

found that monarch caterpillars can sequester the highly toxic cardiac glycosides present in the milkweed plants on which they feed, thereby providing a highly effective defense against bird predators not only for the caterpillar but also for the adult butterfly. Thus, the monarch butterfly has evolved the ability to feed on a plant that is unpalatable to other insects, and it also uses the plant poison for its own protection against predators. It can be assumed that the numerous cases of mutualism described in the next section involve coevolution at various levels.

3 Evolution of Cooperation: Group Selection

Statement

To account for the incredible diversity and complexity of the biosphere, scientists have postulated that natural selection operates beyond the species level and beyond coevolution. **Group selection**, accordingly, is defined as natural selection between groups or assemblages of organisms that are not necessarily closely linked by mutualistic associations. Group selection theoretically leads to the maintenance of traits favorable to populations and communities that may be selectively disadvantageous to genetic carriers within populations. Conversely, group selection may eliminate, or keep at low frequencies, traits unfavorable to the survival of the species but selectively favorable within populations or communities. Group selection involves positive benefits that an organism may exert on the community organization required for that organism's continued survival.

Explanation and Examples

The "struggle for existence" and "survival of the fittest" (T. H. Huxley 1894) are not just a matter of "dog eat dog." In many cases, survival and successful reproduction are based on cooperation rather than competition. How cooperation and elaborate mutualistic relationships get started and become genetically fixed has been difficult to explain in evolutionary theory, because when individuals first interact, it is nearly always advantageous for each individual to act in its own interest rather than to cooperate. Axelrod and Hamilton (1981) analyzed the evolution of cooperation and devised a model based on the *prisoner's dilemma* game and on the theory of reciprocal genetic theory. In the prisoner's dilemma game, two "players" decide whether to cooperate or not on the basis of immediate benefits. On the first encounter, a decision *not* to cooperate (to *defect*) yields the highest reward for each individual, regardless of what the other individual does. However, if *both* choose not to cooperate, they both do worse than if both had cooperated. If individuals continue to interact (the "game" continues), the probability is that cooperation may be selected on a trial basis and its advantages recognized. Deductions from the model show that cooperation based on such reciprocity can get started in an asocial environment and then develop and persist once fully established. Constant close contact between numerous individuals such as microorganisms and plants enhances the possibilities for interaction with mutual benefit, such as has evolved between nitrogen-fixing bacteria and legumes.

It has also been suggested that *altruism*—sacrifice of fitness by one individual for the benefit of another—in related individuals (such as parents and offspring) can be the start of an evolution toward cooperation (even in unrelated species). Once genes favoring reciprocity have become established by kin selection, cooperation can spread into circumstances of less and less relatedness.

David Sloan Wilson (1975, 1977, 1980) stated the case for group selection as follows (1980, p. 97):

Populations routinely evolve to stimulate or discourage other populations upon which their fitness depends. As such over evolutionary time an organism's fitness is largely a reflection of its own effect on the community and the reaction of the community to that organism's presence. If this reaction is sufficiently strong, only organisms with a positive effect on their community persist.

Wilson argued that selection between "structured demes" (closely knit genetic segments of a population) facilitates group selection. He also drew an analogy between the paradox of individual versus community fitness in biological communities and private benefit compared with public benefit in human communities.

Predator-prey and parasite-host interactions tend to become less negative over time. Gilpin (1975) proposed group selection in the development of a "prudence" trait that leads predators and parasites not to overexploit their prey or hosts, because to do so could lead to the extinction of both species involved in the interaction. The history of the myxomatosis virus introduced to control European rabbits (actually hares) in Australia is an example of selection for reduced virulence. When first introduced, the parasite killed the rabbit within a few days. Subsequently, the virulent strain was replaced by a less virulent one that took two to three times as long to kill the host; hence, the mosquitoes that transmit the virus had a longer time to feed on infected rabbits. Because the avirulent strain did not destroy its food resource (rabbit) as rapidly as the virulent strain, more and more avirulent-type parasites were produced and were available for transmission to new hosts. Thus, interdemic selection favored the avirulent over the virulent strain; otherwise, both parasite and host would eventually have become extinct.

Although few doubt that group selection occurs, its importance in evolutionary history remains controversial. The organized complexity that has developed in the natural world is difficult to explain solely by selection at the individual and species level; hence, higher-level selection and the process of self-organization have to play major roles. For more on group selection, see E. O. Wilson (1973, 1980, 1999), D. S. Wilson (1975, 1977, 1980), and Maynard Smith (1976).

4 Interspecific Competition and Coexistence

Statement

Competition in the broadest sense refers to the interaction of two organisms striving for the same resource. **Interspecific competition** is any interaction that adversely affects the growth and survival of two or more species populations. Interspecific competition can take two forms: (1) *interference competition*; and (2) *exploitation competition*. The tendency for competition to bring about an ecological separation of closely

related or otherwise similar species is known as the *competitive exclusion principle*. Simultaneously, competition triggers many selective adaptations that enhance the coexistence of a diversity of organisms in a given area or community.

Explanation and Examples

Ecologists, geneticists, and evolutionists have written much about interspecific competition. Generally, the word *competition* is used in situations in which negative influences are due to a shortage of resources used by both species. Interspecific competition is frequently discussed in terms of direct physical interaction versus exploitation competition. **Interference competition** occurs when two species come into direct contact with each other, such as fighting or defending a territory. **Exploitation competition** occurs when one species exploits a resource, such as food, space, or prey, in common with another species but without direct contact with that species. This indirect exploitation of resources can provide a competitive advantage for one species against another.

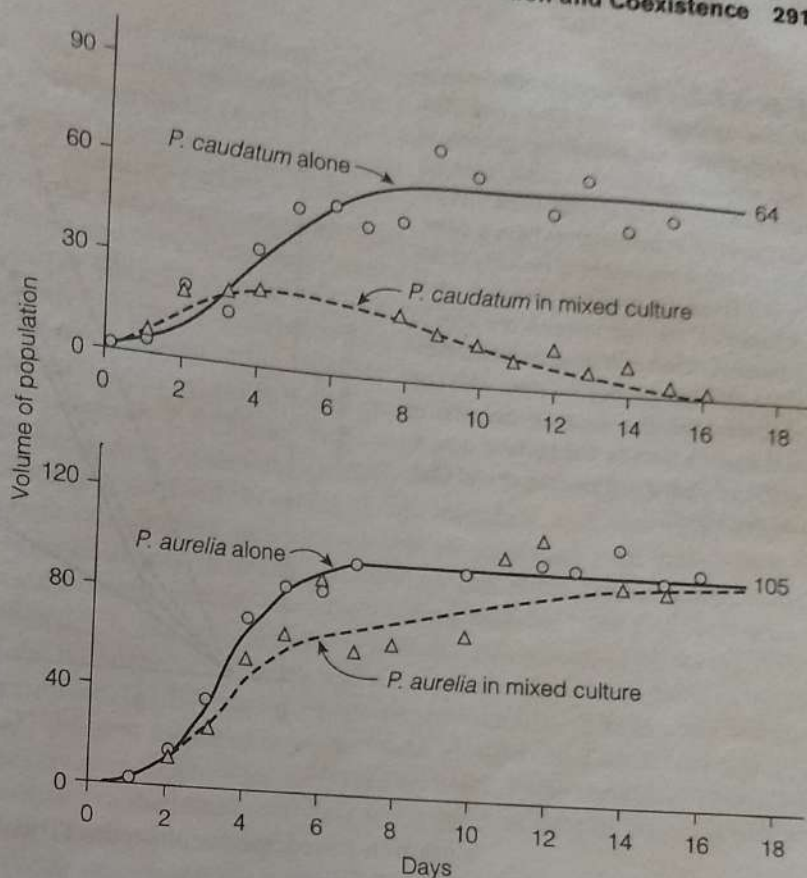
The competitive interaction can involve space, food or nutrients, light, waste materials, susceptibility to carnivores, disease, and many other types of mutual interactions. The results of competition are of interest to evolutionary biologists and have been much studied as one of the mechanisms of natural selection. Interspecific competition can result in equilibrium adjustments between two species or, if severe, in one species population replacing another, or forcing the other to occupy another space or to use another food (whatever was the basis of the original competitive action). Closely related organisms having similar habits or morphologies often do not occur in the same places. If they do occur in the same places, they frequently use different resources or are active at different times. The explanation for the ecological separation of closely related (or otherwise similar) species has come to be known as the **Gause principle** (Gause 1932), after the Russian biologist who first observed such separation in experimental cultures (see Fig. 7-2), or the **competitive exclusion principle**, as designated by Hardin (1960).

One of Gause's original experiments with ciliates (Gause 1934, 1935) is a classic example of competitive exclusion (Fig. 7-2). *Paramecium caudatum* and *Paramecium aurelia*, two closely related ciliate protozoans, when grown in separate cultures, exhibited typical sigmoid population growth and maintained a constant population level in culture medium that was maintained with a fixed density of food items (bacteria that did not themselves multiply in the medium and thus could be added at frequent intervals to keep the food density constant). When both protozoans were placed in the same culture, however, *P. aurelia* alone survived after 16 days. Neither organism attacked the other or secreted harmful substances; *P. aurelia* populations simply had a more rapid growth rate (higher intrinsic rate of increase) and thus "out-competed" *P. caudatum* for the limited amount of food under the existing conditions (a clear case of exploitation competition). By contrast, both *Paramecium caudatum* and *Paramecium bursaria* were able to survive and reach a stable equilibrium in the same culture medium. Although they were competing for the same food, *P. bursaria* occupied a different part of the culture, where it could feed on bacteria without competing with *P. caudatum*. Thus, the habitat proved to be sufficiently different for the two species to coexist, even though their food was identical.

Some of the most widely debated theoretical aspects of competition theory re-

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Figure 7-2. Competition between two closely related species of protozoa that have similar niches. When separate, *Paramecium caudatum* and *Paramecium aurelia* exhibit normal sigmoid growth in controlled cultures with constant food supply; when both are cultured together, *P. caudatum* is eliminated (after Gause 1932).



volve around what has become known as the **Lotka-Volterra equations**, so termed because the equations were proposed as models by Lotka (1925) and Volterra (1926) in separate publications. They are a pair of differential equations similar to the one outlined in Section 1. Such equations are useful for modeling predator-prey, parasite-host, competition, or other two-species interactions. In terms of competition within a limited space where each population has a definite K or equilibrium level, the simultaneous growth equations can be written in the following forms, using the logistic equation as a basis:

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

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

where N_1 and N_2 are the numbers of Species 1 and 2, respectively, α is the *competition coefficient* indicating the inhibitory effect of Species 2 on Species 1, and β is the corresponding competition coefficient signifying the inhibition of Species 1 on Species 2.

To understand competition, one must consider not only the conditions and population attributes that may lead to competitive exclusion but also the situations under which similar species coexist, because large numbers of species do share common resources in the open systems of nature. Figure 7-3 presents what might be termed the *Tribolium-Trifolium model*, which includes an experimental demonstration of ex-