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long a coral reef off the north coast of Jamaica, threespot damselfish guard small territories of less than 1 m^2 (fig. 10.1). These small territories are regularly dispersed across the reef and contain most of the resources upon which the damselfish depend: nooks and crannies for shelter against predators, a carefully tended patch of fast-growing algae for food, and in the territories of males, an area of coral rubble kept clean for spawning. The damselfish constantly patrol and survey the borders of their territories, vigorously attacking any intruder that presents a threat to their eggs and developing larvae, or to their food supply. If you look carefully, however, you may find that not all members of the population have a territory. Damselfish without territories live in marginal areas around the territorial members, wandering from one part of the reef to another.

If you create a vacancy on the reef by removing one of the damselfish holding a territory, other damselfish appear within minutes to claim the vacant territory. Some of the new arrivals are threespot damselfish like the original resident, and some are cocoa damselfish, which generally live a bit higher on the reef face. These new arrivals fight fiercely for the vacated territory. The damselfish chase each other, nip each other's flanks, and slap each other with their tails. The melee ends within minutes, and life among the damselfish settles back into a kind of tense tranquillity. The new resident, which may have driven off a half dozen rivals, is usually another threespot damselfish.

This example demonstrates several things. First, individual damselfish maintain possession of their territories through ongoing competition with other damselfish, and this competition takes the form of **interference competition**, which involves direct aggressive interaction between individuals. Second, though it may not appear so to the casual observer, there is a limited supply of suitable space for damselfish territories, a condition that ecologists call **resource limitation**. Third, the threespot damselfish are subject to **intraspecific competition**, competition with members of their own species, as well as **interspecific competition**, competition between individuals of two species that reduces the fitness of both. The effects of competition on the two competitors may not be equal, however. The individuals of one

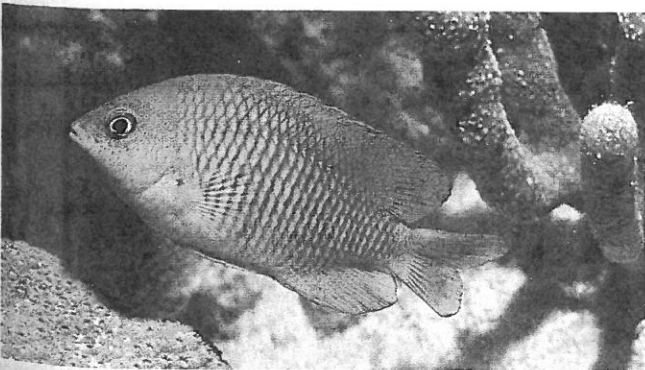


FIGURE 10.1 Territorial reef fish, such as this threespot damselfish, *Eupomacentrus planifrons*, compete intensely for space.

species may suffer greatly reduced fitness while those of the second are affected very little. The observation that threespots generally win in aggressive encounters with cocoa damselfish suggests this sort of competitive asymmetry.

Competition is not always as dramatic as fighting damselfish nor is it always resolved so quickly. In a mature white pine forest in New Hampshire, tree roots grow throughout the soil taking up nutrients and water as they provide support. In 1931, J. Toumey and R. Kienholz designed an experiment to determine whether the activities of these tree roots suppress the activities of other plants. The researchers cut a trench, 0.92 m deep, around a plot 2.74 m by 2.74 m in the middle of the forest. In so doing, they cut 825 roots, which removed potential competition by these roots for soil resources. They also established control plots on either side of the trenched plot and then watched as the results of their experiment unfolded. The experiment continued for 8 years, with retrenching every 2 years and over 100 roots cut each time. By retrenching, the researchers maintained their experimental treatment, suppression of potential root competition.

In the end, this 8-year experiment paid off because it yielded results as dramatic as those with the damselfish. Vegetative cover on the section of forest floor that had been released from root competition was 10 times that present on the control plots. Apparently the roots of white pines exert interspecific competition for some combination of nutrients and water that is strong enough to suppress the growth of forest floor vegetation (fig. 10.2). In addition, the growth of young



FIGURE 10.2 Competition in a forest can be as intense as competition on a coral reef. However, much of the competition in a forest takes place underground, where the roots of plants compete for water and nutrients.

white pines was also much greater within the trenched plots than in the control plots. Therefore, considerable intraspecific competition also occurred on the forest floor.

Ecologists have long thought that both interspecific and intraspecific competition are pervasive in nature. For instance, Darwin thought that interspecific competition was an important source of natural selection. While ecologists have shown that interspecific competition substantially influences the distribution and abundance of many species, they have also questioned the assumption that competition is an all-important organizer of nature. Such questioning has stimulated more careful research and more rigorous testing of the influence of competition on populations, and while this testing continues, sufficient evidence has accumulated to make some tentative generalizations.



- Studies of intraspecific competition provide evidence for resource limitation.
- The niche reflects the environmental requirements of species.
- Mathematical and laboratory models provide a theoretical foundation for studying competitive interactions in nature.
- Competition can have significant ecological and evolutionary influences on the niches of species.

CASE HISTORIES: resource competition



Studies of intraspecific competition provide evidence for resource limitation.

In chapter 9, we saw that slowing population growth at high densities produces a sigmoidal, or S-shaped, pattern in which population size levels off at carrying capacity. Our assumption in that discussion was that intraspecific competition for limited resources plays a key role in slowing population growth at higher densities. The effect of intraspecific competition is included in the model of logistic population growth. If competition is an important and common phenomenon in nature, then we should be able to observe it among individuals of the same species, individuals with identical or very similar resource requirements. Thus we begin our discussion of competition with intraspecific competition.

Intraspecific Competition Among Herbaceous Plants

In chapter 6, we reviewed experiments by David Tilman and M. Cowan (1989) that showed how plants alter root:shoot ratios in response to availability of soil nitrogen. The plants in these experiments reduced their allocation to roots as soil nitrogen concentration increased. The experiments also included evidence for intraspecific competition. Tilman and Cowan grew the grass *Sorghastrum nutans* at low density (7 plants per pot) and high density (100 plants per pot). The results showed that the root:shoot ratios are higher when the plants are grown at high density, suggesting that competition for nutrients was more intense under these conditions.

The results of Tilman and Cowan's experiments also show that soil nitrogen concentration and population density substantially influence growth rates and individual plant weight. For example, the weight of *S. nutans* increased with increased soil nitrogen (fig. 10.3). Therefore, we can conclude that both these responses were limited by nitrogen availability at the lower concentrations in the experiment. Now compare the growth rates and plant weights shown by plants grown at low and high densities. How are they different? Both growth rate and plant weight are higher in the low-density populations, and we can conclude that competition for nutrients (resources) is more intense at the higher plant population density. Such competition for limited resources in natural populations usually leads to mortality among the competing plants.

Self-Thinning in Plant Populations

The development of a stand of plants from the seedling stage to mature individuals suggests competition for limited resources. Each spring as the seeds of annual plants germinate, their population density often numbers in the thousands per square

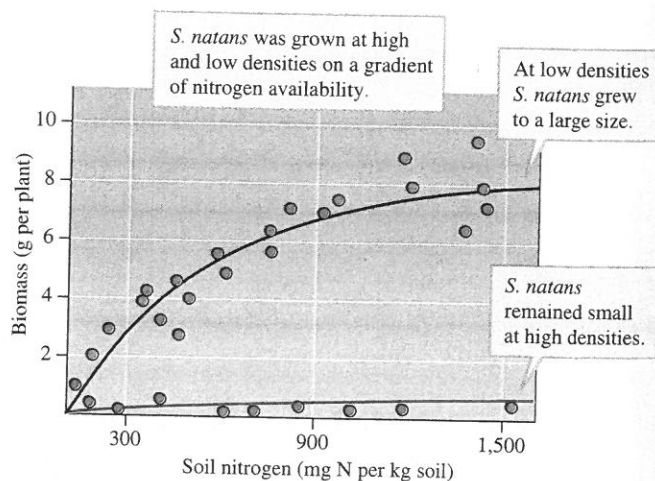


FIGURE 10.3 Population density, soil nitrogen, and the size attained by the grass *Sorghastrum nutans* (data from Tilman and Cowan 1989).

meter. However, as the season progresses and individual plants grow, population density declines. This same pattern occurs in the development of a stand of trees. As the stand of trees develops, more and more biomass is comprised of fewer and fewer individuals. This process is called **self-thinning**.

Self-thinning appears to result from intraspecific competition for limited resources. As a local population of plants develops, individual plants take up increasing quantities of nutrients, water, and space for which some individuals compete more successfully. The losers in this competition for resources die, and population density decreases, or "thins," as a consequence. Over time the population is comprised of fewer and fewer large individuals.

One way to represent the self-thinning process is to plot total plant biomass against population density. If we plot the logarithm of plant biomass against the logarithm of plant density, the slope of the resulting line averages around $-1/2$. In other words, there is an approximately one-unit increase in total plant biomass with each two-unit decrease in population density; plant population density declines more rapidly than biomass increases (fig. 10.4).

Another way to represent the self-thinning process is to plot the average weight of individual plants in a stand against density (fig. 10.5). The slope of the line in such plots averages around $-3/2$. In this case, average plant weight increases 1.5 units for each unit decrease in density; average plant weight increases faster than population density declines. Because self-thinning by many species of plants comes close to a $-3/2$ relationship, this relationship has come to be called the **$-3/2$ self-thinning rule**. The $-3/2$ self-thinning rule was first proposed by K. Yoda and colleagues (1963) and amplified by

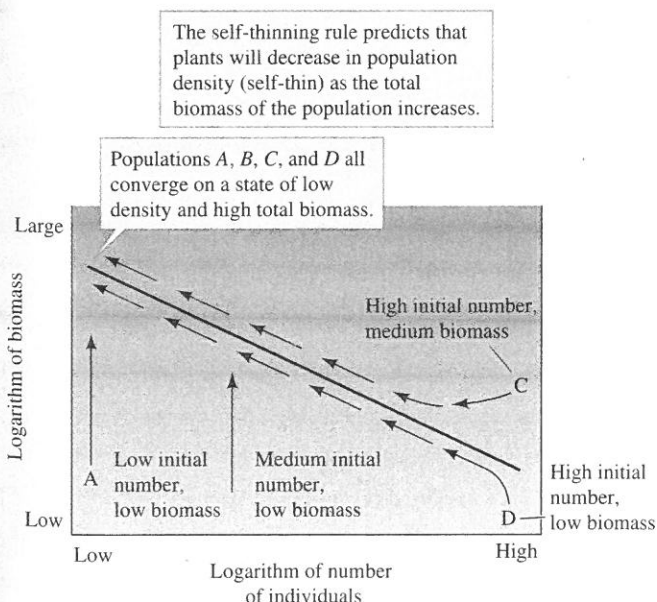


FIGURE 10.4 Self-thinning in plant populations (data from Westoby 1984).

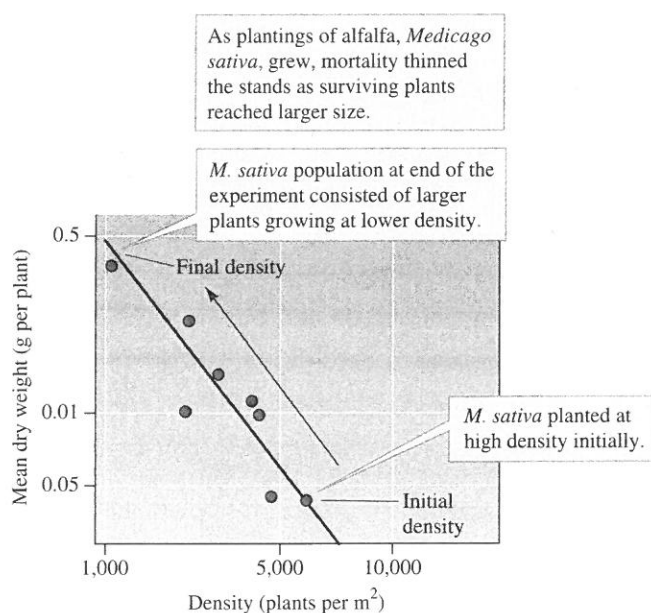


FIGURE 10.5 Self-thinning in populations of alfalfa, *Medicago sativa* (data from White and Harper 1970).

White and Harper (1970), who provided many additional examples (e.g., fig 10.5). Subsequently, the self-thinning rule became widely accepted among ecologists.

Recent analyses have shown that self-thinning in some plant populations deviates significantly from the $-3/2$ (or $-1/2$ for biomass-numbers) slope. However, regardless of the precise trajectory followed by different plant populations, self-thinning of plant populations has been demonstrated repeatedly. The important point, from the perspective of our present discussion, is that self-thinning occurs and appears to be the consequence of intraspecific competition for limited resources. Resource limitation has also been demonstrated in experiments on intraspecific competition within animal populations.

Intraspecific Competition Among Planthoppers

Ecologists have often failed to demonstrate that insects, particularly herbivorous insects, compete. However, one group of insects in which competition has been repeatedly demonstrated are the Homoptera, including the leafhoppers, planthoppers, and aphids. Robert Denno and George Roderick (1992), who studied interactions among planthoppers (Homoptera, Delphacidae), attribute the prevalence of competition among the Homoptera to their habit of aggregating, to rapid population growth, and to the mobile nature of their food supply, plant fluids.

Denno and Roderick demonstrated intraspecific competition within populations of the planthopper *Prokelesia marginata*, which lives on the salt marsh grass *Spartina alterniflora*

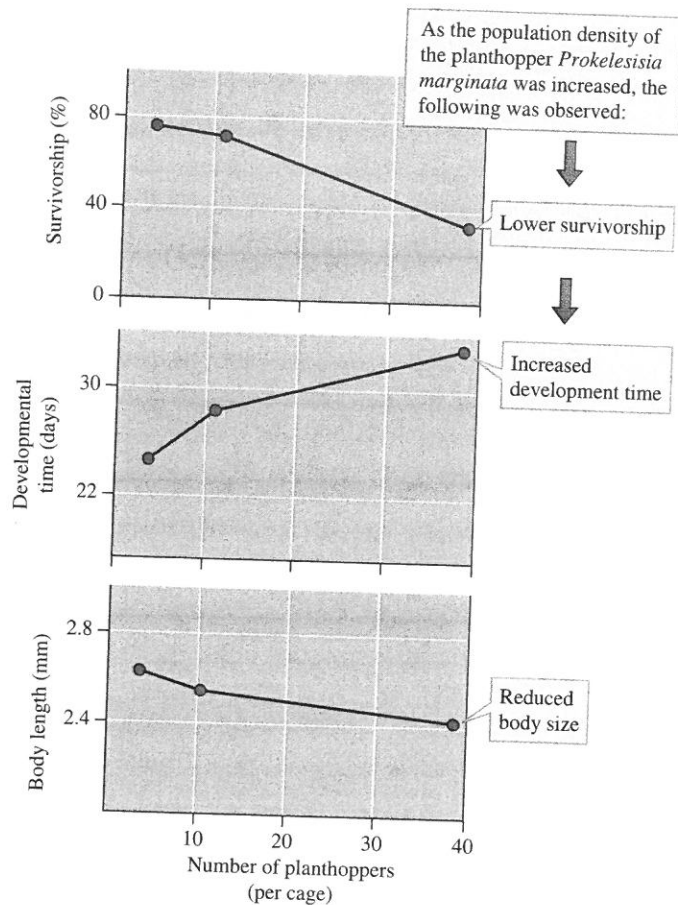


FIGURE 10.6 Population density and planthopper performance (data from Denno and Roderick 1992).

along the Atlantic and Gulf coasts of the United States. The population density of *P. marginata* was controlled by enclosing the insects with *Spartina* seedlings at densities of 3, 11, and 40 leafhoppers per cage, densities that are within the range at which they live in nature. At the highest density, *P. marginata* showed reduced survivorship, decreased body length, and increased developmental time (fig. 10.6). These signs of intraspecific competition were probably the result of reduced food quality at high leafhopper densities. Plants heavily populated by planthoppers show reduced concentrations of protein, chlorophyll, and moisture. Therefore, competition between these leafhoppers was probably the result of limited resource supplies. However, as demonstrated in the following example, intraspecific interference competition may occur in the absence of obvious resource limitation.

Interference Competition Among Terrestrial Isopods

Edwin Grosholz (1992) used a field experiment to study the effects of a wide range of biotic interactions on the population biology of the terrestrial isopod *Porcellio scaber*. This organ-

ism, which is associated with human activities such as farming and gardening and is found throughout the world, sometimes lives at densities in excess of 2,000 individuals per square meter. Such high densities suggest a strong potential for intraspecific competition.

Grosholz conducted his experiments on an outdoor grid of 48, 0.36 m² plots enclosed by aluminum flashing. To control isopod movements, he buried the flashing 12.5 cm into the soil and extended it 12.5 cm above the soil surface. Two experimental treatments were used: (1) to test for food limitation, the food within the enclosures was supplemented by adding sliced carrots and potatoes, and (2) to test for density effects, study plots were stocked with either 100 or 50 *P. scaber*. Supplementing food had no effect on survival by *P. scaber*. However, survival was lower at the higher population density (fig. 10.7). Grosholz attributed lower survival at the higher density to cannibalism, a common occurrence in terrestrial isopods.

Do you think increasing the population densities in the experiment might have changed the results? Since densities in nature sometimes exceed 2,000 per square meter, food limitation might not be observed until such densities are approached. How might the interpretation of the experiment have been altered if other indicators of competition, such as growth rate, size, and reproductive rate, were measured? While food supplements did not affect survival, these other unmeasured attributes may have been affected. Despite these limitations, the study offers interesting insights into the role that interference may play in intraspecific competition, even in the absence of obvious resource limitation.

As we move from discussions of intraspecific to interspecific competition, we need to back up a bit and consider

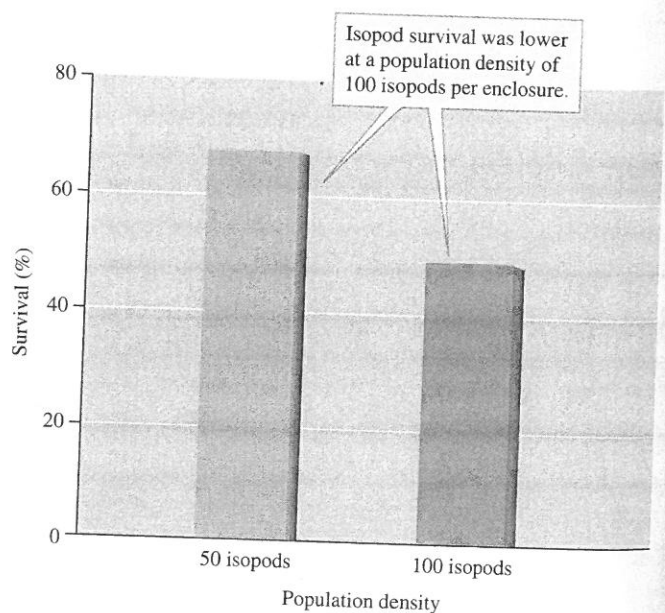


FIGURE 10.7 Population density and survival in populations of a terrestrial isopod, *Porcellio scaber* (data from Grosholz 1992).

how we might portray the environmental requirements of species. We do this because interspecific competition usually occurs among species with similar environmental requirements, that is, among species with similar niches.

CASE HISTORIES: niches



The niche reflects the environmental requirements of species.

The word *niche* has been in use a long time. Its earliest and most basic meaning was that of a recessed place in a wall where one could set or display items. For about a century, however, ecologists have given a broader meaning to the word. To the ecologist, the **niche** summarizes the environmental factors that influence the growth, survival, and reproduction of a species. In other words, a species' niche consists of all the factors necessary for its existence—approximately when, where, and how a species makes its living.

The niche concept was developed independently by Joseph Grinnell (1917, 1924) and Charles Elton (1927), who used the term *niche* in slightly different ways. In his early writings, Grinnell's ideas of the niche centered around the influences of the physical environment, while Elton's earliest concept included biological interactions as well as abiotic factors. However their thinking and emphasis may have differed, it is clear that the views of these two researchers had much in common and that our present concept of the niche rests squarely on their pioneering work.

The niche concept was developed over a period of several decades; however, it was within the context of interspecific competition that the importance of the niche concept was fully realized. It was the work of G. F. Gause (1934), whose principal interest was interspecific competition, that ensured a prominent place for the niche concept in modern ecology. Particularly important was Gause's **competitive exclusion principle**, which states that two species with identical niches cannot coexist indefinitely. Gause experimented with competition in the laboratory and obtained results indicating that when two species compete, one will be a more effective competitor for limited resources. As a consequence, the more effective competitor will have higher fitness and eventually excludes all individuals of the second species. The competitive exclusion principle set the niche concept in a broader context. After Gause, describing the niches of species was no longer an end in itself but a stepping-stone to understanding interactions between species—a potential key to understanding the organization of nature.

Though the work of Gause played a central role in the development of the niche concept, a rigorous definition of the niche awaited later ecologists. We can now point to a single

paper authored by G. Evelyn Hutchinson (1957) as the agent that crystallized the niche concept and stimulated the work of an entire generation of ecologists. In this seminal paper titled simply, "Concluding Remarks," Hutchinson defined the niche as an *n-dimensional hypervolume*, where *n* equals the number of environmental factors important to the survival and reproduction by a species. Hutchinson called this hypervolume, which specifies the values of the *n* environmental factors permitting a species to survive and reproduce, as the **fundamental niche** of the species. The fundamental niche defines the physical conditions under which a species might live, in the absence of interactions with other species. However, Hutchinson recognized that interactions such as competition may restrict the environments in which a species may live and referred to these more restricted conditions as the **realized niche**. While Hutchinson was particularly concerned with the influence of competition on the realized niche, later authors have pointed out that other interactions such as predation, disease, and parasitism may also be important in restricting the distribution of species.

In a single word, *niche* captures most of what we discussed in sections II and III, where we considered how environment affects the growth, survival, reproduction, distribution, and abundance of species. So, why introduce the niche concept here? The reason is that we, like the first ecologists to use the term, need a concept that represents all the environmental requirements of a species. The niche concept carries us beyond the details of individual species' requirements to a position where we can more easily consider the ecology of interactions between species, interactions such as competition, predation, and mutualism.

Do you think it's possible to completely describe Hutchinson's *n*-dimensional hypervolume niche for any species? Probably not, since there are so many environmental factors that potentially influence survival and reproduction. Fortunately, it appears that niches are often determined mostly by a few environmental factors and so ecologists are able to apply a simplified version of Hutchinson's comprehensive niche concept. In studies of animals, ecologists have frequently described niches in terms of their feeding biology.

The Feeding Niches of Galápagos Finches

As we saw in chapter 8, availability of suitable food significantly affects the survival and reproduction of Galápagos finches. In other words, food has a major influence on the niches of Galápagos finches. Because the kinds of food used by birds is largely reflected by the form of their beaks, Peter Grant (1986) and his colleagues were able to represent the feeding niches of Galápagos finches by measuring their beak morphology. For instance, differences in beak size among small, medium, and large ground finches translate directly into differences in diet. The large ground finch, *Geospiza mag-nirostris*, eats larger seeds, the medium ground finch, *G. fortis*,

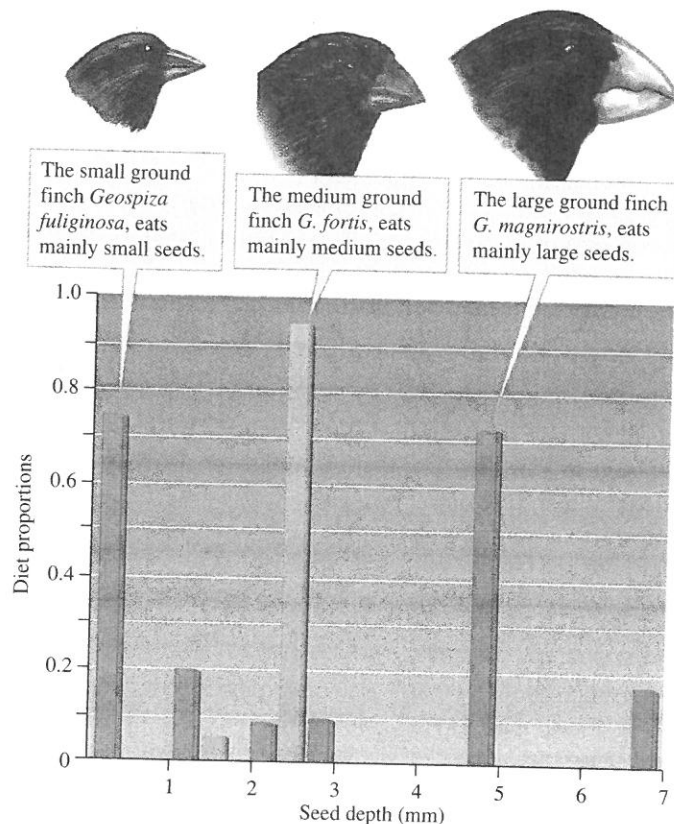


FIGURE 10.8 Relationship between body size and seed size in Galápagos finch species (data from Grant 1986).

eats medium-sized seeds, while the small ground finch, *G. fuliginosa*, eats small seeds (fig. 10.8).

The size of seeds that can be eaten by Galápagos finches can be estimated by simply measuring the depths of their beaks. Studies of seed use by *G. fortis* on Daphne Major showed clearly that even within species, beak size affects the composition of the diet. Within this population, individuals with the deepest beaks fed on the hardest seeds, while individuals with the smallest beaks fed on the softest seeds (fig. 10.9).

The importance of beak size to seed use was also demonstrated by the effects of the 1977 drought on the *G. fortis* population of Daphne Major. In chapter 9, we saw how this drought caused substantial mortality in this population (see fig. 9.16). However, this mortality did not fall equally on all segments of the population. As seeds were depleted, the birds ate the smallest and softest seeds first, leaving the largest and toughest seeds (fig. 10.10). In other words, following the drought not only were seeds in short supply, the remaining seeds were also tougher to crack. Because they could not crack the remaining seeds, mortality fell most heavily on smaller birds with smaller beaks. Consequently, at the end of the drought, the *G. fortis* population on Daphne Major was dominated by larger individuals that had survived by feeding on hard seeds (fig. 10.11).

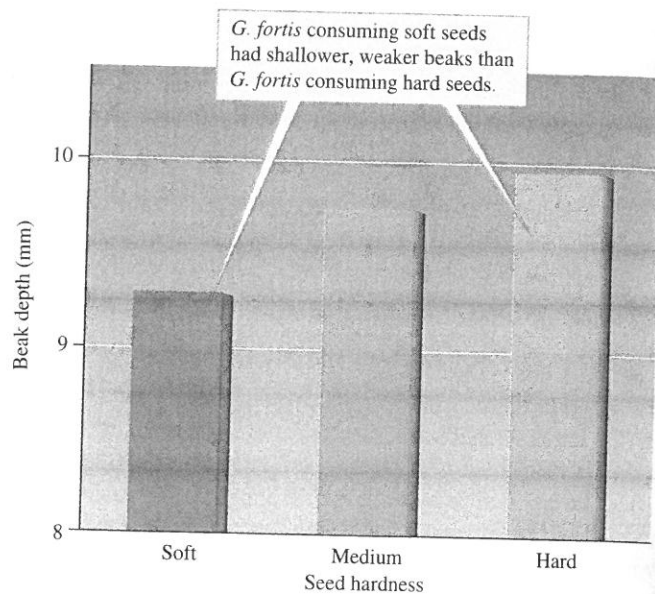


FIGURE 10.9 Relationship between the hardness of seeds eaten by medium ground finches, *Geospiza fortis*, and beak depth (data from Boag and Grant 1984).

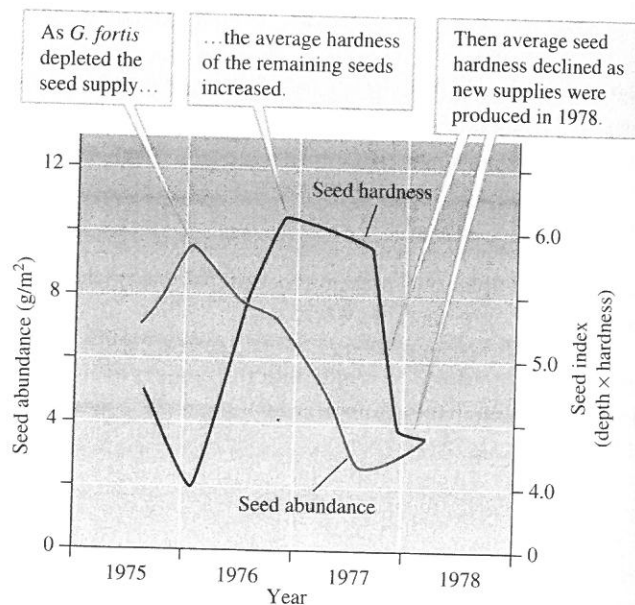


FIGURE 10.10 Seed depletion by the medium ground finch, *Geospiza fortis*, and average seed hardness (data from Grant 1986).

These studies show that beak size provides significant insights into the feeding biology of Galápagos ground finches. Since food is the major determinant of survival and reproduction among these birds, beak morphology gives us a very good picture of their niches. However, the niches of other kinds of organisms are determined by entirely different environmental factors. Let's consider the niche of a dominant species in salt marshes.

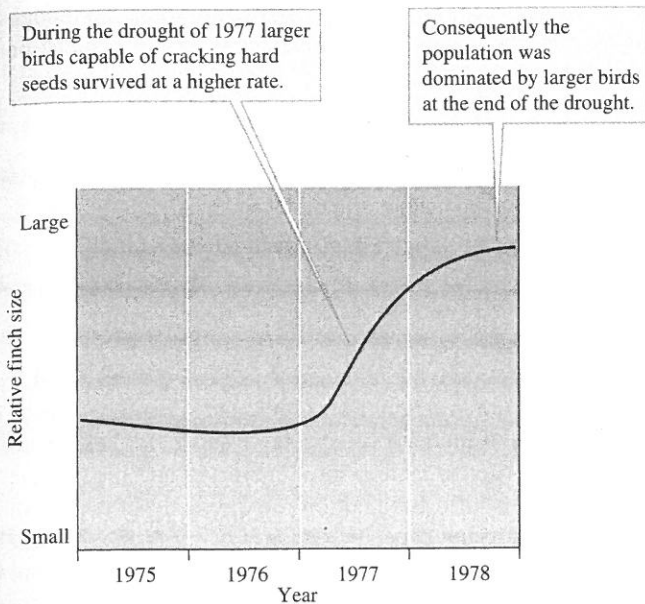


FIGURE 10.11 Selection for larger size among medium ground finches, *Geospiza fortis*, during a drought on the island of Daphne Major (data from Grant 1986).

The Habitat Niche of a Salt Marsh Grass

Biologists discovered *Spartina anglica* approximately one century ago, as a new species recently produced by **allopolyploidy** (fig. 10.12). Allopolyploidy is a process of speciation initiated by hybridization of two different species. *S. anglica* arose initially as a cross between *S. maritima*, a European species, and *S. alterniflora*, a North American species. At least one of these hybrid plants later doubled its chromosome number, making it capable of sexual reproduction, and produced a new species: *S. anglica*. From its center of origin in



FIGURE 10.12 The salt marsh grass *Spartina anglica*.

Lymington, Hampshire, England, *S. anglica* spread northward along the coasts of the British Isles. During this same period, it colonized the coast of France and was widely planted elsewhere in northwest Europe as well as along the coasts of New Zealand, Australia, and China. The Chinese population of this salt marsh grass, established from only 21 plants in 1963, grew to cover 36,000 ha by 1980. *S. anglica* is extensively planted for stabilizing mudflats because it is more tolerant of periodic inundation and water-saturated soils than most other salt marsh plants. This environmental tolerance is reflected in the distribution of the plant in northwestern Europe, where it generally inhabits the most seaward zone of any of the salt marsh plants.

The local distribution of *S. anglica* in the British Isles is well predicted by a few physical variables related to the duration and frequency of inundation by tides and waves. The lower and upper intertidal limits of the grass are mainly determined by the magnitude of tidal fluctuations during spring tides. Where tidal fluctuations are greater, both the lower and upper limits are higher on the shore. However, throughout its British range, the grass generally occupies the intertidal between mean high-water spring tides and mean high-water neap tides (fig. 10.13). A second factor that determines the local distribution of *S. anglica* is the **fetch** of the estuary. The fetch of a body of water is the longest distance over which wind can blow and is directly related to the maximum size of waves that can be generated by wind. All other factors being equal, larger waves occur on estuaries with greater fetch. The larger the fetch the higher *S. anglica* must live in an estuary to avoid disturbance by waves.

The upper limit of *S. anglica*'s distribution within the intertidal zone is also negatively correlated with latitude. In northerly locations within the British Isles, the grass does not occur quite as high in the intertidal zone as it does in the south.

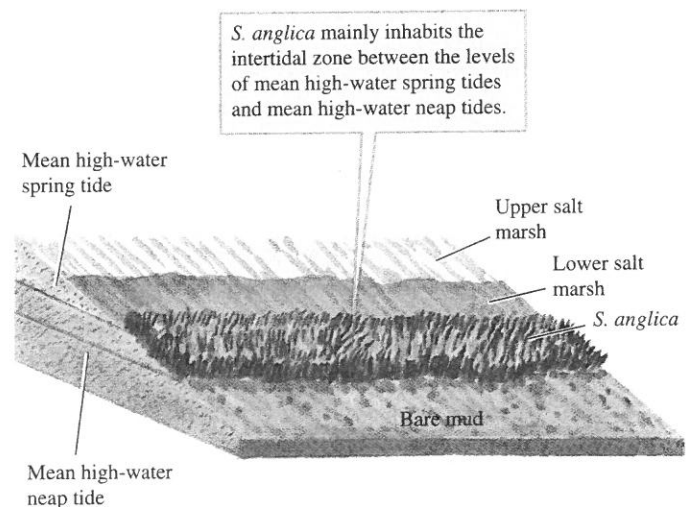


FIGURE 10.13 The niche of *Spartina anglica* is related to tidal fluctuations.

What factors might restrict the distribution at northern sites? One factor we should consider is that *S. anglica* is a C_4 plant. Remember from chapter 6 that C_4 grasses generally do better in warm environments. In northerly locations, *S. anglica* is replaced in the upper intertidal zone by C_3 plants. Could it be that competition with these C_3 plants at northern sites excludes *S. anglica* from the upper intertidal zone? We'll take up this question later in the chapter when we discuss experimental approaches to the study of competition.

Stop

CASE HISTORIES: mathematical and laboratory models



Mathematical and laboratory models provide a theoretical foundation for studying competitive interactions in nature.

As ecologists have used models to explore the ecology of competition, mathematical and laboratory models have played complementary roles. Both mathematical and laboratory models are generally much simpler than the natural circumstances the ecologist wishes to understand. However, while sacrificing accuracy, this simplicity offers a degree of control that ecologists would not have in most natural settings.

D. B. Mertz (1972) began a review of four decades of research on *Tribolium* beetle populations with an astute summary of the characteristics of models in general and of the "Tribolium model" in particular: 1. It is an abstraction and simplification, not a facsimile, of nature; 2. except for the beetles themselves, it is a man-made construct, partly empirical and partly deductive; and 3. it is used to provide insights into natural phenomena." The predictions of these simplified models can be tested in natural systems and either supported or falsified. If falsified, a theory can be modified to accommodate the new information. Ideally, scientific understanding proceeds as a consequence of this dialog between theory and observation, between theoretician and empiricist.

Modeling Interspecific Competition

As we saw in chapter 9, the model of logistic population growth includes a term for intraspecific competition but can be expanded to include the influence of interspecific competition on population growth. The first to do so was Vito Volterra (1926), who was interested in developing a theoretical basis for explaining changes in the composition of a marine fish community in response to reduced fishing during World War I. Alfred Lotka (1932) independently repeated Volterra's analysis and extended it using graphics to represent changes in the population densities of competing species during competition.

Let's retrace the steps of Lotka's and Volterra's modeling exercise, beginning with the logistic model for population growth discussed in chapter 9:

$$\frac{dN}{dt} = r_m N \left(\frac{K - N}{K} \right)$$

We can express the population growth of two species of potential competitors with the logistic equation:

$$\frac{dN_1}{dt} = r_{m1} N_1 \left(\frac{K_1 - N_1}{K_1} \right) \text{ and } \frac{dN_2}{dt} = r_{m2} N_2 \left(\frac{K_2 - N_2}{K_2} \right)$$

Where N_1 and N_2 are the population sizes of species 1 and 2, K_1 and K_2 are their carrying capacities, and r_{m1} and r_{m2} are the intrinsic rates of increase for species 1 and 2. In these models, population growth slows as N increases and the relative level of intraspecific competition is expressed as the ratio of numbers to carrying capacity, either N_1/K_1 or N_2/K_2 . The assumption here is that resource supplies will diminish as population size increases due to intraspecific competition for resources. Resource levels can also be reduced by interspecific competition.

Lotka and Volterra included the effect of interspecific competition on the population growth of each species as:

$$\frac{dN_1}{dt} = r_{m1} N_1 \left(\frac{K_1 - N_1 - \alpha_{12} N_2}{K_1} \right)$$

and

$$\frac{dN_2}{dt} = r_{m2} N_2 \left(\frac{K_2 - N_2 - \alpha_{21} N_1}{K_2} \right)$$

In these models, the rate of population growth of a species is reduced both by conspecifics (individuals of the same species) and by individuals of the competing species, that is, interspecific competition. The effects of intraspecific competition ($-N_1$ and $-N_2$) are already included in the logistic models for population growth. The effect of interspecific competition is incorporated into the Lotka-Volterra model by $-\alpha_{12} N_2$ and $-\alpha_{21} N_1$. The terms α_{12} and α_{21} are called **competition coefficients** and express the competitive effects of the competing species. Specifically, α_{12} is the effect of an individual of species 2 on the rate of population growth of species 1, while α_{21} is the effect of an individual of species 1 on the rate of population growth of species 2. In this model, interspecific competitive effects are expressed in terms of intraspecific equivalents. If, for example, $\alpha_{12} > 1$, then the competitive effect of an individual of species 2 on the population growth of species 1 is greater than that of an individual of species 1. If, on the other hand, $\alpha_{12} < 1$, then the competitive effect of an individual of species 2 on the population growth of species 1 is less than that of an individual of species 1.

In general, the Lotka-Volterra model predicts coexistence of two species when, for both species, interspecific competition is weaker than intraspecific competition. Otherwise, one species is predicted to eventually exclude the other. These conclusions come from the following analysis.

Balanus had no effect on survivorship by the second species because the population density of *Balanus* was too low to compete seriously. Connell's results provide direct evidence that *Chthamalus* is excluded from the middle intertidal zone by interspecific competition with *Balanus*.

How does interspecific competition affect the niche of *Chthamalus*? In the absence of *Balanus*, it can live over a broad zone from the upper to the middle intertidal zones. Using the terminology of Hutchinson (1957), we can call this broad range of physical conditions the fundamental niche of *Chthamalus*. However, competition largely restricts *Chthamalus* to the upper intertidal zone, a more restricted range of physical conditions constituting the species' realized niche (fig. 10.21).

Does variation in interspecific competition completely explain the patterns seen by Connell? At the lowest levels in the lower intertidal zone, *Chthamalus* suffered high mortality even in the absence of *Balanus* (see fig. 10.20). What other factors might contribute to high rates of mortality by *Chthamalus* in the lower intertidal zone? Experiments have shown that this species can withstand periods of submergence of nearly 2 years, so it seems that it is not excluded by physical factors. It turns out that the presence of predators in the lower intertidal zone introduces complications that we will discuss

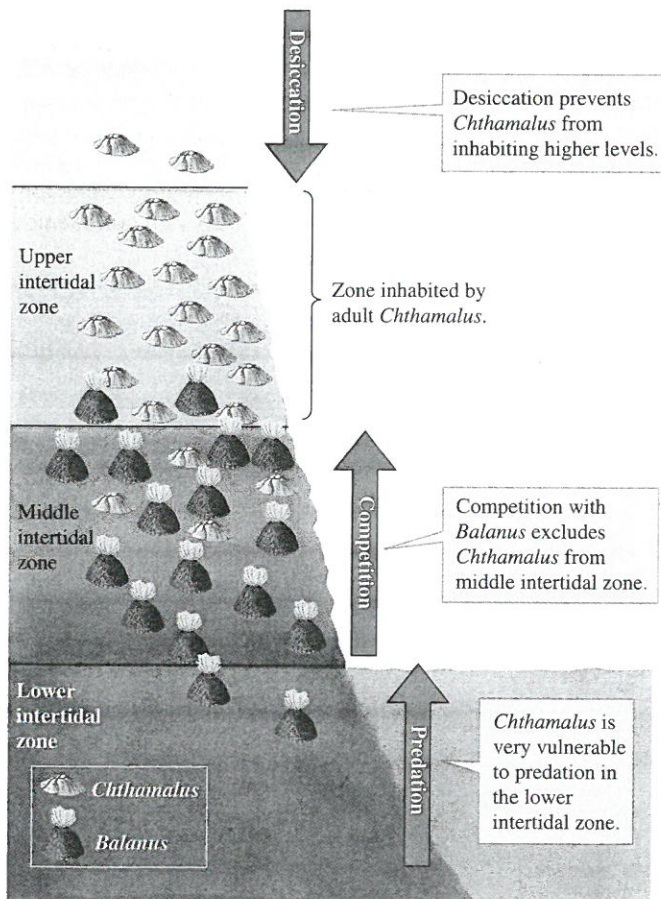


FIGURE 10.21 Environmental factors restricting the distribution of *Chthamalus* to the upper intertidal zone.

in chapter 11 when we examine the influences of predators on prey populations.

Competition and the Habitat of a Salt Marsh Grass

How do you think competition might affect populations of the salt marsh grass *Spartina anglica*, whose niche we discussed earlier in the chapter? Field experiments have demonstrated that *S. anglica*, like *Chthamalus*, is restricted to its typical intertidal zone partly by interspecific competition with other salt marsh plants. In contrast to *Chthamalus*, however, *S. anglica* receives competitive pressure from the landward side of its intertidal distribution (Scholten and Rozema 1990, Scholten et al. 1987).

Does this reversal in the direction of competitive pressure make sense? It should, since in the case of barnacles we have marine organisms for which greater physical challenge occurs as they inhabit areas higher in the intertidal zone. In the case of the salt marsh plants, we are dealing with organisms descended from terrestrial ancestors that are met with increasing physical challenge as they inhabit areas lower in the intertidal zone. Similar experiments have been conducted on competition among desert rodents.

Competition and the Niches of Small Rodents

One of the most ambitious and complete of the many field experiments ecologists have conducted on competition among rodents focused on desert rodents in the Chihuahuan Desert near Portal, Arizona. This experiment, conducted by James H. Brown and his students and colleagues (Munger and Brown 1981, Brown and Munger 1985), is exceptional in many ways. First, it was conducted at a large scale; the 20 ha study site includes 24 study plots each 50 m by 50 m (fig. 10.22). Second, the experimental trials have been well replicated, both in space and in time. Third, the project has been long term; it began in 1977 and is ongoing. These three characteristics combine to demonstrate subtle ecological relationships and phenomena that would not otherwise be apparent.

The rodent species living on the Chihuahuan Desert study site can be divided into groups based upon size and feeding habits. Most members of the species are **granivores**, rodents that feed chiefly on seeds. The large granivores consist of three species of kangaroo rats (fig. 10.23a) in the genus *Dipodomys*—*D. spectabilis*, 120 g; *D. ordi*, 52 g; and *D. merriami*, 45 g. In addition, the study site is home to four species of small granivores (fig. 10.23b)—*Perognathus penicillatus*, 17 g; *P. flavus*, 7 g; *Peromyscus maniculatus*, 24 g; *Reithrodontomys megalotis*, 11 g—and two species of small insectivorous rodents—*Onychomys leucogaster*, 39 g; and *O. torridus*, 29 g.

In one experiment, Brown and his colleagues set out to determine whether large granivorous rodents (*Dipodomys* spp.)

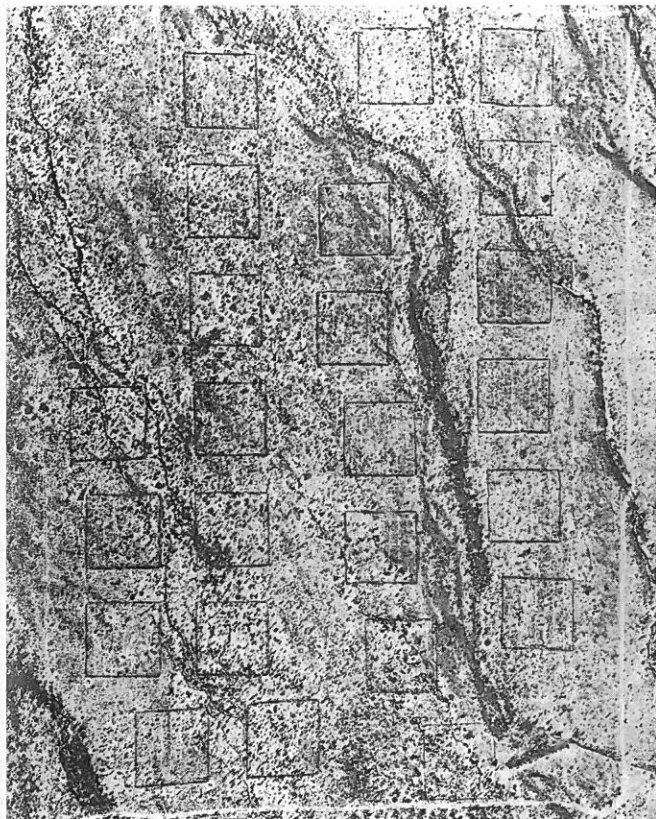
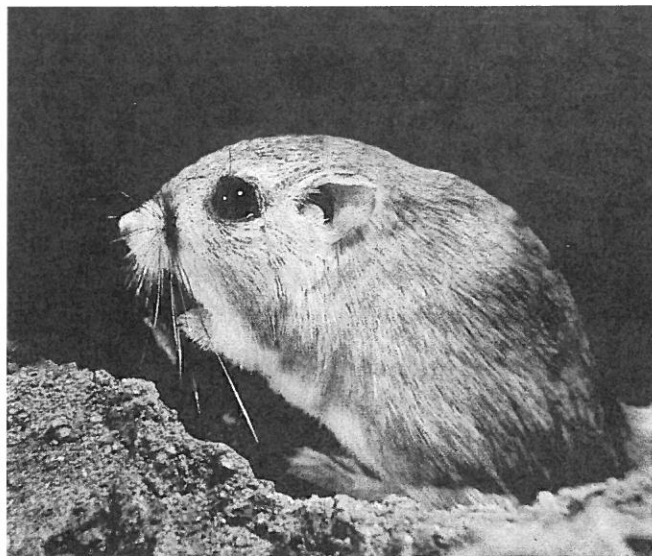


FIGURE 10.22 Aerial photo showing the placement of 24 study plots, each 50 m by 50 m, in the Chihuahuan Desert near Portal, Arizona (courtesy of J. H. Brown).

limit the abundance of small rodents on their Chihuahuan Desert study site. They also wanted to know whether the rodents might be competing for food. The researchers addressed their questions with a field experiment in which they enclosed 50 m by 50 m study plots with mouse-proof fences. The fences were constructed with a wire mesh with 0.64 cm openings, which were too small for any of the rodent species to crawl through. They also buried the fencing 0.2 m deep so the mice couldn't dig under it, and they topped the fences with aluminum flashing so the mice couldn't climb over it. This may sound like a lot of work, but to answer their questions, the researchers had to control the presence of rodents on the study plots.

The researchers next cut holes 6.5 cm in diameter in the sides of all the fences to allow all rodent species to move freely in and out of the study plots. With this arrangement in place, the rodents in the study plots were trapped live and marked once a month for 3 months. Following this initial monitoring period, the holes on four of eight study plots were reduced to 1.9 cm, small enough to exclude *Dipodomys* but large enough to allow free movement of small rodents. Brown and his colleagues refer to these fences with small holes as semipermeable membranes, since they allow the movement of small rodents but exclude *Dipodomys*, the large granivores in this system.



(a)



(b)

FIGURE 10.23 Two species of granivorous rodents living in the Chihuahuan Desert: (a) the kangaroo rat, *Dipodomys* sp., a large granivore; (b) a pocket mouse, *Perognathus* sp., a small granivore.

If *Dipodomys* competes with small rodents, how would you expect populations of small rodents to respond to its removal? The density of small rodent populations should increase, right? If food is the limiting resource, would you expect granivorous and insectivorous rodents to respond differently to *Dipodomys* removal? The researchers predicted that if competition among rodents is mainly for food, then small granivorous rodent populations would increase in response to *Dipodomys* removal, while insectivorous rodents would show little or no response.

The results of the experiment were consistent with the predictions. During the first 3 years of the experiment, small granivores were approximately 3.5 times more abundant on the *Dipodomys* removal plots compared to the control plots, while populations of small insectivorous rodents did not increase significantly (fig. 10.24).

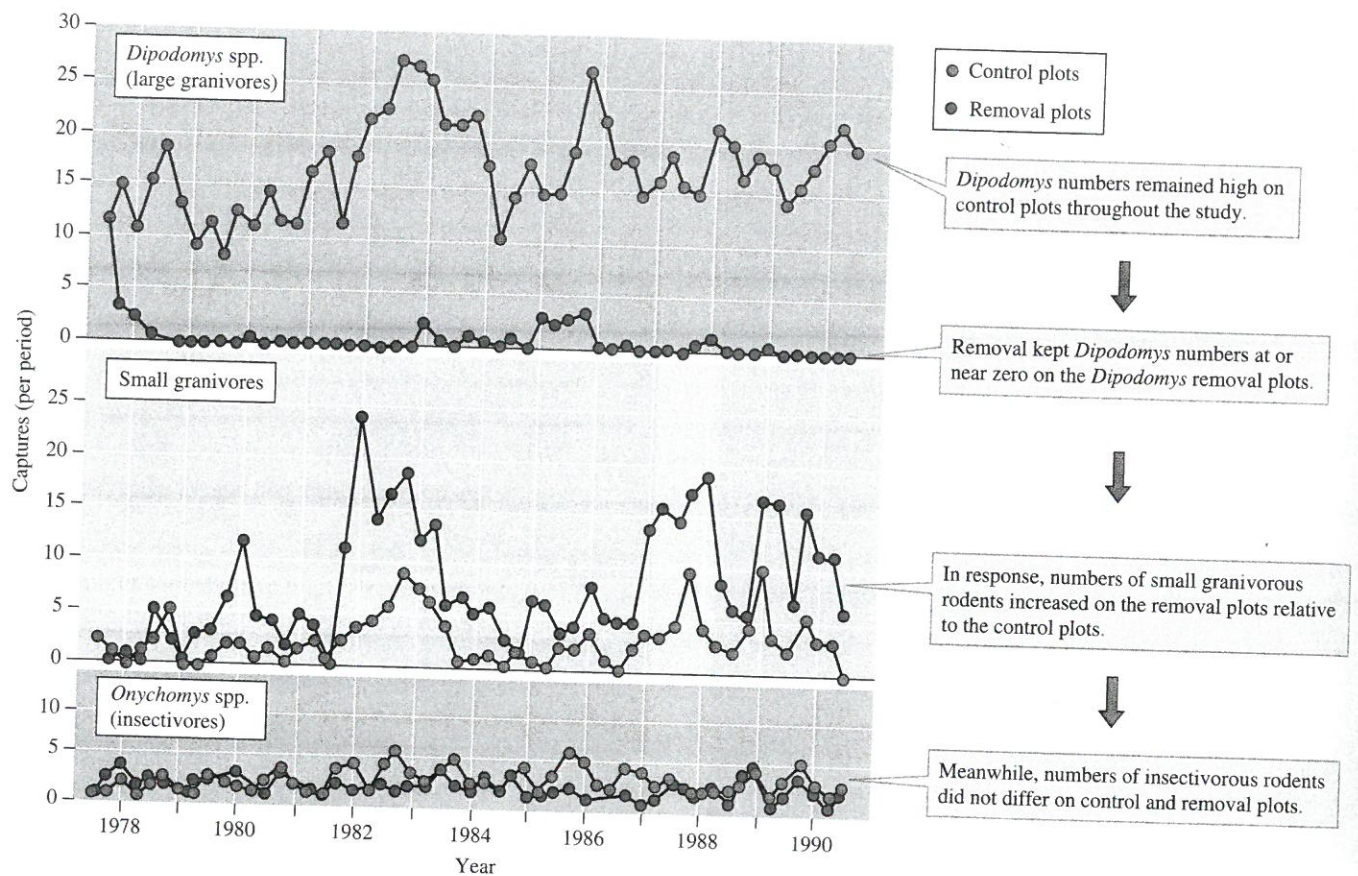


FIGURE 10.24 Responses by small granivorous and insectivorous rodents to removal of large granivorous *Dipodomys* species (data from Heske, Brown, and Mistry 1994).

The results presented in figure 10.24 support the hypothesis that *Dipodomys* spp. competitively suppress populations of small granivores. But would they do so again in response to another experimental manipulation? We cannot be certain unless we repeat the experiment. That's just what Edward Heske, James H. Brown, and Shahroukh Mistry (1994) did. In 1988, they selected eight other fenced study plots that they had been monitoring since 1977, installed their semipermeable barriers on four of the plots, and removed *Dipodomys* from them. The result was an almost immediate increase in small granivore populations on the removal plots (fig. 10.25). By reproducing the major results of the first experiment, this second experiment greatly strengthens the case for competition between large and small granivores at this Chihuahuan Desert site.

Character Displacement

Because interspecific competition reduces the fitness of competing individuals, those individuals that compete less should have higher fitness than individuals that compete more. Because the degree of competition is assumed to depend upon the degree of niche overlap, interspecific competition has been predicted to lead to directional selection for reduced niche overlap. This process of evolution toward niche divergence in the face of competition is called **character displacement**.

The Galápagos finches *Geospiza fortis*, the medium ground finch, and *G. fuliginosa*, the small ground finch, provide one of the most convincing cases of character displacement. These two species occur apart from each other, that is, they are **allopatric**, on Daphne Major and Los Hermanos Island and occur together, that is, they are **sympatric**, on the island of Santa Cruz (fig. 10.26). Where the two species are allopatric, they have very similar beak sizes. However, where they are sympatric, the sizes of their beaks do not overlap. The allopatric *G. fortis* on Daphne Major have smaller beaks than those sympatric with *G. fuliginosa* on Santa Cruz, while the *G. fuliginosa* on Los Hermanos Island have beaks that are significantly larger than those sympatric with *G. fortis* on Santa Cruz. Since beak size correlates with diet in Galápagos finches, we can say that the sympatric populations of the two species on Santa Cruz have different feeding niches. Natural selection has apparently favored divergence in the feeding niches of these sympatric populations (Lack 1947, Schluter, Price, and Grant 1985, and Grant 1986).

A few other studies have demonstrated similar patterns of character displacement among a variety of animal species, including *Cnemidophorus* lizards on islands off Baja California, *Anolis* lizards on Caribbean islands, and sticklebacks inhabiting small lakes around Vancouver Island, Canada. Character displacement has also been observed in laboratory