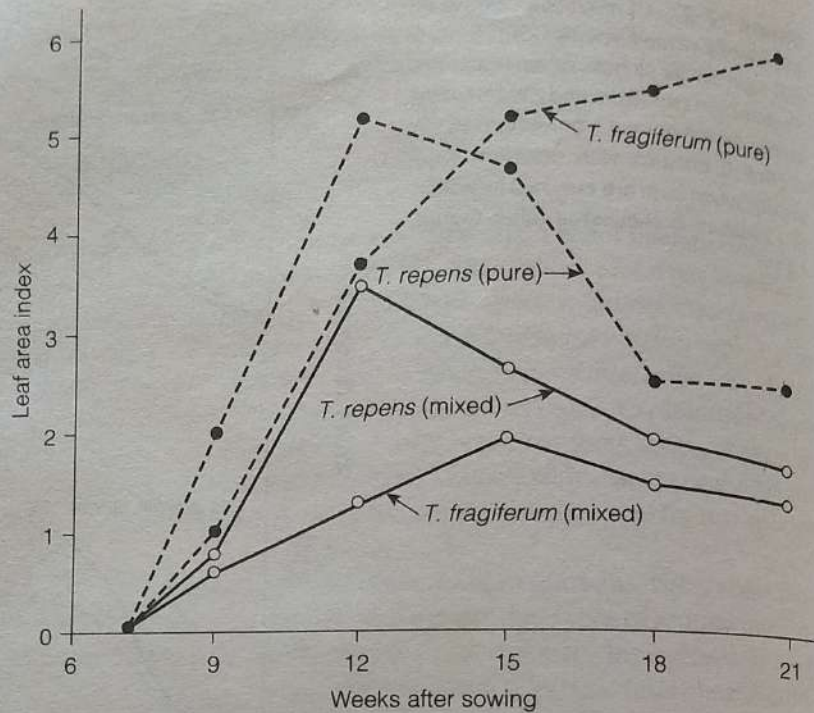


Figure 7-3. The case for coexistence in populations of clover (*Trifolium*). The graph shows the population growth of two species of clover in pure (growing alone) and in mixed stands. Note that the two species in pure stands have a different growth form, reaching maturity at different times. Because of this and other differences, the two species are able to coexist in mixed stands at reduced density, even though they interfere with one another. Leaf area index is the ratio of leaf surface area to soil surface area in cm^2/cm^2 (redrawn from Harper and Clatworthy 1963).



clusion in paired species of beetles (*Tribolium*) and of coexistence in two species of clover (*Trifolium*).

One of the most thorough long-term experimental studies of interspecific competition was carried out at the University of Chicago in the laboratory of Thomas Park (Park 1934, 1954). Park and his students and associates worked with flour beetles, especially those belonging to the genus *Tribolium*. These small beetles can complete their entire life history in a very simple and homogeneous habitat, namely, a jar of flour or wheat bran. The medium in this case is both food and habitat for larvae and adults. If fresh medium is added at regular intervals, a population of beetles can be maintained for a long time. In energy flow terminology, this experimental setup is a stabilized heterotrophic ecosystem in which imports (subsidies) of food energy balance respiratory losses.

The investigators found that when two different species of *Tribolium* were placed in this homogeneous microcosm, one species invariably was eliminated sooner or later, whereas the other continued to thrive. One species always "wins," or to put it another way, two species of *Tribolium* cannot survive in this particular one-habitat microcosm. The relative number of individuals of each species originally placed in the culture (the *stocking rate*) does not affect the eventual outcome, but the climate imposed on the ecosystem does have a great impact on which species of the pair wins out. One species (*T. castaneum*) always wins under conditions of high temperature and humidity, whereas the other (*T. confusum*) always wins under cool and dry conditions, even though either species can live indefinitely in any of the six climates, provided it is alone in the culture. Population attributes measured in one-species cultures help explain some of the outcomes of the competitive action. For example, the species with the highest rate of increase, r , under the conditions of existence in question was usually found to win if the species difference in r was rather large. If the

growth rates differed only moderately, the species with the highest rate did not always win. The presence of a virus in one population could easily tip the balance. Feener (1981) described a case in which a parasitic fly altered the competitive balance between two species of ants. Also, genetic strains within the population may differ greatly in competitive ability.

Some of the most interesting experiments in plant competition were reported by J. L. Harper and associates, researching at the University College of North Wales (see J. L. Harper 1961; J. L. Harper and Clatworthy 1963). The results of one of these studies, shown in Figure 7-3, illustrate how a difference in growth form allows two species of clover to coexist in the same environment (same light, temperature, and soil). Of the two species, *Trifolium repens* grows faster and reaches a peak in leaf density sooner. However, *T. fragiferum* has longer petioles and higher leaves and can overtop the faster-growing species, especially after *T. repens* has passed its peak, and thus avoid being shaded out. In mixed stands, therefore, each species inhibits the other, but both can complete their life cycle and produce seed, even though each coexists at a reduced density. In this case, the two species, although competing strongly for light, could coexist because their morphology and the timing of their growth maxima differed. J. L. Harper (1961) concluded that two species of plants can persist together if the populations are independently controlled by one or more of the following mechanisms: (1) different nutritional requirements (such as legumes and non-legumes); (2) different causes of mortality (such as differential sensitivities to grazing); (3) sensitivity to different toxins (different responses to secondary chemicals); and (4) sensitivity to the same controlling factor (such as light or water) at different times (like the clover just described).

Brian (1956) was among the first to distinguish between *indirect* or *exploitation competition* and *direct* or *interference competition*. Interference competition appears more frequently as we move up the phylogenetic tree of animal life, from simple filter-feeding protozoans and cladocerans, which usually compete in gathering food, to vertebrates, with their elaborate behavioral patterns of aggression and territoriality. Slobodkin (1964) concluded on the basis of competition experiments with *Hydra* that these two types of competition overlap but that it is useful to distinguish between the two processes on theoretical grounds. A general pattern emerging from the literature on competition is that competition is most severe—and competitive exclusion most likely to occur—in systems where immigration and emigration are absent or reduced, such as in laboratory cultures or mesocosms or on islands or other natural systems with substantial barriers to inputs and outputs. The probability of coexistence is higher in the more typical open systems of nature.

Interspecific competition in plants in the field has been much studied and is generally believed to be an important factor in bringing about a succession of species (as will be described in Chapter 8). The strongest evidence regarding the importance of competition in nature comes from studies of how species respond to experimental additions or removals of potential competitors (Connell 1961, 1972, 1975; Paine 1974, 1984; Hairston 1980). Connell's (1961) classic study of competition among barnacles in natural settings is a splendid example of a well-designed field experiment. Connell's investigation was conducted on the rocky coast of Scotland, where two barnacle species typically occupy different locations in the intertidal zone. The smaller of the two species, *Chthamalus stellatus*, occurs higher in the intertidal zone than the larger species, *Balanus glandula*. Figure 7-4A presents a "barnacle model" based on the experimental studies of J. H. Connell. The intertidal zone on a rocky eastern seacoast

Robert Paine at the University of Washington demonstrated that predation played a major role in shaping the structure of biological communities by influencing the outcome of competitive interactions between prey species. The intertidal zone on an exposed rocky shore on the West Coast of the United States harbors several species of barnacles, mussels, limpets, and chitons. These species are preyed on by the sea star *Pisaster ochraceus*. Following the removal of sea stars from experimental plots, the number of prey species in the removal plots decreased rapidly from 15 to 8 by the end of the investigation. Diversity decreased because populations of barnacles and mussels, superior competitors for space in the absence of predators (sea stars in this case), crowded out many of the prey species. This elegant study demonstrated how predation shaped the biological community and regulated biotic diversity (Paine 1974).

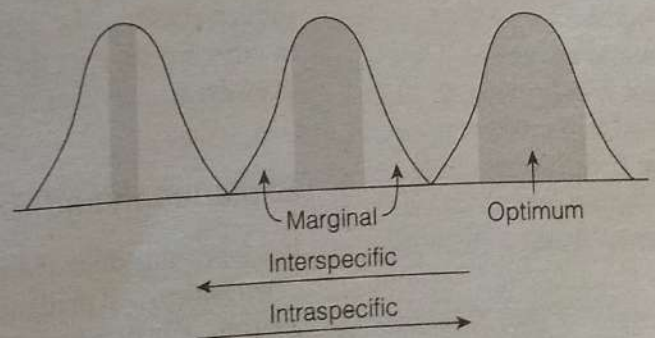
Morphological differences that enhance ecological separation may arise by an evolutionary process termed **character displacement**. For example, in central Europe, six species of titmice (small birds of the genus *Parus*) coexist, segregated partly by habitat and partly by feeding areas and size of prey, which is reflected in small differences in length and width of the bill. In North America, more than two species of titmice are rarely found in the same locality, even though seven species are present on the continent as a whole. Lack (1969) suggested that the American species of titmice are at an earlier stage in their evolution than the European species, and their differences in beak, body size, and feeding behavior are adaptations to their respective habitats and are not yet adaptations for permitting coexistence in the same habitat.

The general theory of the role of competition in habitat selection is summarized in Figure 7-5. The curves represent the range of habitat that can be tolerated by the species, with optimum and marginal conditions indicated. Where there is competition with other closely related or ecologically similar species, the range of habitat conditions that the species occupies generally becomes restricted to the optimum (that is, to the most favorable conditions under which the species has an advantage in some manner over its competitors). Where interspecific competition is less severe, intraspecific competition generally brings about a wider choice of habitats.

Islands are good places to clearly observe the tendency for a wider selection of habitats to occur when potential competitors fail to colonize. For example, meadow voles (*Microtus*) often occupy forest habitats on islands where their forest competitors, the red-backed voles (*Clethrionomys*), are absent.

Just because closely related species are sharply separated in nature does not, of course, mean that competition is actually operating continuously to keep them separated; the two species may have evolved different requirements or preferences that effectively reduce or eliminate competition. For example, in Europe, one species of

Figure 7-5. The effect of competition on habitat distribution. When intraspecific competition dominates, the species spreads out and occupies less favorable (marginal) areas; where interspecific competition is intense, the species tends to be restricted to a narrower range, representing the optimum conditions.



Rhododendron (*R. hirsutum*), is found on calcareous soils, whereas another species (*R. ferrugineum*) is found on acidic soils. The requirements of the two species are such that neither can live at all in the opposite type of soil, so there is never any actual competition between them. Teal (1958) made an experimental study of habitat selection of species of fiddler crabs (*Uca*), which are usually separated in their occurrence in salt marshes. One species, *U. pugilator*, is found on open, sandy flats; another, *U. pugnax*, is found on muddy substrates covered with marsh grass. Teal found that one species would tend not to invade the habitat of the other even in the absence of the other, because each species would dig burrows only in its preferred substrate. The absence of active competition, of course, does not mean that competition in the past can be ruled out as a factor in originally bringing about the isolating behavior.

Two closely related species of aquatic birds, the shag (*Phalacrocorax aristotelis*) and the cormorant (*P. carbo*), are found together in England during the breeding season, but feed on entirely different kinds of fish. Therefore, they are not in direct competition for food resources (that is, the niche of the two species is different). This is an example of **neutralism** (0 0) as described in Table 7-1 and illustrated in Figure 7-1.

5 Positive/Negative Interactions: Predation, Herbivory, Parasitism, and Allelopathy

Statement

Predation and *parasitism* are familiar examples of interactions between two populations that result in negative effects on the growth and survival of one population and positive or beneficial effects on the other. When the predator is a primary consumer (usually an animal), and the prey or "host" is a primary producer (plant), the interaction is termed **herbivory**. When one population produces a substance harmful to a competing population, the term **allelopathy** is commonly used for the interaction. Accordingly, there are a variety of + - relationships.

The negative effects tend to be quantitatively small when the interacting populations have had a common evolutionary history in a relatively stable ecosystem. In other words, natural selection tends to lead either to a reduction in detrimental effects or to the elimination of the interaction altogether, as the continued severe depression of a prey or host population by the predator or parasite population can only lead to the extinction of one or both populations. Consequently, a severe impact of predation or parasitism is most frequently observed when the interaction is of recent origin (when two populations have just become associated) or when large-scale or sudden changes have occurred in the ecosystem (as might be produced by humans). In other words, over the long term, parasite-host or predator-prey interactions tend to evolve to coexistence (recall the discussion of reward feedback in Chapter 4).

Explanation and Examples

It is frequently difficult for students, or for people in general, to approach the subject of parasitism and predation objectively. People have a natural aversion to parasitic organisms, whether bacteria or tapeworms. Although human effects on Earth as pred-