plants, we replace some of those seeds with seeds from different species (or genotype), say blue-flowering plants. We grow them all together and then weigh both plants at the end.

FIGURE 12.4A Suppose we have 100 red-flowering plants that have been grown in a common area and weigh 100 grams. At the start of this experiment, we choose 25 seeds at random, mark them, and weigh the resulting plants at the end of the experiment. How much would the plants be expected to weigh?

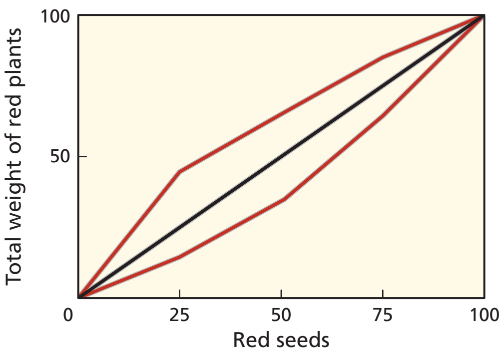
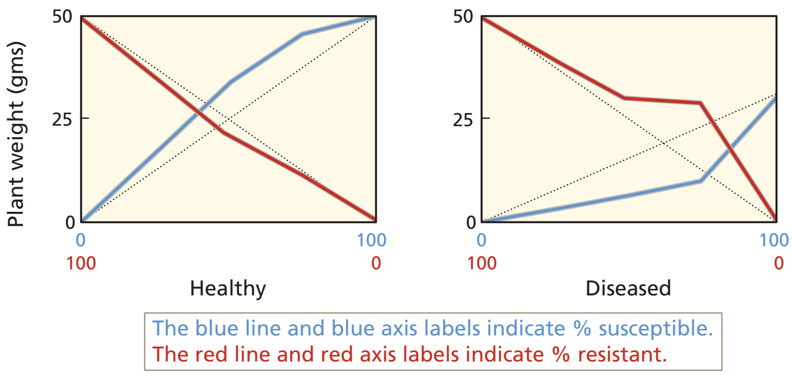


FIGURE 12.4B What's the outcome of the experiment in Figure 12.4A? This figure shows two possible outcomes from the experiment. If the red line is above the black line, then the red plants are better competitors than the blue plants. If the red line is below the black line, the red plants are inferior competitors to the blue plants.

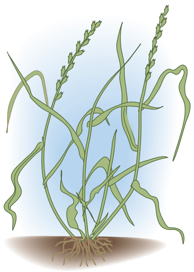
Plants interact with a variety of fungi. In some cases these interactions are beneficial to the plant, and in other cases the fungi are pathogens. Rust fungi are pathogens to many plants, and occasionally plants develop a genetically based resistance to the rust. Burdon and his colleagues studied two genotypes of the skeleton weed, one resistant to rust and the other susceptible (see Figure 12.4C). When the plants were not exposed to rust, the susceptible genotype revealed a slight competitive advantage. However, if both genotypes were exposed to rust during their growth, the resistant genotype had a tremendous advantage in competitive situations.

Mycorrhizae are fungi that infect the roots of many plants and often increase the ability of the plant roots to absorb nutrients such as phosphorus and potassium. The presence of mycorrhizae may significantly affect the outcome of competition. In one experiment, two different species of plants were raised under competitive conditions with and without inoculations of mycorrhizal fungi (see Figure 12.4D). In the absence of mycorrhizae, an index of competitive ability showed little difference between the two plants. However, with mycorrhizae, one plant (*Holcus*) demonstrated a clear competitive advantage. ❖




Skeleton weed, *Chondrilla juncea*

FIGURE 12.4C Competition between Different Genotypes Burdon competed two genotypes of skeleton weed. One genotype was susceptible to a rust fungus, the other was resistant. When both plants were healthy, the susceptible type is a better competitor. Not surprisingly, when both plants are exposed to the fungus, the resistant genotype is a much better competitor.


Lolium perenne
Perennial rye grass


Holcus lanatus
Velvet grass

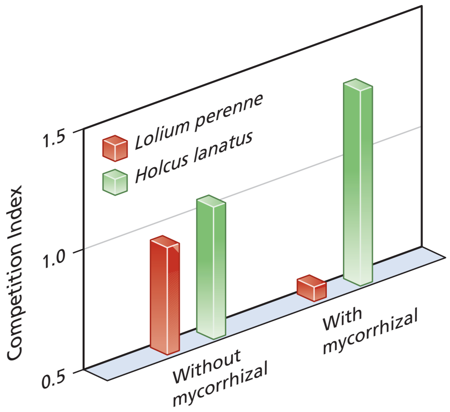


FIGURE 12.4D *Lolium* and *Holcus*, when planted together, compete for phosphorus and potassium uptake through their roots. Inoculating the roots with mycorrhizal fungi increases the competitive ability of *Holcus* for these limiting nutrients.

12.5 Intraspecific competitive ability responds to natural selection

Is competitive ability affected by natural selection? Two important attributes of competitive ability suggest that it is. First, relative competitive ability affects survival and thus fitness. Any genetically based trait that improves competitive ability will increase the fitness of its carriers. Secondly, there appears to be genetically based variation for competitive ability, at least in fruit flies.

> *Note that an important feature of experiments in evolutionary ecology is the replication of whole populations.*

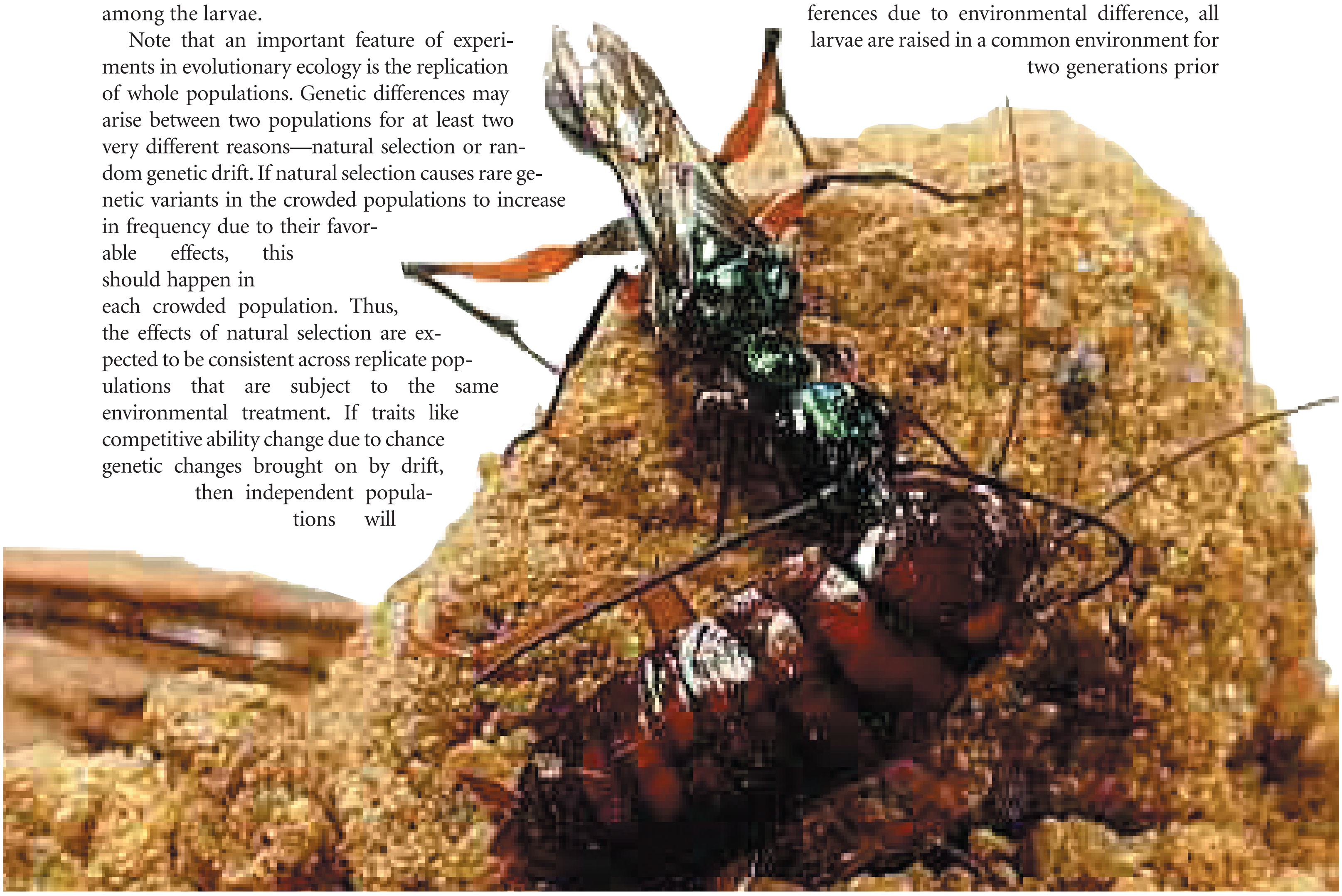
To test whether competitive ability responds to natural selection, it would seem best to place one population in an environment where competitive ability is at a premium. This can be accomplished by crowding individuals so the level of food resources per individual is low. A control would consist of similar populations in an environment with abundant resources.

Figure 12.5A outlines an experiment with fruit flies using three replicate experimental populations (*K*'s) where adults and larvae were extremely crowded. The control populations (*r*'s) had abundant food resources, especially among the larvae.

Note that an important feature of experiments in evolutionary ecology is the replication of whole populations. Genetic differences may arise between two populations for at least two very different reasons—natural selection or random genetic drift. If natural selection causes rare genetic variants in the crowded populations to increase in frequency due to their favorable effects, this should happen in each crowded population. Thus, the effects of natural selection are expected to be consistent across replicate populations that are subject to the same environmental treatment. If traits like competitive ability change due to chance genetic changes brought on by drift, then independent populations will not necessarily change in the same fashion. If the experiment used only one experimental population and one control population, we could never determine if genetically based differences that arise over time are due to selection or drift. Replication is essential.

After many generations of evolution in the *r*- and *K*-environments, the competitive ability of larvae from these populations was measured (using the technique illustrated in Section 12.2) For each set of populations, competitive ability was greater in the populations that evolved with scarce resources (*K*'s) than in their controls (*r*'s). As expected, the populations that have adapted to scarce resources have improved competitive ability.

How do we know that the differences between the *r*- and *K*-populations are genetically based? It is certainly possible for phenotypic differences to arise due to environmental differences. For instance, larvae in crowded cultures typically grow slowly and are smaller compared to larvae raised in uncrowded environments. To eliminate phenotypic differences due to environmental difference, all larvae are raised in a common environment for two generations prior



to the measurement of competitive ability. Why two generations? If this was done for just one generation, then the larvae to be tested would come from eggs that might have different levels of nutritional resources because their mothers came from the two very different environments. To eliminate the possibility of this type of *maternal effect*, larvae are raised in a common environment for two consecutive generations.

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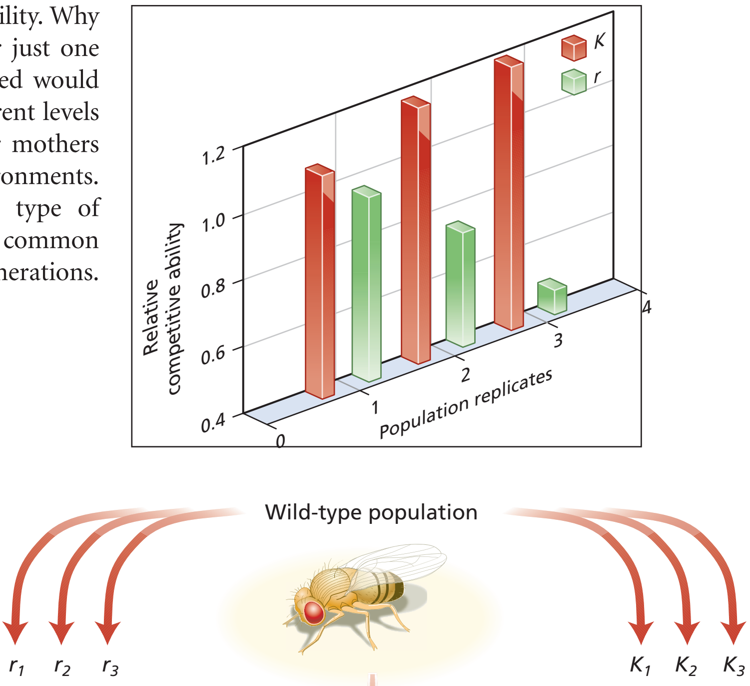


Six replicate populations were created from a single source population. Replicate populations are used to aid in sorting out genetic changes due to natural selection vs. those due to random genetic drift.

One group of populations, called *r*'s, were kept at low adult and larval densities and served as controls. The other group, called *K*'s were kept at high larval and adult densities. Food was especially scarce for the growing larvae.

After 128 generations in these environments, larval competitive ability for food was measured. Prior to these measurements the *r*- and *K*-populations were cultured for two generations in a common environment. The common environment for the first generation should remove any effects that the different densities may cause. However, since the mothers of the first generation may produce eggs that are affected by their density environment, a second generation is used to remove these maternal effects.

FIGURE 12.5A **Evolution of Competitive Ability**

Alexander J. Nicholson (1895–1969)

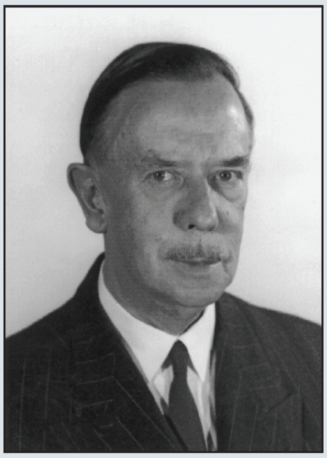


FIGURE 12.5B
Alexander J. Nicholson

A. J. Nicholson (Figure 12.5B) was an Australian entomologist with interests in host-parasite models, population regulation, and experimental population ecology. Nicholson was a strong proponent of the use of theoretical models in ecology. Nicholson thought that ecology would advance through the combination of observations of nature, model construction, and experiments.

In 1935, with physicist Victor A. Bailey, Nicholson published an important paper that developed host-parasite models that are still referred to today. A central concern of Nicholson's was to describe the forces that regulate population numbers. He became convinced that intraspecific competition was one of the most important factors regulating populations. In his writings he coined the terms *contest* and *scramble* competition to distinguish between territorial and nonterritorial animals.

Nicholson also carried out some of the most extensive laboratory experiments with populations of blowflies (*Lucilia cuprina*). Under his culture techniques, these blowflies produced dramatic cycles in population numbers. These blowfly data are still the subject of theoretical analysis 50 years later.

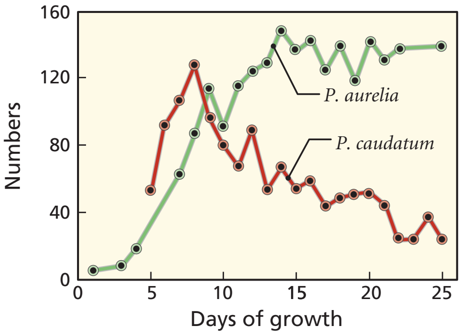
THE CONSEQUENCES OF COMPETITION

12.6 Gause developed his competitive exclusion principle from experiments with *Paramecium*

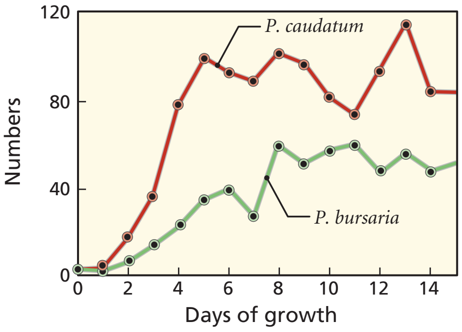
In the previous module we reviewed the effects of competition on survival of individuals of the same species as well as on individuals of different species. What would happen to the distribution and abundance of two competing species if they competed over a prolonged period of time? Several answers seem plausible. (1) While negative competitive effects may reduce the numbers of each species, they may nevertheless coexist indefinitely. (2) The effects of competition on survival may be so severe that one or perhaps both species would go extinct over time. (3) For many animal species that are mobile, one species may simply leave the area in which competition occurs to avoid the negative effects. In this module we will see that ecological theory may help us answer these questions.

The outcome of two-species competition has been studied carefully in the laboratory as far back as the 1930s. In 1934 George F. Gause published an account of these experiments in his historic book, *The Struggle for Existence*. In these experiments, Gause utilized small ecosystems, called microcosms, to study competition between different species of unicellular organisms called *Paramecium*. In these simple microcosms, different species of *Paramecium* feed on a growing bacterial population.

Gause's experiments documented two of the possible consequences of competition we noted earlier. When *P. aurelia* and *P. cuadatum* were placed in the same culture, both populations initially increased in numbers. At first, when the densities of the two



In this experiment *P. caudatum* declines and eventually goes extinct due to the superior competitor, *P. aurelia*.



In this experiment both species *P. caudatum* and *P. bursaria* are able to stably coexist.

FIGURE 12.6A **Gause's Experiments**

species are low, there should be adequate resources for both species. However, when resources become limiting and competition ensues, we see in the first experiment (at top in Figure 12.6A) that the numbers of *P. caudatum* start to decrease, and *P. aurelia* continues to increase and eventually level off. Although not shown, *P. caudatum* is eventually driven to extinction.

In the second experiment shown in Figure 12.6A, *P. cuadatum* is raised with a third species, *P. bursaria*. In this case, both species increase in numbers and then level off. Both species are able to coexist despite the limited resources.

Gause noted that exclusion of one species often occurred between closely related species when they were placed in highly simplified environments. These simple environments essentially forced the two species to compete for exactly the same resources. The simple environment also prevented the two species from moving and avoiding competition. This finding led Gause to propose that no two species can coexist if they use the environment in precisely the same fashion. This prediction is sometimes called the **competitive exclusion principle**.

Gause's proposal implies that a key to understanding the consequences of competition is to know the various resource and habitat requirements of a species. A description of all such requirements for a species is sometimes called the **ecological niche**. In this final section of the chapter, we will explore in more detail the concept and evaluation of ecological niches. The important connection we wish to make here is the relationship between the consequences of competition and the idea of an ecological niche.

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12.7 Interspecific competition affects population dynamics

The logistic model of population growth, discussed in Chapter 10, summarizes the impact of intraspecific competition on population dynamics. Competition between individuals of the same species results in declining survival and fertility. Similar effects may follow from competition between different species. The population dynamic consequences of interspecific competition can be studied with the **Lotka-Volterra model**.

In Figure 12.7A the Lotka-Volterra equation is developed following the same process used to derive the logistic equation in Chapter 10. In fact the Lotka-Volterra model looks just like the logistic equation, but with the addition of a term, $r_1\alpha_{12}N_t^{(2)}/K_1$, that reflects how population growth of species 1 is slowed by competing species 2.

The coefficient α_{12} is called the **competition coefficient**. It is a positive number that measures the effect of species 2 on the growth of species 1. If $\alpha_{12} = 1$, then each individual of species 2 has the same effect on the growth rate of species 1 as an individual from species 1. If $\alpha_{12} > 1$, then each member of species 2 has a more severe effect on the growth of species 1 than on their own members. If species 2 is a very weak competitor, then $\alpha_{12} < 1$. When $\alpha_{12} = 0$, species 2 has no effect on the growth of species 1.

The Lotka-Volterra equations can be used to study the outcome of competition. With two species there are three possible outcomes of competition: (1) Species 1 grows to its carrying capacity (K_1) and species 2 is eliminated (goes extinct). (2) Species 2 grows to its carrying capacity (K_2) and species 1 is eliminated. (3) Both species coexist at population sizes less than their carrying capacity. These different possibilities can be inferred from a graph that plots combinations of $N^{(1)}$ and $N^{(2)}$ that yield no growth of species 1 and species 2. Such a graph appears in Figure 12.7B.

For species 1, the blue line in the graph in Figure 12.7B illustrates these zero-growth combinations. The shape of this line is determined by using the equations in Figure 12.7A and finding values of $N^{(1)}$ and $N^{(2)}$ that make the expression in braces $\{\}$ equal to 1.0. When this term is equal to 1.0, then every individual of species 1 will just replace itself, leading to no net growth of the population. If $N^{(1)}$ and $N^{(2)}$ are below the blue line, then $N^{(1)}$ will increase. For population size combinations above the line, $N^{(1)}$ decreases. ❖

$$N_{t+1}^{(1)} = \lambda(N_t^{(1)}, N_t^{(2)})N_t^{(1)}$$

This equation looks similar to the equation for the basic model of growth except there are now superscripts next to the N's. These refer to the two different species under study. So $N^{(1)}$ will be the number of species 1 and $N^{(2)}$ the numbers of species 2.

Population growth for species 1

$$N_{t+1}^{(1)} = \left\{\underbrace{1 + r_1 - \frac{r_1 N_t^{(1)}}{K_2}} - \frac{r_1\alpha_{12}N_t^{(2)}}{K_2}\right\}N_t^{(1)}$$

This is the usual logistic part of the reproductive rate.

This term reflects the effects of competition. The net reproductive rate of species 1 declines as the density of species 1 declines as the density of species 2 increases and as the competitive effect of species 2 on species 1 (α_{12}) increases.

Population growth for species 2

$$N_{t+1}^{(2)} = \left\{1 + r_2 - \frac{r_2 N_t^{(2)}}{K_2} - \frac{r_2\alpha_{21}N_t^{(2)}}{K_2}\right\}N_t^{(2)}$$

This equation for species 2 looks exactly like that for species 1 except every 1 has been replaced by a 2, and vice versa.

FIGURE 12.7A The Lotka-Volterra Competition Model In the Lotka-Volterra model the net reproductive rate (λ) of each species depends not only on its density but also on the density of the competing species.

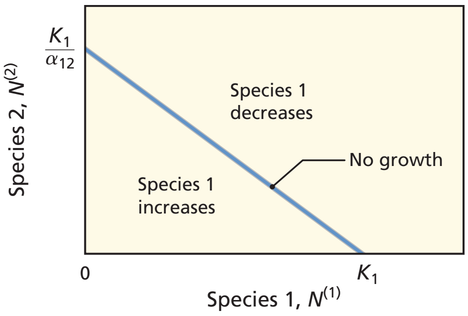

FIGURE 12.7B Find values of $N^{(1)}$ and $N^{(2)}$ that make the reproductive rate of species 1 exactly 1 (that is, where there is no net growth of species 1). The blue line represents combinations of $N^{(1)}$ and $N^{(2)}$ where there is no net growth of species 1. Combinations of $N^{(1)}$ and $N^{(2)}$ above the blue line result in species 1 decreasing in size. Combinations below the line permit species 1 to increase in numbers.

An Application of the Lotka-Volterra Equations

Suppose there are two competing species, and species 1 is characterized by the following parameter values:

intrinsic rate of increase, r_1: 1.2
carrying capacity, K_1: 1000
competition coefficient, α_{12}: 1.25

If $N_t^{(1)} = 500$ and $N_t^{(2)} = 900$, will $N_{t+1}^{(1)}$ be greater or smaller than 500? In other words, are the numbers of species 1 increasing or decreasing?

From Figure 12.7B we can infer that if $N_t^{(2)} > K_1/\alpha_{12}$, species 1 will be in the region where its population size decreases. Since $K_1/\alpha_{12} = 1000/1.25 = 800$, and $N_t^{(2)}$ is greater than this value, the number of individuals in the species 1 population will decrease in the next time interval.

12.8 The Lotka-Volterra model of competition predicts competitive exclusion or stable coexistence

What useful ecological predictions can we make from from the Lotka-Volterra model? How do these predictions match up with our intuition of competition? Figures 12.8A through 12.8C show three cases of interspecific competition. Each figure shows the lines describing no growth for both species 1 and species 2.

In Figure 12.8A we see that if population sizes of species 1 and species 2 fall below the red line, then both populations increase in size. If their population sizes are above the blue line, then both populations decrease in size. The interesting area in this figure is where the points fall between the red and blue lines. Here we are above the zero-growth line of species 2, so species 2 will decrease in size. However, we are below the zero-growth line of species 1, so species 1 will increase. The Lotka-Volterra dynamics will push the system into the area between the two lines, no matter where we start. (In other words, if we start with both populations increasing in size, they will eventually grow to the sizes represented by the area between the lines. If we start with both species decreasing, they will eventually shrink to sizes represented by the areas between the lines.) As a result, the numbers of species 2 dwindle down to zero, and species 1 increases to its carrying capacity.

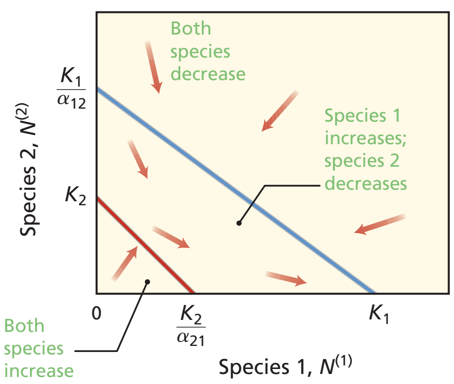

FIGURE 12.8A Predicted Outcome of Two-Species Competition: Species 1 Eliminates Species 2 In this and Figures 12.8B and 12.8C, the blue line is the no-growth curve for species 1 and the red line is the no-growth curve for species 2. The black arrows show the general direction of change in $N^{(1)}$ and $N^{(2)}$ from different starting points.

Why does this happen? It helps to look at the competition coefficients α for species 1 and species 2. If we examine the points at which the blue and red lines intercept the y- and x-axis in Figure 12.8A, we see that $K_1/\alpha_{12} > K_2$ and $K_1 > K_2/\alpha_{21}$. Let's assume the two carrying capacities are the same ($K_1 = K_2$), so then the inequalities are reduced to expressions that we can interpret: $1 > \alpha_{12}$ and $\alpha_{21} > 1$. Roughly speaking, this means that species 2 exerts a weak effect on species 1 (since $\alpha_{12} < 1$); in fact, its effect is less than the effect of species 1 on itself. (Recall from Section 12.7 that when the competition coefficient α equals 1, then members of the second species have the *same effect* on the growth of members of the first species as do other members of that first species.). Another way of saying this is that the interspecific competitive effects of species 2 on species 1 are weaker than the intraspecific competitive effects of species 1.

What about the effects of species 1? Species 1 is a strong competitor (since $\alpha_{21} > 1$) and reduces the growth rate of

species 2 more than species 2 individuals reduce their own growth rate. In other words, the interspecific competitive effects of species 1 on species 2 are stronger than the intraspecific competitive effects of species 2. Not surprisingly, the Lotka-Volterra equations are saying that if one species is a very strong competitor and the second is very weak, the strong competitor can drive the weak one to extinction. The meanings of *strong* and *weak* are made explicit by this theory.

Figure 12.8B shows the same process of competitive elimination of one species, but now species 2 is the superior competitor. See if you can derive relationships that the competition coefficients (α's) must satisfy, as we did earlier.

Figure 12.8C shows the very interesting case of coexistence of both species. Because we do find competing species coexisting in nature, it is important to understand the conditions under which this outcome is expected. If we again assume that $K_1 = K_2$, examination of Figure 12.8C reveals that $1 > \alpha_{12}$ and $1 > \alpha_{21}$. This condition suggests that both species exhibit levels of interspecific competition that are weaker than the levels of intraspecific competition. When interspecific competition is symmetrically attenuated in this fashion, both species may coexist.

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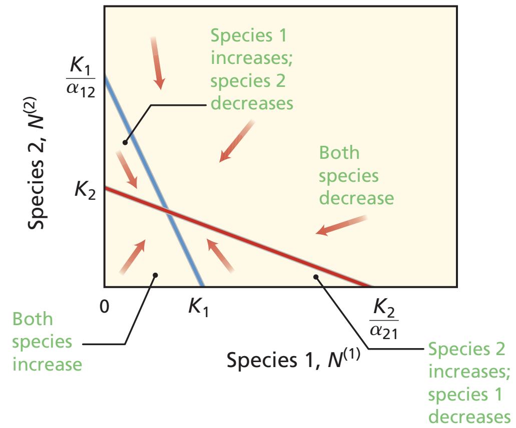
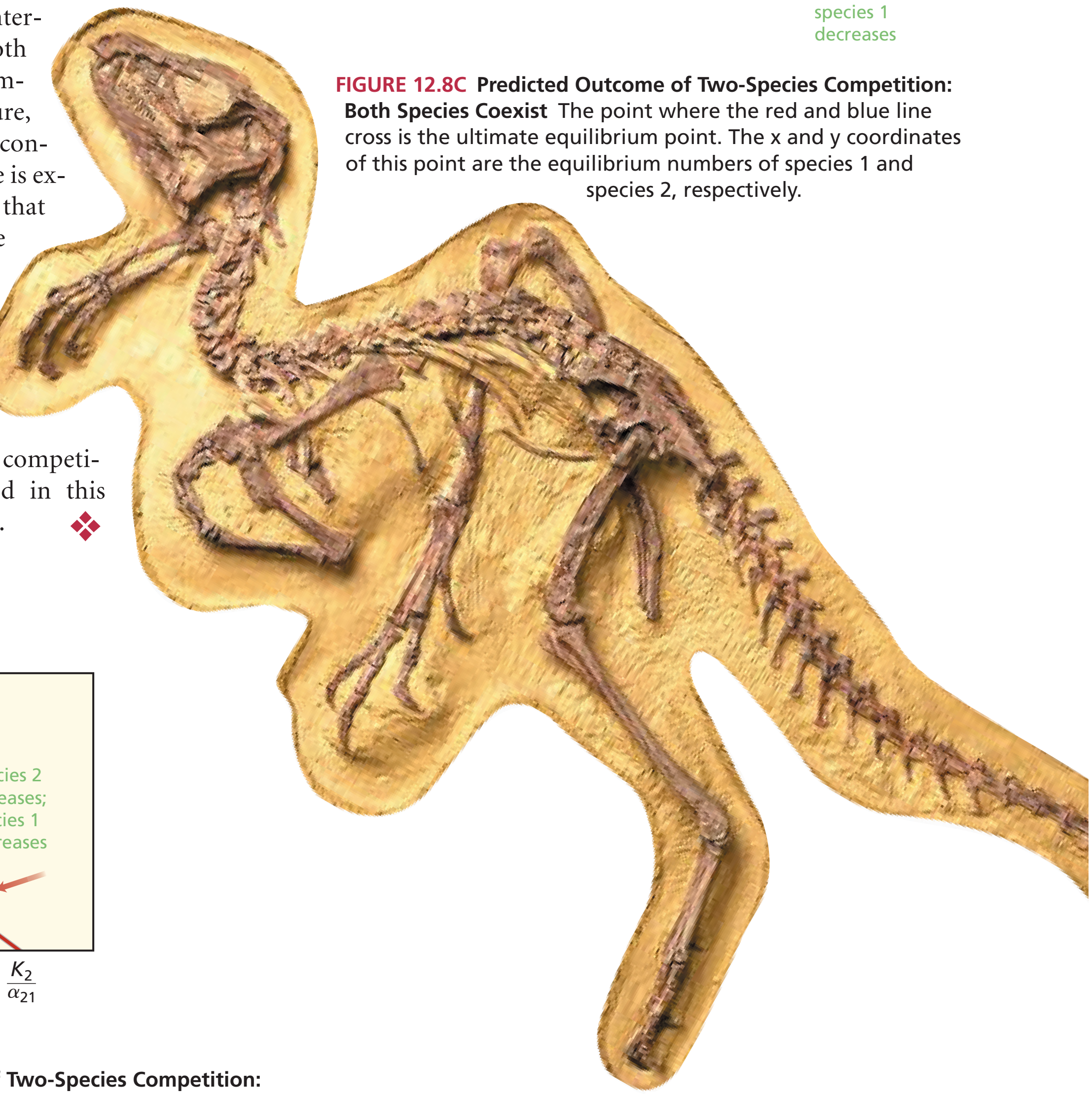


FIGURE 12.8C Predicted Outcome of Two-Species Competition: Both Species Coexist The point where the red and blue line cross is the ultimate equilibrium point. The x and y coordinates of this point are the equilibrium numbers of species 1 and species 2, respectively.



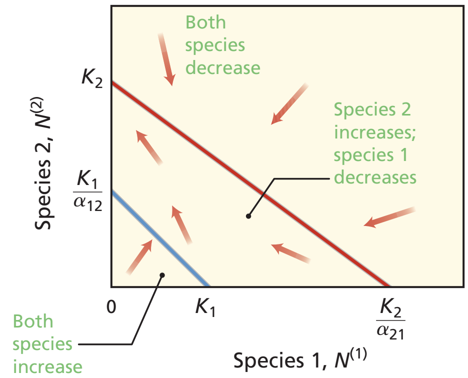


FIGURE 12.8B Predicted Outcome of Two-Species Competition: Species 2 Eliminates Species 1

Predicting the Outcome of Competition from the Lotka-Volterra Equations

Suppose two species grow according to the Lotka-Volterra competition equations and have the following parameter values:

K_1	K_2	α_{12}	α_{21}	K_1/α_{12}	K_2/α_{21}
1000	2000	0.4	1.6	2500	1250

What is the ultimate outcome of competition? By examination of Figures 12.8A through 12.8C, it is clear that the values of *r* do not affect the outcome of competition. We need to look at the ratios of the carrying capacities to the appropriate competition coefficient and compare these ratios to the carrying capacities. In this case we see that $K_1/\alpha_{12} > K_2$ and $K_1 < K_2/\alpha_{21}$. This corresponds to Figure 12.8C or stable coexistence of both species, as you can determine by looking at the carrying capacity and the ratio on each axis of the graph.

12.9 Competition affects the distribution of species

The Lotka-Volterra model of competition predicts the demise of a species in the presence of strong competition. Is there any way for a species to avoid such a fate? The predictions from the Lotka-Volterra model assume those two competing species are constrained to a physical environment where competition is unavoidable. Real organisms may not be constrained in this fashion. The negative effects of competition may be reduced or eliminated if the two species can avoid each other. Joseph Connell (1961) first demonstrated this response to competition for two species of barnacles on the coast of Scotland.

Chthamalus stellatus is found in the upper region of the intertidal zone that is most removed from the splash of waves and most exposed to air and sun. *Balanus balanoides* is found lower in the intertidal zone, less exposed to the drying conditions of air and sun. Both animals make their living by firmly attaching themselves to rock surfaces and then filtering food particles from the waves that splash over them. Observations of young settling barnacles showed that there is extensive overlap in the location of both species (Figure 12.9A). By the time the barnacles have become adults, however, there is very little overlap in the distribution of the two species (see figure).

Connell observed that when an individual *Balanus* came into contact with a neighboring *Chthamalus,* the *Balanus* barnacle shell would actually grow underneath the *Chthamalus* shell and dislodge it. In other instances *Balanus* would simply grow over the shell of *Chthamalus*. This appeared to be competition, but another possible explanation was that *Chthamalus* were weakened because they cannot live in this middle region of the intertidal zone, so the direct contact with and apparent removal of *Chthamalus* by *Balanus* was not the ultimate reason *Chthamalus* did not live there. Connell reasoned that he could directly test the effects of competition by physically removing *Balanus* from the middle of the intertidal range. *Chthamalus* larvae settled in the middle range, but would they persist in the absence of *Balanus*? Connell found that indeed they did. The absence of *Chthamalus* adults in the middle intertidal zone is a direct consequence of the competitive effects of *Balanus*. The environment in this middle range is perfectly suitable for *Chthamalus,* but competition restricts their distribution to the high end of the intertidal.

Balanus, on the other hand, is unable to persist in the high intertidal due to environmental conditions. The prolonged periods of exposure to air, wind, and sun require that plants and animals living in the high intertidal resist desiccation, or loss of water. *Balanus* is unable to survive in these conditions, and in effect provides *Chthamalus* with a refuge from competition.

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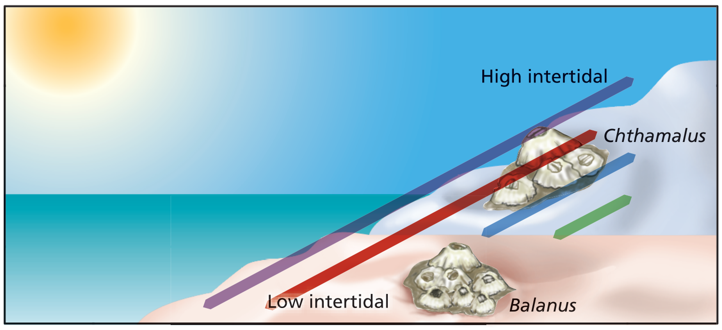
The distribution of larval *Balanus* and *Chthamalus* along the intertidal is shown by the colored lines.



The distribution of adult *Balanus* and *Chthamalus*

FIGURE 12.9A Competition between Barnacles in the Intertidal Zone. When the larvae of *Balanus* and *Chthamalus* settle in the intertidal, there is extensive overlap in the distribution. As the larvae develop and become adults, their distribution along the intertidal changes. The adult *Balanus* are not found at the very high end of the intertidal, due to dry conditions. Adult *Chthamalus* retreat from the middle of the intertidal zone due to competition with *Balanus*.

Social Darwinism

Charles Darwin had described evolution by invoking powerful images of competition between species and a struggle for survival. These powerful images and the logic of Darwin's ideas had very far-reaching consequences. For example, G. F. Gause's research in 1934 on competition was clearly motivated by Darwin and an interest in understanding the mechanisms of evolution.

Darwin's ideas spread, however, and were embraced by fields other than biology. Many economists and anthropologists could not resist using Darwinian phrases like "survival of the fittest" and the "struggle for existence" to support and lend credence to their own theories. This misapplication of Darwin's ideas to fields for which they were unintended has been called **social Darwinism**.

Some economists, for instance, tried to argue that there is a natural order to economic systems, just as there is in biological systems, and that governments should not interfere with this natural order. They predicted that economic systems left to their own devices would experience competition between companies, and the victors of this competition would improve the overall quality of the economy. We can get the flavor of these arguments from the words of the classical French economist, Yves Guyot, who wrote in 1881 that "Darwin speaks of the struggle for existence. It is the struggle for economic existence that has been the cause of all material progress. Competition rouses from the apathy of content, and unceasingly stimulates the effort to improve. It is the grand agent of evolution. Competition fixes the natural level of prices."

THE ECOLOGICAL NICHE

12.10 Several ecologists contributed to the development of the ecological niche concept

Long before Gause used the Lotka-Volterra theory of competition to understand competition between *Paramecium,* ecologists were collecting information on the habitats and feeding relationships of many plants and animals. This purely descriptive activity gave ecologists an appreciation for the ways in which many organisms differed in their requirements for space, food and light. In 1913 Joseph Grinnell (Figure 12.10A) was the first to use the word **niche** to describe the specific habitat, requirements, and ecological role of a species. From Grinnell's writing it is clear that he considered the niche as a description of both the spatial and dietary dimensions of a species. For instance, many plants and animals cannot live in desert environments, because it is too hot and dry. Some animals may have very specific food requirements. For example, not only are Koala bears herbivores, but they eat only the leaves from a few species of eucalyptus trees.

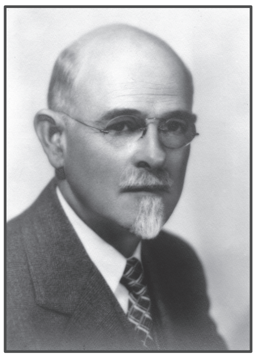
Grinnell also recognized that aspects of a species' ecological niche were not only related to its nutritional requirements but also may be related to its need to avoid predators. Although Gause is typically given credit for formulating the competitive exclusion principle, Grinnell expressed a similar idea in 1917 when he said, "It is, of course, axiomatic that no two species regularly established in a single fauna have precisely the same niche relationship." Gause developed this notion more thoroughly by connecting the niche relationships to species extinction through his experiments.

Charles Elton also used the concept of niche extensively, but in a somewhat different fashion than Grinnell did. In Elton's 1927 book, *Animal Ecology,* he emphasized the feeding role and activity of animals in defining their niche. Thus, according to Elton it is important to know what an animal eats and who eats that animal.

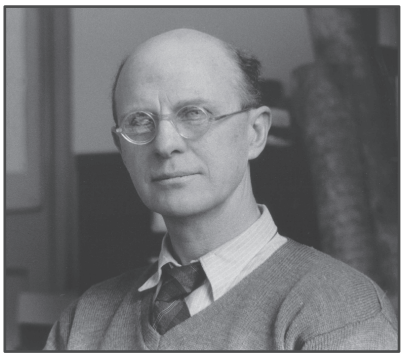
There are many similarities between the two ecologists' concepts of niche. (1) Both considered the niche to be a constant, immutable aspect of species ecology. (2) They included dietary requirements as an important aspect of the niche. (3) They saw avoiding predators as an important aspect of the niche for many animals. Yet neither Grinnell nor Elton provided a conceptually simple, precise definition of the niche.

George Evelyn Hutchinson was next to tackle the problem of defining a species' niche, with the goal of being more precise and concrete. The details of Hutchinson's theory of the niche were outlined in a paper entitled "Concluding remarks," delivered at a symposium at Cold Spring Harbor, New York, in 1957. He suggested that every important environmental and ecological aspect of a species be numerically quantified. Each of these variables would represent a different axis of a geometric figure. The range of variables for each axis would be the limits required for the species to successfully survive and reproduce.

If we consider just three axes, we could in fact draw the three-dimensional shape that represents what Hutchinson



Joseph Grinnell (1877–1939). Grinnell obtained his undergraduate degree from Throop Polytechnic Institute, now known as California Institute of Technology, and his graduate degree from Stanford University in 1913. He was appointed Assistant Professor at the University of California, Berkeley and served as Director of the Museum of Vertebrate Zoology until his death. He was especially interested in the natural history of birds and mammals and published over 500 papers during his career.



Charles Elton (1900–1991). A British ecologist who helped start the Nature Conservancy Council in 1949, had concerns about the impact of introduced species on natural populations. He completed two important books in ecology, *Animal Ecology* and The *Pattern of Animal Communities*. He also developed the concept of the pyramid of numbers, which stated that large predators were rare (top of the pyramid) and small animals were abundant and at the bottom of the food chain.

George Evelyn Hutchinson (1903–1991). Born in Cambridge, England, Hutchinson was interested in ponds and nature at an early age. He published his first scientific paper at the age of 15. He spent most of his academic career at Yale. His interests were in limnology. However, he is best known for his papers synthesizing important concepts in ecology including his formulation of the ecological niche.

FIGURE 12.10A **Major Contributors to the Concept of the Niche** called the **fundamental niche**. Thus, the x-axis might represent the range of temperatures at which the organism can survive. The y-axis could be the range of food sizes an animal might be able to feed on. Finally, the z-axis could be the range of altitudes over which the animal can live. Figure 12.10B shows an example.

The **realized niche** differs from the fundamental niche in that it reflects the impact of other species. The realized niche is the part of the niche volume that does not overlap the fundamental niche of any other species; it also includes the areas that overlap, but in which the first species is able to survive anyway. The realized niche is a subset of the fundamental niche; that is, the realized niche is totally included within the volume of the fundamental niche. Using Hutchinson's definition of *niche,* we would restate Gause's competitive exclusion principle in this way: No two species may have exactly the same realized niche.

Following up on Elton's concept of niche, ecologists often group together species that make their living in a similar fashion. These groups are referred to as **guilds**. Seed-eating birds might form a guild, for example, as might insects that live in decaying fruit. There is a good deal of latitude in the use of the word *guild,* and the common thread that defines a group may vary from one ecologist to the next. In this book, the context in which a group is considered a guild should be clear from the discussion. ❖

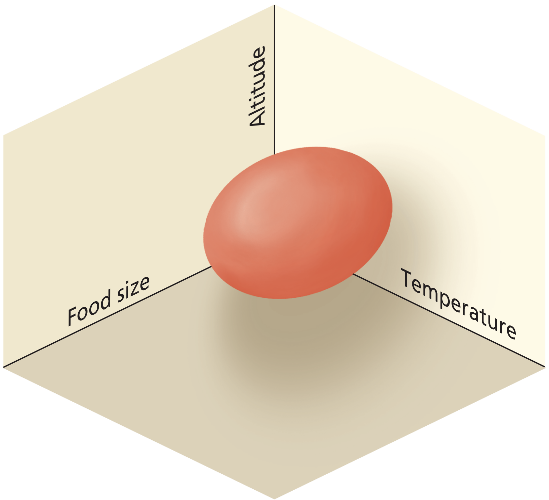


FIGURE 12.10B **A Fundamental Niche**

12.11 Determination of the realized niche can reveal how different species avoid competition

In 1956 Robert MacArthur had set out to study the ecology of five closely related species of warblers in the forests of Maine. These five species were all similar in size (three are shown Figure 12.11A) and tended to eat the same species of insects. It also appeared that the numbers of warblers were resource limited. Not only did all five species live in the same forest, but they could be found feeding on the same tree. In light of Gause's competitive exclusion principle, MacArthur could not explain how it was possible for all five species to coexist.

He decided to collect detailed information on the feeding behavior of these birds. This involved long and tedious observations of the birds in their natural habitat. MacArthur carefully timed the duration, and location within a tree, of the foraging behavior of each species.

The picture that emerged is shown in Figure 12.11B for three of the five species studied by MacArthur. Although the birds would eat the same species of insects, they foraged in different parts of the tree. Thus, the myrtle warbler (now called Audubon's warbler) spent most of its time

Bay-breasted warbler
Dendroica castanea

Cape May warbler
Dendroica tigrina

Myrtle warbler
Dendroica coronata

FIGURE 12.11A **Species of Warblers**

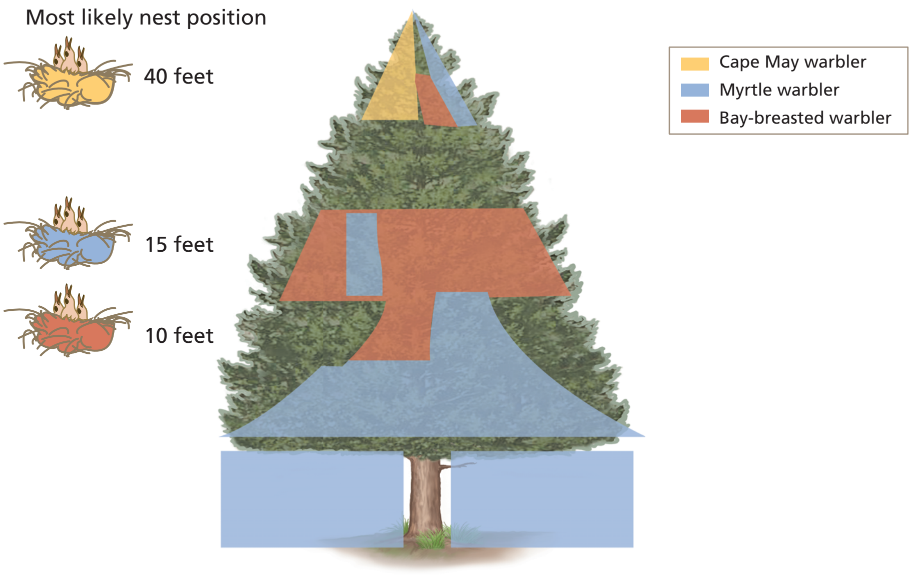


FIGURE 12.11B **Foraging Position of Three Species of Warblers in Maine** The different colors show where each bird species spent most of its time searching for food and feeding. While all three species can be found in the same forest and trees, Cape May warblers tend to feed near the top of the trees, Bay-breasted warblers in the center, and myrtle warblers at the bottom or underneath the tree.

feeding at the bottom of the tree—or actually on the ground underneath the tree. When the myrtle warbler fed higher up on the tree, it tended to forage close to the trunk of the tree. The bay-breasted warbler would feed at the middle heights, both close to the trunk and at the tips of branches. Finally, the Cape May warbler usually fed at the top of the tree and on the outer branches. Even the location of each bird's nest was roughly related to its preferred area of foraging.

Since the species of insects were unlikely to move between these different regions, each bird had its own food resource pool that overlapped little with the resource pools of the other species. In this fashion, the magnitude of competition and the negative impact of one species on the next was reduced.

By today's standards, MacArthur's study is lacking several important components. For instance, he never showed directly that if two species foraged in the same location, there would be insufficient food for both; and thus they would suffer from the effects of this competition. However, MacArthur's interpretation of the distribution patterns of birds was novel, and it inspired many ecologists to more thoroughly study the effects of competition in many other natural systems.

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12.12 The number of species that exist in a particular environment may be determined by competition

When we think about the observations made by MacArthur, a natural question is: How many species of warblers could coexist in the same forest? Even very large trees have a limit regarding how finely space can be divided among different species. Thus, there will be a limit to how many species can coexist in—or be packed into—a particular ecological space. One way to think about this problem is to consider competition at the simplest level—one essential resource. We will assume that this resource varies on a scale that we can quantify, for instance, the size of seeds or insects eaten by birds. It seems reasonable that a given species would have a preferred—or most commonly used—resource value, and that its use of larger or smaller resources might decrease.

We show this type of relationship in Figure 12.12A. Each of three species has a bell-shaped utilization of the single resource, but the mean or preferred resource value is different for each species. The degree of overlap of each of these curves roughly indicates the level of competition that is expected between species. The first graph shows weak competition, as indicated by the small colored areas. The second graph shows much higher levels of competition. Not only is the colored area greater, but the difference in the preferred resource level from one species to the next is smaller. Because the three species have only a small difference in their preferred resource level, we say these species are *tightly packed* in this environment.

If there were only two species in a particular guild, could a third species be packed between them on this single resource axis? Another way of posing this question is to ask if a third species could successfully invade this guild. This question can be answered theoretically by using the Lotka-Volterra competition equations, and by using the resource utilization curves to estimate competition coefficients. This is fairly complicated theory, so we will simply review the possible outcomes. As Figure 12.12B shows, there are basically three different possible outcomes of this invasion: (1) The third species successfully invades, and all three species coexist. (2) The third species successfully invades, but one or both of the resident species is driven to extinction. (3) The invading species cannot displace either of the residents and is itself driven to extinction.

If this type of invasion were to occur repeatedly, we might expect that after awhile, the existing array of species would be packed on the critical resource axis as tightly as possible within the limits prescribed by competition. Is there evidence that resource utilization by organisms is structured in this fashion by competition?

For birds, the types of foods consumed is related to the bird's size. In local environments where two species of sandpipers are found, the difference in the size of birds can be expressed as the ratio of the larger species to the size of the smaller species. The observations show that the relative size of the two species varies greatly, but there is a marked peak in the range of 1.2–1.3 (Figure 12.12C). We can see that if the pool of species were simply placed together at random, there should be no peak at 1.2–1.3. These results suggest that some process is preventing two competing species from being too similar or too different. This is exactly what we would expect if competition were determining these size differences. ❖

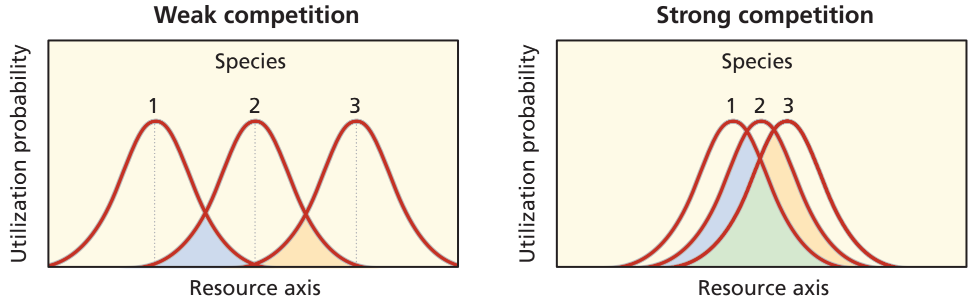
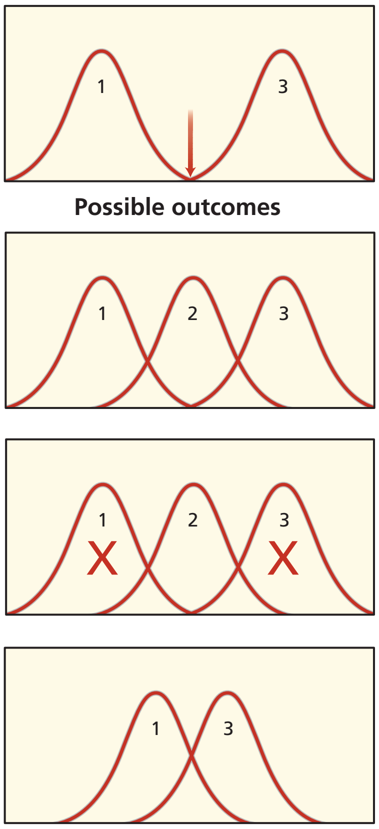


FIGURE 12.12A How Tightly Can Species Be Packed? The blue area indicates the relative intensity of competition between species 1 and species 2. The yellow indicates the relative intensity of competition between species 3 and species 2. The green indicates the relative intensity of competition between all three species.



In a two species-guild can a third species invade and successfully coexist if its resource utilization is between the two existing species?

YES. Now all three species are tightly packed on the resource axis.

YES. but species 1, or species 3, or both species 1 and 3 go extinct.

NO. If the two species are already tightly packed, the invading species will be driven to extinction.

FIGURE 12.12B Can a Third Species Invade?

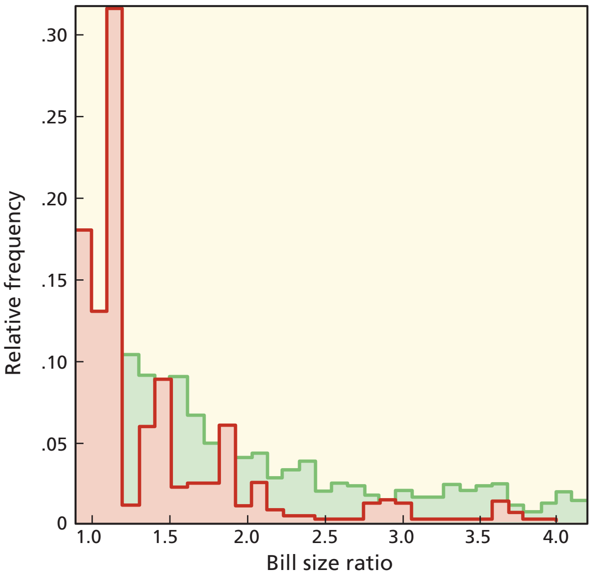


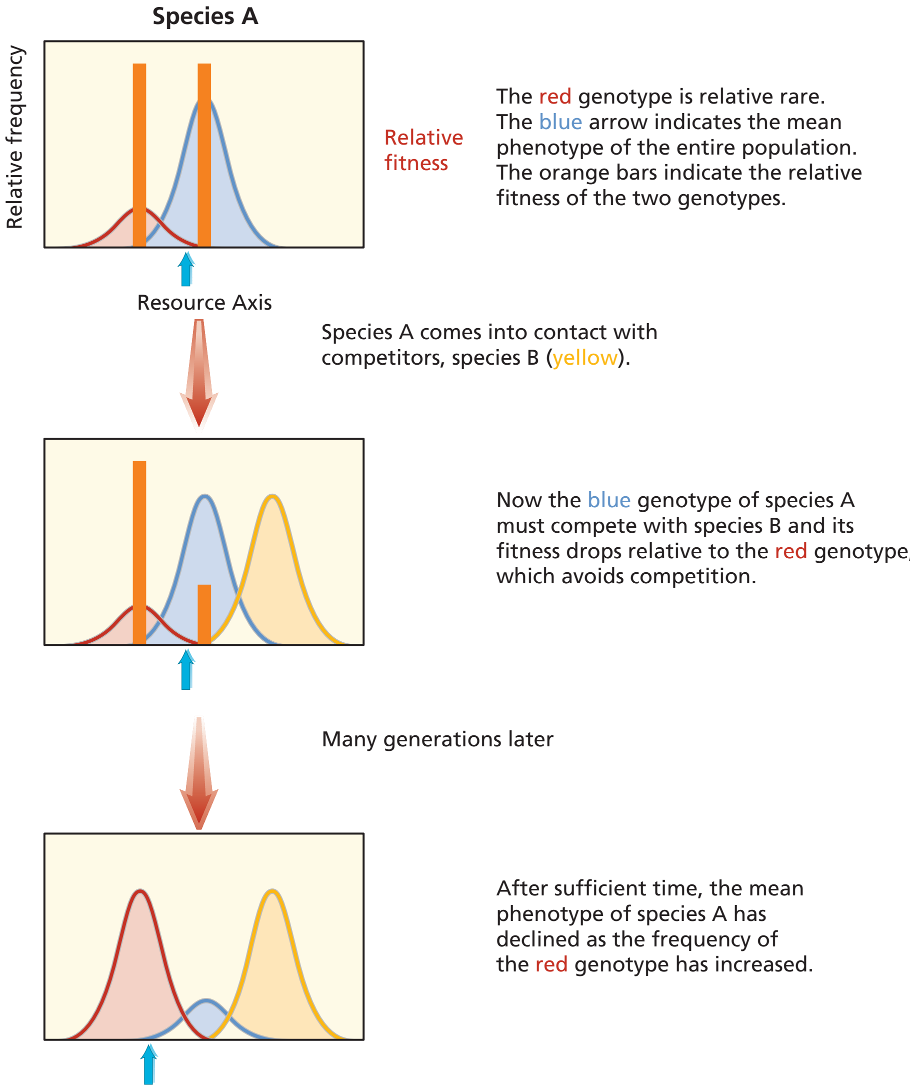
FIGURE 12.12C The red bars show the actual distribution of bill size ratios among North Dakota sandpipers. The green bars show the expected ratios if these pairs of species were randomly placed together. The observed peak ratio at 1.2–1.3 is much higher than expected and may indicate the influence of competition between the bird species.

12.13 Important morphological or behavioral traits may evolve, reducing levels of competition between species in a process called character displacement

Are competing species forever doomed to suffer reduced fitness if their competitors cannot be driven to extinction? The answer is not necessarily. One way for a species to escape the negative effects of competition is to avoid it altogether. One way to accomplish this is to relocate to someplace without competitors. However, if this is not possible, evolution may over time cause changes in morphology or behavior in one or both competing species. Such changes will ultimately reduce the level of competition. If they were to occur, we would say that the morphological or behavioral character has been *displaced* due to the competitive interactions.

Figure 12.13A shows how **character displacement** might happen. As with other models of natural selection, we start by assuming that there is genetic variation in the population. In this case we assume, for simplicity, that competition depends on a single resource and that there is genetic variation for resource usage. On the top graph, we see that in species A, the rare, red genotype uses smaller values of this key resource than does the blue genotype. In the absence of competitors, the fitness of these two genotypes is equal (as the orange bars show), so there is no change in their relative frequencies.

What happens if species A is suddenly confronted with a competitor, species B? As the orange bars on the middle graph show, the relative fitness of species A's red and blue genotypes changes. Since the resource utilization curve of the blue genotype overlaps more extensively with species B, the blue genotype suffers disproportionately. As a result, the relative fitness of the red genotype is now greater than that of the blue genotype. The result of this change is the gradual increase in the frequency of the red genotype at the expense of the blue genotype. After sufficient time has gone by, the average resource utilization of species A is now much lower than it had previously been because of the increased frequency of the red genotype, as the bottom graph shows.



The red genotype is relative rare. The blue arrow indicates the mean phenotype of the entire population. The orange bars indicate the relative fitness of the two genotypes.

Species A comes into contact with competitors, species B (yellow).

Now the blue genotype of species A must compete with species B and its fitness drops relative to the red genotype which avoids competition.

Many generations later

After sufficient time, the mean phenotype of species A has declined as the frequency of the red genotype has increased.

FIGURE 12.13A Character Displacement

In small coastal lakes of southwestern British Columbia, several different species of three-spined sticklebacks are found. Two species are co-occurring in some lakes. In these lakes, one species prefers to forage near the surface of the lake; that species is referred to as limnetic (Figure 12.13B). The second species forages near the bottom of the lake and is called benthic. One genetically based character that can be used to distinguish these two species is the length of the gill raker (see Figure 12.13B). The limnetic species has longer gill rakers than those of the benthic species. In other lakes there is just a single stickleback species whose gill raker size is between those of the benthic and limnetic species. By examining the stomach contents of these fish, ecologists can infer the diet of each species. In the two-species lakes, the benthic species has a diet dominated by invertebrates that are found only on the lake bottoms, while the limnetic species derives almost all of its diet from species that live near the lake surface. In the solitary lakes the single stickleback species has a diet that is almost equal in its distribution of bottom- and plankton-derived species.

These observations suggest that the ancestral species of the benthic and limnetic species had gill rakers and feeding preferences similar to those of the solitary species. However, when the species were placed together, the levels of competition favored the differentiation of the two species such that they specialized on feeding in different localities of the same lake.

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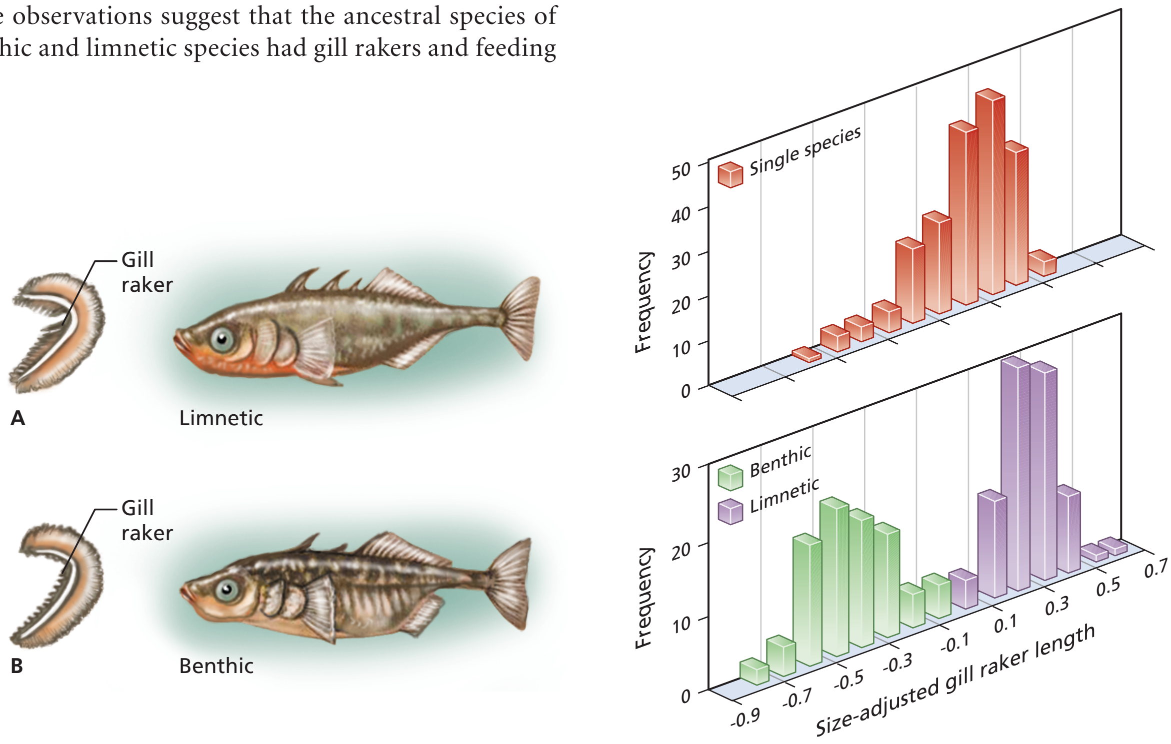


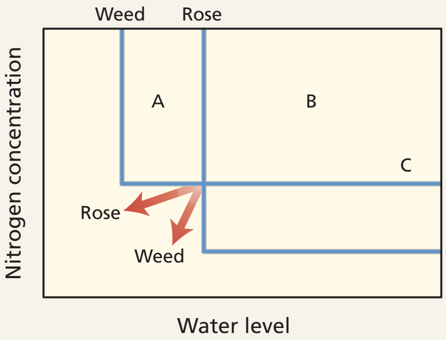
FIGURE 12.13B **Character Displacement in the Sticklebacks**

SUMMARY

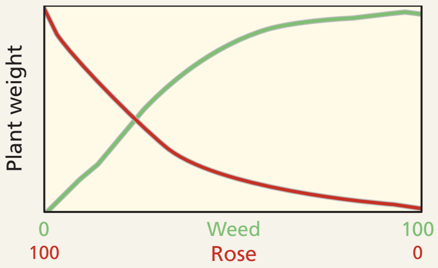
1. The mechanisms of competition are typically different in animals and plants.
   - **a.** Animals compete through two mechanisms, called contest and scramble competition. Contest competition often involves competition for territory.
   - **b.** Plants are affected most strongly by their nearest neighbors. This is due to several factors common to plants: They are sedentary, they vary tremendously in size, and they often compete for common resources.
2. When resources are limited, it is expected that natural selection will favor increased competitive ability. One of the few direct demonstrations of this simple prediction has been made with populations of fruit flies.
3. Early studies of competition between different species of *Paramecium* showed that extinction of one species was one possible outcome of competition. When two species coexisted, it was due to differential use of resources in the environment; this led G. F. Gause to suggest that no two species using the environment in exactly the same manner may coexist. This prediction is referred to as Gause's competitive exclusion principle.
4. A description of the ecological requirements of a species is called its niche.
5. The Lotka-Volterra model is a mathematical summary of the interactions of competing species. For two species with the same carrying capacity, the Lotka-Volterra model predicts extinction of one species when the effects of interspecific competition are stronger than the effects of intraspecific competition. The two species may coexist when each species competitively affects the other to a lesser degree than it affects itself.
6. The effects of competition can also be used to understand the number of competing species that can stably coexist in a particular environment.
7. In some situations, competition between different species may lead to the evolution of behavioral or morphological characters that will ultimately diminish the intensity of competition between the species. This process, called character displacement, appears to account for morphological differences among three-spined sticklebacks.

REVIEW QUESTIONS

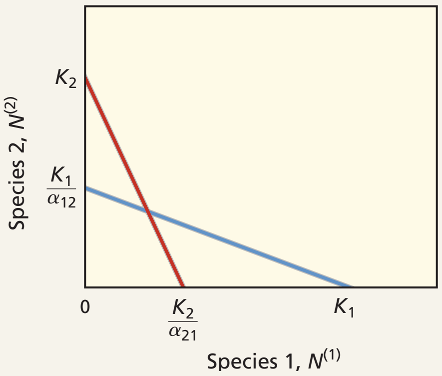
1. In this figure, the blue lines show the equilibrium growth lines for a rose and a weed species. The red arrows show the consumption rates for water and nitrogen for each species. What do you predict the outcome of competition will be if the supply point for these resources is located at either point A, B, or C?



2. In this figure, seeds from a weed and a rose are grown in different proportions, from 0 to 100 percent of each. The weights of the final plants are determined and recorded by the colored lines. Which plant appears to be the better competitor? Why?



3. In Module 12.8 we considered several possible outcomes of competition according to the Lotka-Volterra model. In this graph we show a set of conditions not considered previously. Try to predict the outcome of competition in this case. Hint: There is more than one outcome.



4. Review and explain how the meaning of the niche concept has changed over time.
5. In Module 12.12 we described how character displacement would proceed when a genetically variable species encountered a strong competitor. How would you modify this description if the second species also contained genetic variation similar to the variation present in the first species?

KEY TERMS

apparent competition
character displacement
competition
competition coefficient
competitive exclusion principle
contest competition
ecological niche
fundamental niche
guild
interspecific competition
intraspecific competition
Lotka-Volterra model
mycorrhizae
niche
realized niche
scramble competition
social Darwinism

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