11 Interactions Between Populations

Direct Interactions

The traditional approach to population interactions has been to consider just the direct pairwise interactions. In this simplistic view of things, two populations may or may not affect each other; if they do, the influence may be beneficial or adverse. By designating a detrimental effect with a minus, no effect with a zero, and a beneficial effect with a plus, all possible population interactions can be conveniently classified. When neither of two populations affects the other, the interaction is designated as (0, 0). Similarly, a mutually beneficial relationship is (+, +) and a mutually detrimental one is (–, –). Other possible interactions are (+, –), (–, 0), and (+, 0), making a total of six fundamentally different ways in which populations can interact (Table 11.1).

Table 11.1 Summary of Direct Pairwise Interactions Between Two Populations

Type of Interaction	**Species A**	**Species B**	**Nature of Interaction**
Competition	–	–	Each population inhibits the other
Predation, parasitism, and Batesian mimicry	+	–	Population A, the predator, parasite, or mimic, kills or exploits members of population B, the prey, host, or model
Mutualism, Müllerian mimicry	+	+	Interaction is favorable to both (can be obligatory or facultative)
Commensalism	+	0	Population A, the commensal, benefits whereas B, the host, is not affected
Amensalism	–	0	Population A is inhibited, but B is unaffected
Neutralism	0	0	Neither party affects the other

Source: Adapted from Odum (1959) after Haskell (1947).

Competition (–, –) takes place when each of two populations affects the other adversely. Typically, both require the same resource(s) that is (are) in short supply; the presence of each population inhibits the other. If the resource is another population (a prey species), competition is indirect and mediated by means of resource depression — this type of competition is termed **exploitation competition**. Other kinds of competition also occur. For example, competition can also be direct, as in agonistic encounters such as allelopathy or interspecific territoriality (known as **interference competition**). Predation (+, –) occurs when one population affects another adversely but benefits itself from the interaction. Usually a predator kills its prey and consumes part or all of the prey organism. (Exceptions include lizards losing their tails to predators and plants losing their leaves to herbivores.) Parasitism (+, –) is essentially identical to predation, except that the host (a member of the population being adversely affected) is usually not killed outright but is exploited over some period of time. Thus, parasitism can in some ways be considered as a "weak" form of predation; Batesian mimicry (p. 320) and herbivory could be placed here. Interactions that benefit both populations (+, +) are classified as mutualisms. In some mutualisms, the association is obligatory (neither population can exist without the other), but in others the interaction is facultative because it is not an essential condition for survival of either population (Müllerian mimicry, pp. 320–321, falls under this heading). When one population benefits while the other is unaffected, the relationship is termed commensalism (+, 0). Amensalism (–, 0) is said to occur when one population is affected adversely by another but the second is unaffected. Neutralism (0, 0) occurs when the two populations do not interact and neither affects the other in any way whatsoever; it is thus of little ecological interest. True neutralism is likely to be very rare or even nonexistent in nature because there are probably indirect interactions between all the populations in any given ecosystem, although their significance may be minimal.

Three of the six population interactions, competition, predation, and mutualism, are of overwhelming importance; an entire chapter is devoted to competition and another to predation. Mutualisms are considered later in this chapter.

Complex Population Interactions

Interactions among populations often become quite intricate, particularly in diverse communities. Colwell (1973) studied interactions among four species of nectar-feeding birds, four species of flowering plants, and two species of mites (Figure 11.1) in Costa Rica. Three hummingbirds, *Colibri thalassinus*, *Eugenes fulgens*, and *Panterpe insignis*, compete for nectar and are pollinating vectors for the plants. Flowers of various species differ in corolla lengths and are visited differentially by hummingbirds that differ in beak lengths. Only *Eugenes*, which has the longest

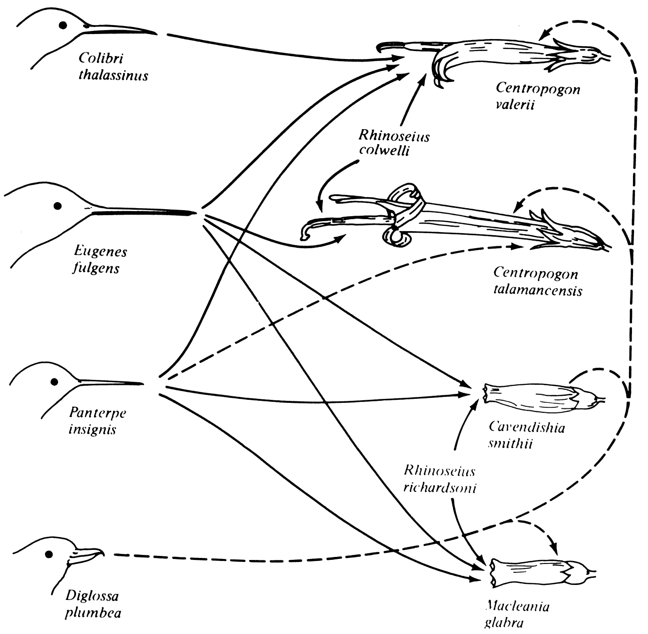


Figure 11.1. Patterns of exploitation of flowers of four species by various birds and mites. Broken lines indicate illegitimate visits by nectar thieves, which pierce the base of the corolla. [From Colwell (1973). Copyright © 1973 by The University of Chicago Press.]

beak, can reach the nectar of *Centropogon talamancensis* through its very long corolla (Figure 11.1). However, *Panterpe* hummingbirds steal nectar from this *Centropogon* species by piercing the base of flower corollas. The fourth species of bird, *Diglossa plumbea*, is a nectar thief that obtains nectar from all four plant species by breaking their corolla bases. Two species of mites live within flowers of different plant species, moving among flowers by climbing up beaks and riding in hummingbird nostrils. Both mite species are found on *Panterpe* and *Eugenes* hummingbirds, which make legitimate pollinating visits through the corollas of flowers of three and four species of plants, respectively. One mite, *Rhinoseius colwelli*, is restricted to flowers of the two species of *Centropogon* and never occurs in either *Macleania* or *Cavendishia* flowers. The second species of mite, *R. richardsoni*, is found only in *Macleania* and *Cavendishia* flowers and never occurs in *Centropogon* flowers. Significantly, avian pollinator visits are structured so that transfers between *Macleania* and *Cavendishia* flowers are frequent, whereas transfers between flowers of these two species and those of *Centropogon* are much more infrequent. Experimental introductions of mites into flowers without mites showed that both species can live and reproduce successfully in the flowers normally occupied only by the other species. Adult male mites are extremely aggressive, particularly in interspecific encounters, and Colwell observed male *R. colwelli* killing *R. richardsoni*. Over evolutionary time, adult male mites may have reinforced the observed species-specific separation on flowers of different species by killing mites of the other species when these made the mistake of leaving their hummingbird carriers to invade a flower of the wrong species containing adult males of the other species of mite. Among these ten species, then, interactions include intense interference competition (between the two species of mites), exploitation competition (among nectarivorous birds), facultative mutualism (between hummingbird pollinators and plants), parasitism (between plants and nectar thieves), and commensalism (between mites and their hummingbird carriers).

Mutualistic Interactions and Symbiotic Relationships

Symbiosis means "living together." Usually the term is used only to describe pairs of organisms that live together without harming one another, thereby excluding parasitism (+, –) and amensalism (–, 0), in which one party is affected adversely (see Table 11.1 for explanation of symbols). Hence, symbiotic relationships include mutualism (+, +), commensalism (+, 0), and neutralism (0, 0). Obligate mutualisms can be distinguished from facultative ones. As pointed out before, these various types of interactions can change in evolutionary time and grade into one another. Although mutualism is a symmetric relationship, there may nevertheless usually be an asymmetry in costs versus benefits to each of the parties concerned (a conflict of interests arises even in mutualistic relationships!). Mutualisms may evolve from parasitic relationships (see p. 324).

As pointed out earlier, true neutralism is uninteresting as well as uncommon and therefore need not be considered. However, mutualism and commensalism are fairly widespread, particularly in diverse communities. Many organisms have formed mutualisms with ants (DeVries 1991, 1992). For example, the bullhorn *Acacia* supports a colony of ants, feeding them both nectar and protein; the ants in turn protect the plant from a wide variety of herbivores (when ants are removed by poisoning them, these plants are quickly defoliated).

Likewise, caterpillars in many different Lepidopteran families have evolved close mutualisms with ants to defend themselves against parasites and predators (Pierce 1985). These caterpillars "sing" to the ants as well as feed them a nutritious protein-rich diet (DeVries 1991, 1992). Numerous other cases are also known. In many legumes such as mesquite, root nodules house bacteria that fix atmospheric nitrogen. Mycorrhizae, or fungal roots, supply mineral nutrients to host plants but in return gain organic carbon from the host.

Many deep-sea fish harbor bioluminescent bacteria, exploiting their light-emission abilities to the fish's own ends in the dark depths of the oceans. Certain types of algae are endozoic, actually living inside the cells of animal hosts, particularly coelenterates such as corals and *Hydra*. In these situations, algal photosynthate is shared with the host. Some invertebrate "hosts" actually digest away most of the alga, retaining ("kidnapping"?) just the chloroplasts, which continue to photosynthesize inside the animal.

Perhaps the ultimate in mutualistic interactions concerns the intriguing theory of endosymbiosis; very strong evidence exists that certain of the cell organelles found in higher organisms (eukaryotes), particularly chloroplasts and mitochondria, are actually the remnants of symbiotic prokaryotic organisms (Ehrman 1983; Margulis 1970, 1974, 1976) that have been permanently incorporated into the eukaryotes.

Some birds ride on the backs of water buffalo (the bird obtains food while the mammal is freed of many insect pests); other small birds pick between the teeth of crocodilians (the bird obtains food while the reptile gets its teeth cleaned). Certain ants exploit aphids for the latter's honeydew, tending their herds of hemipterans much like a shepherd watches over his flock. Other species of ants and termites actually cultivate fungi for food.

An African bird known as the honey guide has formed a unique alliance with the honey badger or ratel (a large skunk-like mammal); the honey guide locates a beehive and leads the honey badger to it, whereupon the mammal tears open the bee's nest and eats its fill of honey and bee larvae. Later the bird has its meal of beeswax and larvae. The honey guide can find beehives with relative ease but cannot open them, whereas the ratel is in just the opposite situation; cooperation clearly increases the efficiency of both species.

In marine environments, certain species of labrid fish are "cleaners," maintaining cleaning stations where other species of larger fish come to be cleaned of ectoparasites and bacteria, sometimes lining up rather like cars at a gas station. Interspecific displays are used in recognition. Cleaner fish are conspicuous and brightly colored. Interestingly, an unrelated fish species in another family, the saber-toothed blenny, has evolved that mimics cleaner fish, but brings woe to the unsuspecting large fish (these blennies eat the vascularized gill tissue of the large fish!).

Because most land plants cannot move, they often exploit animals both for pollination and for seed dispersal (some rely on wind, too). Seeds of many fruits pass unharmed through the intestines of herbivores and germinate to grow a new plant from the droppings of the animal dispersing agent. Colorful flowers with nectar and brightly colored fruits can only be interpreted as having been evolved to attract appropriate animals. Here, as in plant–herbivore interactions, a high degree of plant-animal specificity has arisen. Animals that pollinate a particular plant are referred to as pollinating vectors. As an example, in Central America different species of male euglossine bees are highly specific to particular species of tiny epiphytic orchids; male bees travel long distances between orchids. Different bee species are attracted by different orchid fragrances (Dressler 1968), as can be shown by putting out "baits" of artificially synthesized orchid "fragrances." (These male bees do not obtain nectar from the orchids they visit, but only obtain orchid products that the insects use for production of their own pheromones to attract females.) These bees are probably necessary for, and may have allowed the evolution of, the great diversity of tropical orchids, many of which are evidently quite rare and far apart. Such specificity of pollinating vectors ensures that the plant's pollen is transmitted to the ovules of its own species. Although female euglossine bees are not as specific to the plant species they pollinate as males, individual females travel distances up to 23 kilometers (Janzen 1971a) and regularly move long distances between sparsely distributed plants in gathering nectar and pollen; thus, they probably promote outcrossing among tropical plants at low densities. Indeed, Janzen suggests that such "traplining" by female bees may actually permit the very existence of plant species forced to very low densities by factors such as competition and predation on their seeds and seedlings.

Some pollinators, such as *Heliconius* butterflies (Gilbert 1972), obtain amino acids from the pollen of plants they pollinate. Because production of nectar and pollen (and fruit) requires matter and energy, attracting animal pollinators (and seed dispersers) has its costs to the plant. Nectar and fruits are usually rich in sugars and other carbohydrates but contain relatively little protein; in contrast, pollen and seeds contain considerably greater amounts of nitrogen and other limiting materials. Due to the frequent scarcity of such vital nutrients, carbohydrates are presumably cheaper for a plant to produce than amino acids and proteins. Thus, pollen-eating pollinators presumably cost a plant considerably more than strict nectar feeders. Returns from visiting a flower (or eating a fruit) must be great enough to an animal pollinator or seed disperser to make it worthwhile, yet small enough that the animal will travel the distance necessary to disperse the pollen or seeds. This intricate energetic interplay between plants and their pollinators is reviewed by Heinrich and Raven (1972).

Obligate mutualisms are less common than facultative ones, probably because both populations depend completely on the relationship and neither can survive without the other. A very high degree of interdependency occurs between figs and the agaonid fig wasps that pollinate them (wasp eggs are laid inside fig fruits where larvae develop). There are hundreds of species of figs, each with its own species of wasp (this is a good example of tight, or species-specific, coevolution). Similarly, termites cannot themselves produce enzymes to digest the cellulose in wood, but by harboring in their intestines a population of protozoans that can make such enzymes, the insects are able to exploit wood successfully as a food source. Neither termite nor protozoan could survive without the other. These intestinal endosymbionts are passed on from one generation of termites to the next through exchange of intestinal contents. Large grazing mammals have a rumen in their gut system, an anaerobic chamber that houses endosymbiotic protozoans and bacteria, which similarly assist in digestion. Another putative example of mutualism is lichens, which are composed of a fungus and an alga; the fungus provides the supportive tissue, whereas the alga performs photosynthesis. (Algae of some lichens can be grown without the fungi.)

Commensalism occurs when one population is benefited but the other is unaffected (+, 0). Small epiphytes such as bromeliads and orchids, which grow on the surfaces of large trees without obvious detriment to the tree, might be an example. A well-documented case of commensalism is the association between cattle egrets and cattle (Heatwole 1965). These egrets follow cattle that are grazing in the sun and capture prey (crickets, grasshoppers, flies, beetles, lizards, frogs) that move as cattle approach. The number of cattle egrets associated with cattle is strongly dependent on the activities of the cattle; thus, Heatwole observed fewer egrets than expected on a random basis near resting cattle, but nearly twice as many egrets as expected (if the association were entirely random) accompanied cattle that were actively grazing in the sun. Since the birds seldom take prey (such as ticks and other ectoparasites) directly from the bodies of the cattle, the mammals probably benefit little from their relationship with egrets. Moreover, egret feeding rates and feeding efficiency are markedly higher when these birds are associated with cattle (Table 11.2).

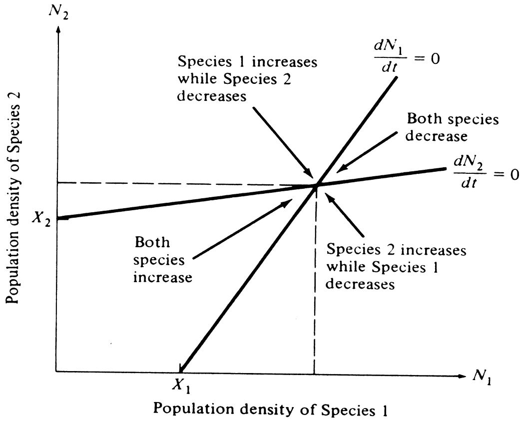


Figure 11.2. Isoclines for two species with a mutually beneficial interaction and a stable joint equilibrium (see text).

Table 11.2 Various Aspects of the Association of Cattle Egrets with Cattle

Category	Number of Cattle	Percent Cattle	Number of Associated Egrets	
			Expected	Observed
Grazing in sun	735	39.1	239	439
Grazing in shade	55	2.9	18	21
Standing in sun	146	7.8	48	46
Standing in shade	257	13.7	84	17
Lying in sun	503	26.8	164	69
Lying in shade	143	7.6	47	17
Walking	39	2.1	13	3
Total	1878	100.0	612	

	Mean Number Per Minute	Number of Times Count Was Higher Than for Opposite Egret	Number of Associated Egrets
Feedings, $N = 84$			
Associated	2.34	58	69
Nonassociated	1.71	26	31
Steps, $N = 62$			
Associated	20.1	7	11
Nonassociated	32.1	55	89
Feeding/step, $N = 59$			
Associated	0.129	52	88
Nonassociated	0.051	7	12

Note: Upper section shows numbers of egrets associated with cattle engaged in different activities. Lower section shows feeding rates, steps taken per prey item (energy expended in foraging), and feeding efficiencies of egrets associated with and not associated with cattle.
Source: From Heatwole (1965).

Because of their plus-plus and symmetric nature, mutualisms exhibit positive feedback and hence can run away — for this reason, they are destabilizing unless the intraspecific negative self-damping is stronger than the interspecific positive mutualistic effects. Mutualistic relationships are easily modeled with equations similar to the Lotka–Volterra competition equations simply by changing the signs of the alphas. (See Chapter 12, p. 241, for variables used in Lotka–Volterra equations.) *K*'s have also been changed to *X*'s since they no longer represent maximal densities.

$$dN_1/dt = r_1N_1\ (\{X_1 - N_1 + \alpha_{12}N_2\}\ /\ X_1) \qquad (1)$$

$$dN_2/dt = r_2N_2\ (\{X_2 - N_2 + \alpha_{21}N_1\}\ /\ X_2) \qquad (2)$$

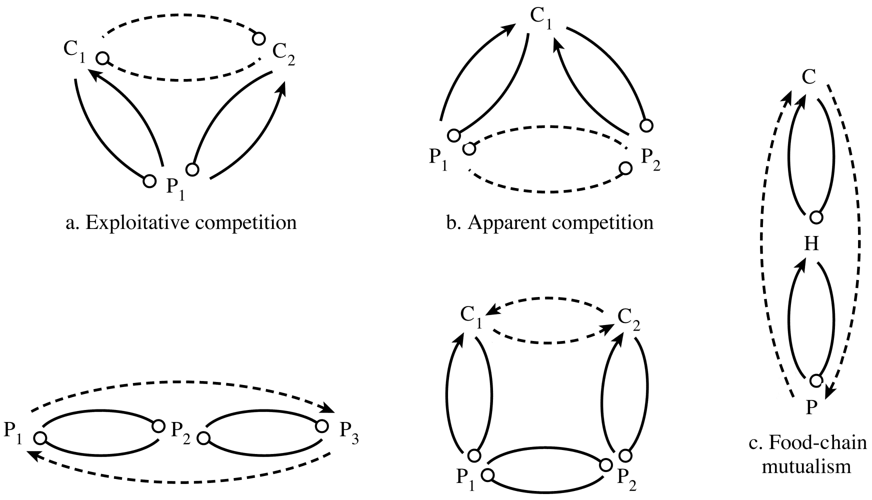
Equilibrium conditions are described by a pair of linear equations and are shown graphically in Figure 11.2.

Populations reach equilibrium at density X_1 or X_2 in the absence of the other species, and each population's equilibrium density is increased by increasing the density of the other species. If both X_1 and X_2 are positive and if α_{12} and α_{21} are chosen so that isoclines cross, the joint equilibrium is stable. More realistic, but also more complex, cost-benefit models of mutualism are discussed by Roughgarden (1975), Vandermeer and Boucher (1978), Dean (1983), Wolin and Lawlor (1984), Wolin (1985), and Post et al. (1985).

Indirect Interactions

Superimposed on direct pairwise interactions, more subtle indirect interactions are mediated through other members of the community concerned. Darwin anticipated the concept of indirect interactions and gave as an example interactions among cats, field mice, humblebees (bumblebees), and red clover. The bees pollinate clover, but field mice raid bee nests and eat bee larvae. Lots of clover grows around villages, presumably because cats keep mice populations down, allowing bumblebees to flourish which in turn assists clover. Darwin's staunch defender Huxley carried Darwin's example farther and noted that spinsters (who have lots of cats) facilitate Britain's naval prowess because strong sailors must be well fed and British beef thrives on clover. Here we have a long string with a path length of seven: spinsters —> cats —o mice —o bees —>clover —>beef —>sailors —>naval prowess!

Five different sorts of indirect interactions involving three or four different species' populations are depicted in Figure 11.3. Pointed arrows indicate beneficial effects whereas circle-headed "arrows" depict detrimental interactions. Solid arrows are direct interactions, dashed arrows represent indirect interactions. Two consumers sharing a common prey may compete indirectly via classical **exploitation competition** (resource depression). Two prey species may appear to compete because if either increases, a shared predator also increases, which operates to the detriment of the other prey population — Holt (1977) called this **apparent competition**. Three species' populations at three different trophic levels result in what has been termed a **food chain mutualism** (such **vertical** interactions have also been called **cascading effects** or **trophic cascades**). The plant and carnivore are indirect mutualists because the plant generates herbivores that constitute food for the carnivore (a "bottom-up" effect). The carnivore reduces herbivory, which benefits the plants (a "top-down" effect). An example was provided by Power et al. (1985): fish-eating bass prey upon herbivorous minnows in pools of an Oklahoma creek. When bass were removed (pools were fenced to keep these predators out) and minnow densities raised, the standing crop of algae diminished. With the re-addition of bass, minnows retreated to shallow water and algal densities increased significantly over the next two weeks.



a. Exploitative competition

b. Apparent competition

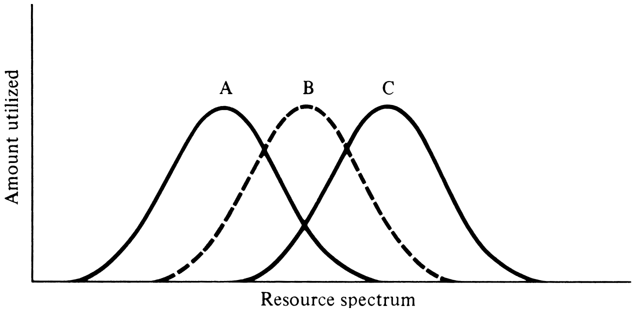
c. Food-chain mutualism

d. Competitive mutualism

e. Facilitation

Figure 11.3. Pointed arrows indicate beneficial effects whereas circle-headed "arrows" depict detrimental interactions. Solid arrows are direct interactions, dashed arrows represent indirect interactions. In all panels except (c) and (d), C's represent consumer species and P's represent prey species. In (c), C = carnivore, H = herbivore, and P = plant. In (d), all three P species are at the same trophic level. Numerous other sorts of indirect interactions are also possible.

Three species' populations at the same trophic level, arranged so that one species (P_2) is sandwiched between two others, can also result in indirect mutualism (referred to as **horizontal interactions**). Populations P_1 and P_3 are indirect mutualists because each inhibits the other's competitor P_2. Such a situation can also arise even when P_1 and P_3 are actually weak competitors, so long as competitive interactions with P_2 are strong (this has been called **competitive mutualism** — Pianka 1981). An alternate depiction of how indirect competitive mutualism arises is shown in Figure 11.4. A four-species system that results in an indirect mutualism is termed **facilitation** (Vandermeer et al. 1985). In this case, consumer populations C_1 and C_2, which do not interact directly but consume different prey species, interact indirectly because their prey compete: if consumer C_1 increases, its prey P_1 decreases, which in turn reduces the competition with P_2, hence allowing an increase in this second prey population (P_2), providing more food for consumer C_2. Many other indirect interactions with still longer path lengths are also possible. For example, in a food chain with four trophic levels (path length = 3), the top-down



effect from the top predator to the bottom trophic level is negative, whereas the bottom-up effect is positive.

Figure 11.4. Conditions that can lead to competitive mutualism between species. Species A and C overlap moderately in their utilization of resources, so that, in isolation, these two species are potentially weak competitors. However, both species overlap more extensively with a third species, Species B, and hence potentially experience intense competition with Species B. Since each species A and C exerts a stronger influence on Species B than they do on one another, when all three species occur together, each exerts strong competition on Species B, thus reducing the intensity of competition between Species B and the other. Resulting *indirect* effects between Species A and C, as mediated through Species B, are beneficial (each species reduces the fitness of a strong competitor of the other species). Hence the net interaction between Species A and C changes qualitatively in the presence or absence of Species B.

An indirect effect can be defined mathematically as the product of all the various direct effects along a directed series of links, or a pathway, in which no species node is passed through more than once (Lane 1985). Such a path product represents the indirect effect between two nodes that may also be connected by a direct effect. Typically, the longer the pathway by which an indirect effect is mediated, the longer the time lag required for the effect to be transmitted from one node to another. Thus, indirect effects typically take longer to occur than direct effects. Positive indirect effects can arise both by means of mutualistic links and by means of products of an even number of negative links. If, however, there are an odd number of negative links in a pathway, the overall indirect effect is negative. Indirect effects are usually weaker than direct effects. However, because there are many more indirect effects than direct ones in a given system, the former can assume paramount importance even though they are weak. Indirect effects may actually oppose direct effects, and if their overall effects are intense enough, the overall net effect of one population on another, sometimes termed the "community effect," can actually be reversed. Although this sort of double thinking seems circuitous and complex, it may prove vital to understanding community organization; opposing direct versus indirect interactions would moderate each other, leaving a target species only weakly affected.

Indeed, an interaction between any given pair of populations depends vitally on the complex network of other interactions within which the pair concerned is embedded. Indirect effects render interpretation of simple experiments and observations extremely difficult.

Selected References

Direct Interactions

Haskell (1947, 1949); Krebs (1972); Levins (1968); MacArthur (1972); MacArthur and Connell (1966); MacArthur and Wilson (1967); Odum (1959, 1971).

Complex Population Interactions

Colwell (1973); Seifert and Seifert (1976).

Mutualistic Interactions and Symbiotic Relationships

Addicot (1985); Allee (1951); Allee et al. (1949); Axelrod and Hamilton (1981); Boucher et al. (1982, 1985); Briand and Yodzis (1982); Colwell (l973); Dean (1983); DeVries (1991a, 1991b, 1992); Dressler (1968); Ehrman (1983); Gilbert (1971, 1972, 1979); Heatwole (1965); Heinrich and Raven (1972); Janzen (1966, 1967, 1971a, 1971b); Margulis (1970, 1974, 1976); May (1982); Pierce (1985); Post et al. (1985); Roughgarden (1975); Seifert and Seifert (1976); Vandermeer (1980); Vandermeer and Boucher (1978); Whittaker (1970); Wolin (1985); Wolin and Lawlor (1984).

Indirect Interactions

Bender et al. (1984); Brown (1987); Brown et al. (1986); Darwin (1857); Higashi and Burns (1991); Holt (1977); Kerfoot and Sih (1987); Lane (1985, 1986); Lawlor (1979, 1980); Levine (1976); Patten (1983); Pianka (1980, 1981b, 1987); Power et al. (1985); Strauss (1991); Vandermeer (1980); Vandermeer and Boucher (1978); Vandermeer et al. (1985); D. S. Wilson (1986); Wooton (1993, 1994).