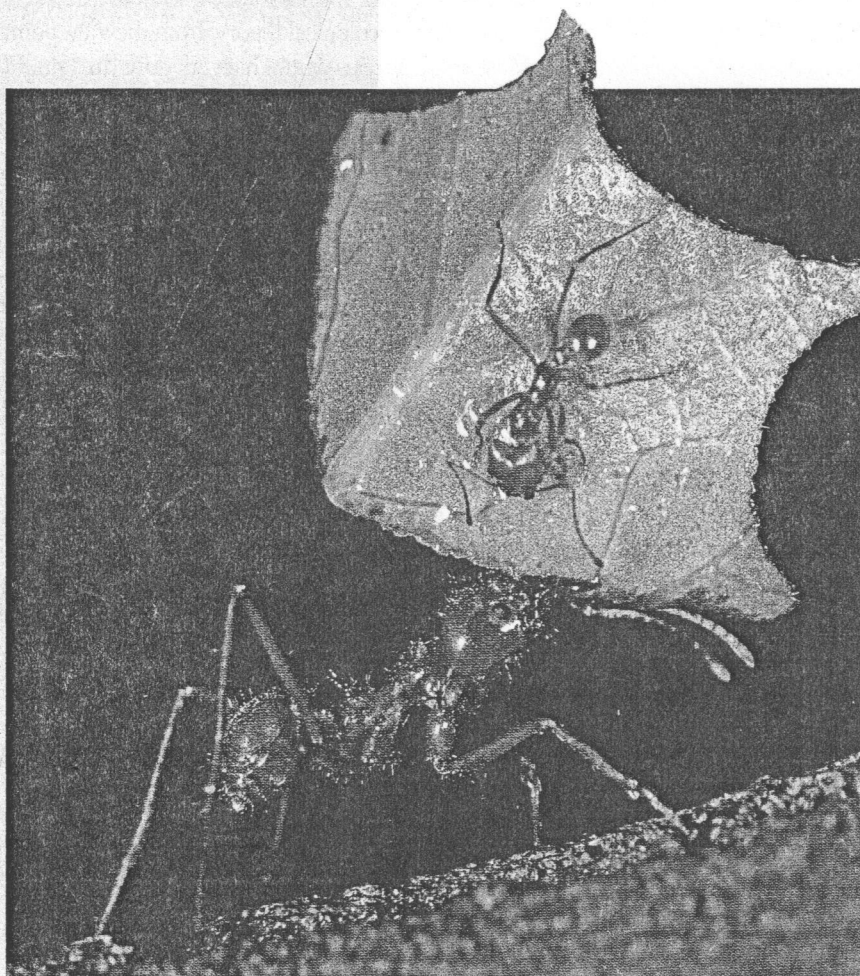


Coevolution: Evolving Interactions among Species



Interspecies interactions.

Atta colombica and other leaf-cutter ants feed only on fungi that they cultivate on fragments of leaves (see Figure 2.4B). The mutually adapted ants and fungi are part of a web of interactions with other fungi and bacteria. (Photo © Gavriel Jecan/AGE Fotostock.)

If you walk through a forest in many parts of tropical America, you are likely to encounter large, reddish ants, each carrying a fragment of a leaf, rushing by the hundreds along their highway, a track worn into the soil by the tramp of many thousands of little ant feet in days and months past. They are leaf-cutter ants, genus *Atta* or *Acromyrmex*, transporting massive amounts of fresh leaf material to their nest, a series of underground caverns as much as 3 meters deep that may house 5 to 10 million worker ants, thousands of larvae, and their mother, the single queen who may live for 15 years and lay many millions of eggs. The ants do not eat

leaves. Rather, small workers in the caverns chew the leaf material into tiny fragments and insert these into gardens of fungi, the sole food of both the larval and adult ants. This species of fungus (see Figure 2.4B) is found nowhere else and is carried by young queens from their natal nest in a special cavity in the pharynx. The fungus, in the family Lepiotaceae, is related to other fungi that digest leaf litter, and the phylogenetically most basal of the fungus-growing ants (tribe Attini) provide their lepiotaceous fungi with bits of dead and decaying leaves, instead of live leaves (Hölldobler and Wilson 1990; Mueller et al. 2005). This exquisite mutualistic symbiosis, however, is threatened by other fungi, in the genus *Escovopsis*, that attack and devastate the fungal garden, and are likewise found only in the nests of attine ants. The ants counter this threat partly by removing *Escovopsis* spores, but mostly by

harboring actinomycete bacteria, *Pseudonocardia*, which produce an antibiotic that inhibits *Escovopsis* growth. The mutualistic bacteria are housed in many small pits on the ants' exoskeletons and are apparently nourished by secretions of glands, unique to attine ants, that open into these pits. These four organisms are thus bound to each other in a web of antagonistic and mutualistic interactions, and have been adapting to each other since the origin of the tribe Attini, about 50 Mya (Currie et al. 2003, 2006).

This is a rather extreme example of reciprocal adaptation of species to each other, but almost all species have adaptations for interacting with other species. Such adaptations, some of which are quite extraordinary, have enhanced the diversity of life and have had profound effects on the structure of ecological communities.

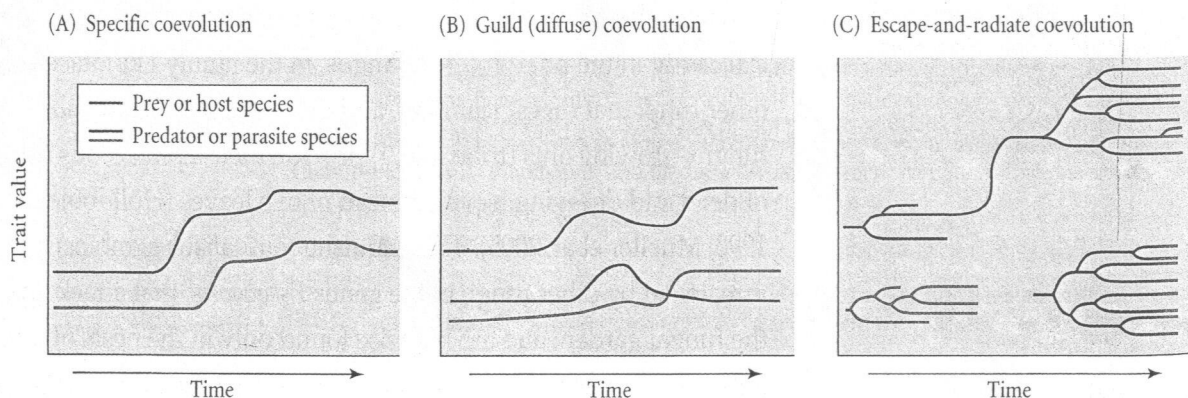
In this chapter, we will consider interactions among species in terms of their effects on the fitness of individual organisms (not, as in some ecological theory, from the viewpoint of their effects on population growth). Most of the species with which an individual might interact can be classified as **RESOURCES** (used as nutrition or habitat), **COMPETITORS** (for resources such as food, space, or habitat), **ENEMIES** (species for which the focal species is a consumable resource), or **COMMENSALS** (species that profit from but have no effect on the focal species). In **MUTUALISTIC** interactions (such as the relation between attine ants and their *Pseudonocardia* bacteria), each species obtains a benefit from the other. Some interactions are more complex, often because they are mediated by a third species. For example, different unpalatable species of butterflies that resemble one another may profit from their resemblance because predators that have learned to avoid one may avoid the other as well (see Figures 12.19 and 19.25). Moreover, the nature and strength of an interaction may vary depending on environmental conditions, genotype, age, and other factors. There is genetic variation, for example, in virulence within species of parasites and in resistance within species of hosts. Some mycorrhizal fungi, associated with plant roots, enhance plant growth in infertile soil but depress it in fertile soil. Thus the selection that species exert on each other may differ among populations, resulting in a "geographic mosaic" of coevolution that differs from one place to another (Thompson 1999).

Figure 19.1 Three kinds of coevolution. In each graph, the horizontal axis represents evolutionary time and the vertical axis shows the state of a character in a species of prey or host and one or more species of predators or parasites. (A) Specific coevolution. (B) Guild, or diffuse, coevolution, in which a prey species interacts with two or more predators. (C) Escape-and-radiate coevolution. One of several prey or host species evolves a major new defense, escapes association with a predator or parasite, and diversifies. Later, a different predator or parasite adapts to the host clade and diversifies.

The Nature of Coevolution

The possibility that an evolutionary change in one species evokes a reciprocal change in another species distinguishes selection in interspecific interactions from selection stemming from conditions in the physical environment. Reciprocal genetic change in interacting species, owing to natural selection imposed by each on the other, is **coevolution** in the narrow sense.

The term "coevolution" includes several concepts (Futuyma and Slatkin 1983; Thompson 1994). In its simplest form—**specific coevolution**—two species evolve in response to each other (Figure 19.1A). For example, Darwin envisioned predatory mammals, such as wolves, and their prey, such as deer, evolving ever greater fleetness, each improvement in one causing selection for compensating improvement in the other, in an "evolutionary arms race" between prey and predator. **Guild coevolution**, sometimes called **diffuse**



coevolution, occurs when several species are involved and their effects are not independent (Figure 19.1B). For example, genetic variation in the resistance of a host to two different species of parasites might be correlated (Hougen-Eitzman and Rausher 1994). In **escape-and-radiate coevolution**, a species evolves a defense against enemies and is thereby enabled to proliferate into a diverse clade (Figure 19.1C). For example, Paul Ehrlich and Peter Raven (1964) proposed that species of plants that evolved effective chemical defenses were freed from predation by most herbivorous insects, and thus diversified, evolving into a chemically diverse array of food sources to which different insects later adapted and then diversified in turn.

Phylogenetic Aspects of Species Associations

The term “coevolution” has also been applied to a history of parallel diversification, as revealed by concordant phylogenies, of associated organisms such as hosts and their parasites or endosymbionts. For example, aphids have endosymbiotic bacteria (*Buchnera*) that live in special cells and supply the essential amino acid tryptophan to their hosts (see Figure 16.22C). The phylogeny of these bacteria is completely concordant with that of their aphid hosts (Figure 19.2). The simplest interpretation of this pattern is that the association between *Buchnera* and aphids dates from the origin of this insect family, that there has been little if any cross-infection between aphid lineages, and that the bacteria have diverged in concert with speciation of their hosts. Differences among host species may reinforce host-specific associations and prevent symbionts from switching to distantly related species. For example, the phylogeny of feather lice in the genus *Columbicola*, which are parasites of pigeons and doves (Columbidae), is not a perfect match with that of their hosts, but it is similar enough to indicate that the lice have cospeciated with their hosts rather frequently, rather than switching from one species of columbid to another (Figure 19.3A). Dale Clayton and colleagues (2003) found that the body size of lice species is correlated with the body size of their host species, which have wider intervals between the adjacent units (barbs) that make up a feather. Therefore, lice fit better into the feathers of their normal host than into the feathers of larger or smaller birds. Lice transferred to smaller species of columbids had reduced survival because the birds could easily remove them by preening their feathers. On birds that could not preen effectively because their bills were fitted with bits, the lice survived quite well (Figure 19.3B). The investigators concluded that lice have seldom switched to bird species that differ in size because colonists would have had low fitness.

Associations between hosts and their parasites or symbionts rarely show much evidence of cospeciation. Instead, there are often mismatches, caused by horizontal transfer,

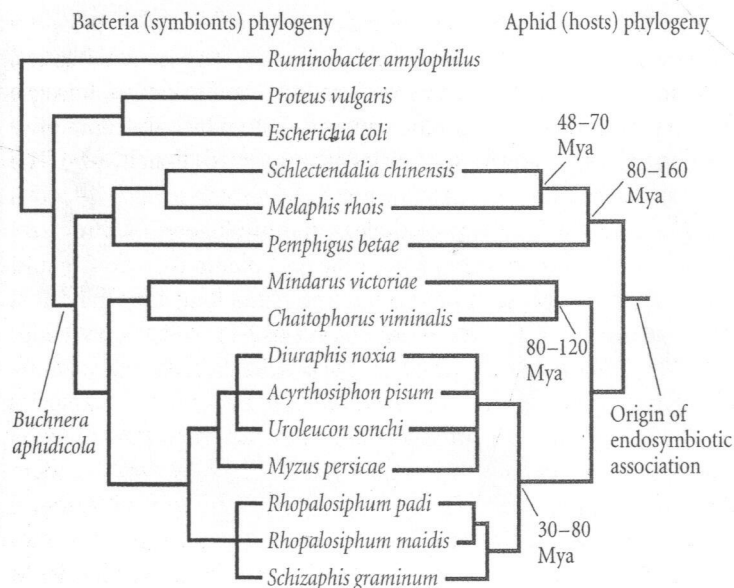


Figure 19.2 The phylogeny of endosymbiotic bacteria included under the name *Buchnera aphidicola* is perfectly congruent with that of their aphid hosts. Several related bacteria (names in red) were included as outgroups in this analysis. Names of the aphid hosts of the *Buchnera* lineages are given in blue. The estimated ages of the aphid lineages are based on fossils and/or biogeography. (After Moran and Baumann 1994.)

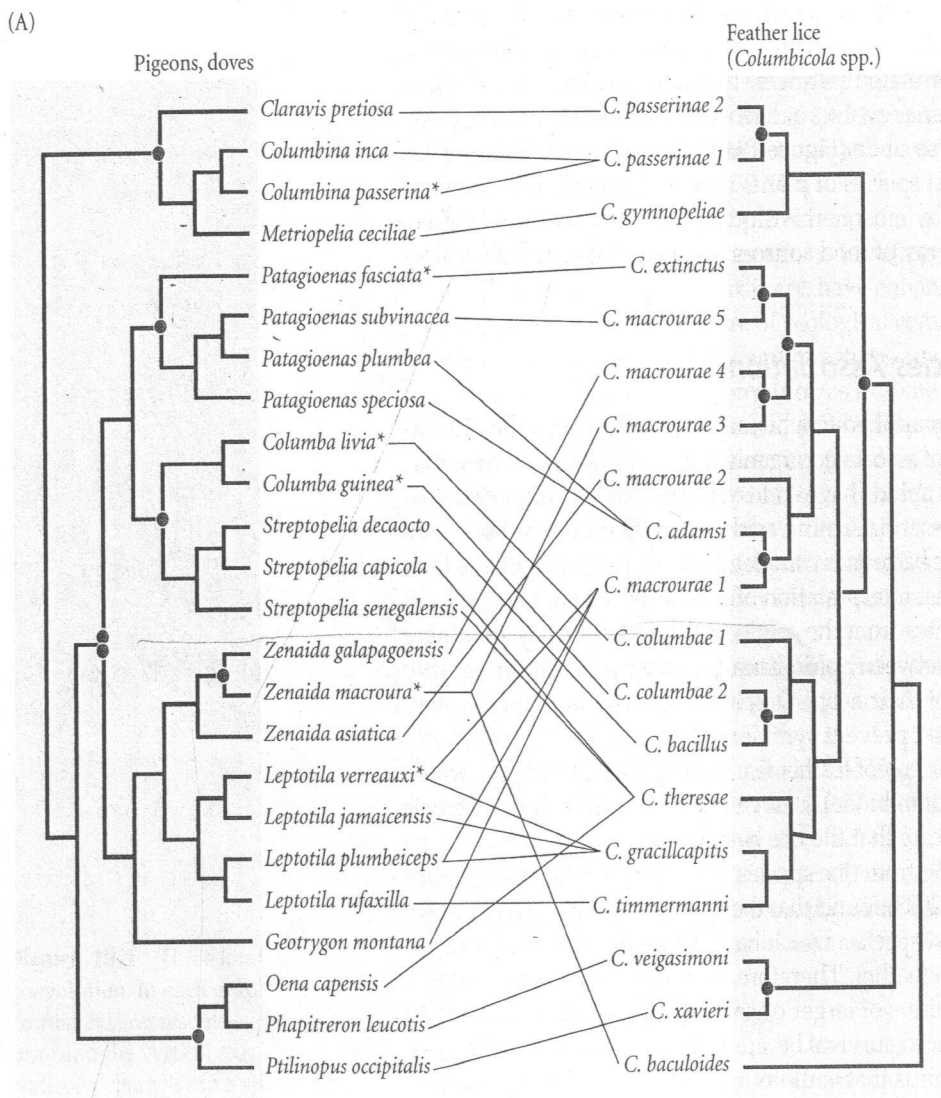
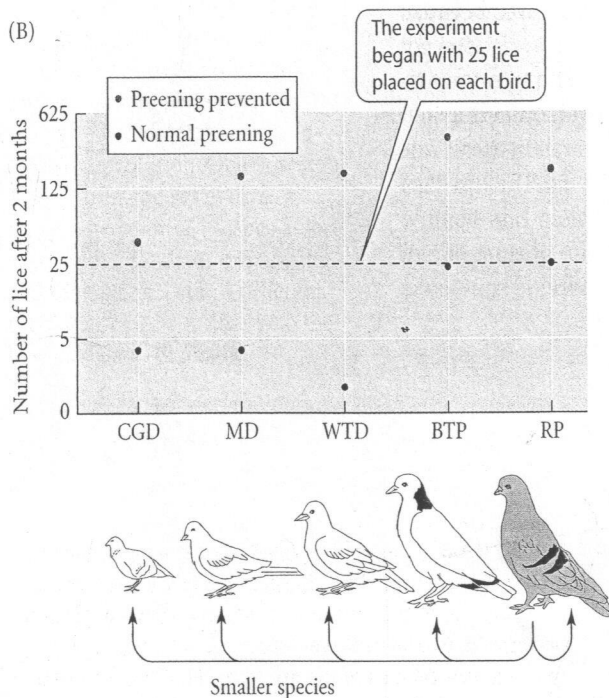


Figure 19.3 (A) A phylogeny of specialized feather lice (right) is mostly congruent with that of their dove and pigeon hosts (left), suggesting a history of cospeciation (with a few exceptions, shown by the crossing of lines that connect parasites to their hosts). Species marked with an asterisk were subjects in the experiment shown in (B). (B) A starting population of 25 lice transferred from rock pigeons (shaded) to other individuals of the same and four different species increased on all of these species when a bit placed on the birds' bills prevented them from preening. Louse populations on birds that could preen normally decreased on the three smaller species. RP, rock pigeon (*C. livia*); BTP, band-tailed pigeon (*P. fasciata*); WTD, white-tipped dove (*L. verreauxi*); MD, mourning dove (*Z. macroura*); CGD, common ground dove (*C. passerina*). (After Clayton et al. 2003).



or HOST SWITCHING, and by several other factors, such as extinction of parasite lineages (Page 2002). Host switching may be likely if parasites disperse from one host to another through the environment, as do plant-feeding insects. Among host-specific herbivorous insects, related species often feed on plants in the same family, and these associations may be very old. For example, phylogenetically basal lineages of leaf beetles, long-horned beetles, and weevils all feed mostly on cycads or conifers—plant lineages that evolved before the angiosperms, with which the more phylogenetically “advanced” beetles are associated (Farrell 1998). The fossil record also attests to the great age of some such associations (Labandeira 2002). Nevertheless, the phylogeny of the insect species seldom matches that of the host plants very closely, and the species of insects have often originated long after their host plant lineages diverged (Futuyma et al. 1995; Winkler and Mitter 2008). Flea beetles in the genus *Blepharida* are associated with the plant family Burseraceae in both Mexico and Africa, an association that is more than 100 Myr old. The beetles are adapted to the terpene-containing resins that appear to be the plants' main defense against nonadapted insects. Judith Becerra (1997) found that in Mexico, closely related host-specialized species of *Blepharida* are more likely to feed on chemically similar species of

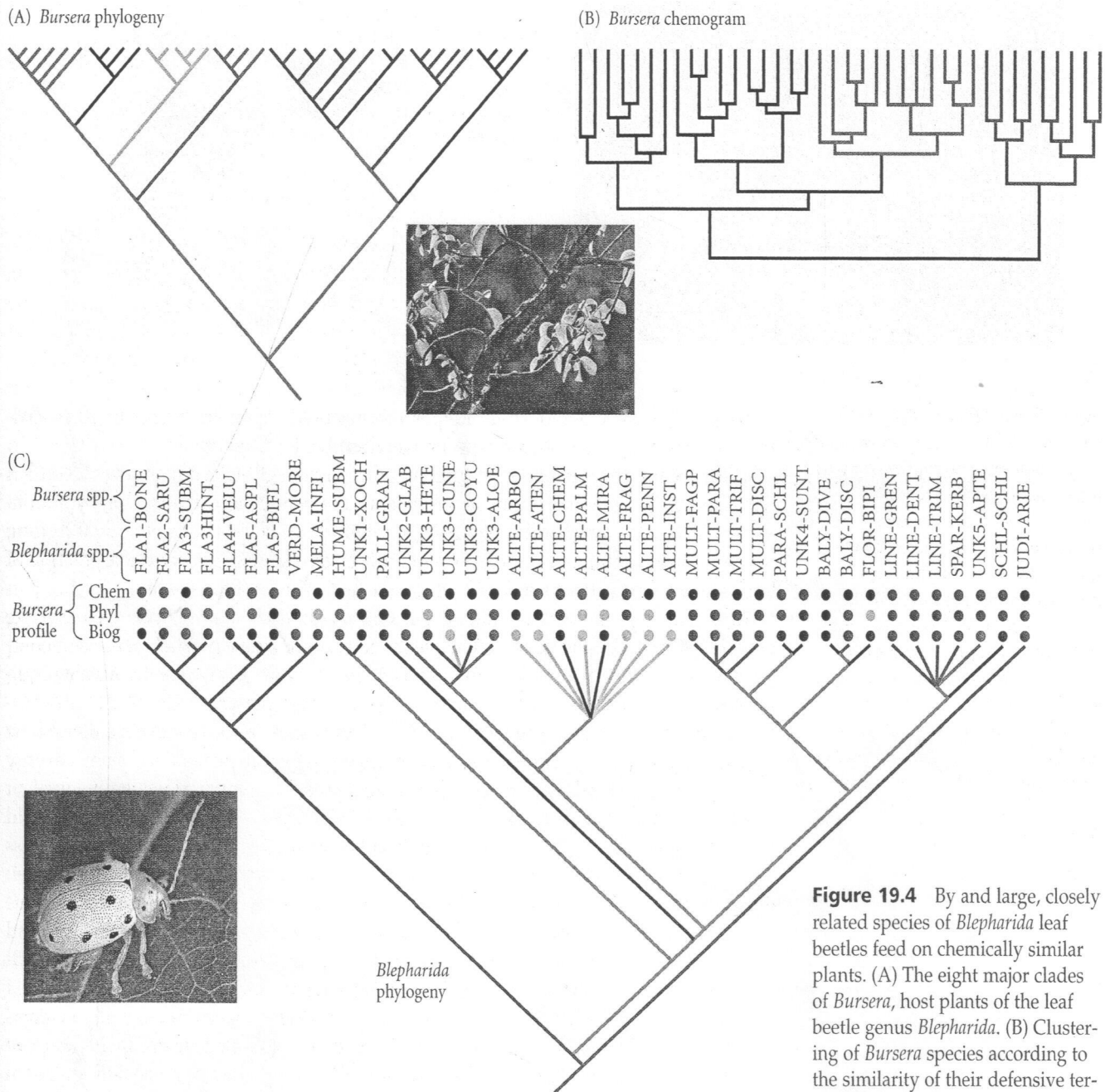


Figure 19.4 By and large, closely related species of *Blepharida* leaf beetles feed on chemically similar plants. (A) The eight major clades of *Bursera*, host plants of the leaf beetle genus *Blepharida*. (B) Clustering of *Bursera* species according to the similarity of their defensive terpenes reveals four major chemically coherent groups of species. (C) Phylogenetic relationships among species of *Blepharida* match the chemical similarity of their host plants more closely than they do the phylogeny or geographic distribution of their host. Colored circles above the tips of the beetle phylogeny profile the chemical group (top), major clade (middle), and major geographic region (bottom) of the beetle's host plant species. (From Becerra and Venable 1999; B, photo © tbkmedia.de/Alamy; C, photo courtesy of Judith Becerra).

Bursera than on phylogenetically closely related species (Figure 19.4). This pattern suggests that newly arisen species of beetles have adapted to plant lineages that had already evolved, and furthermore, that these insects adapt more readily to new hosts that are chemically similar to the beetles' ancestral host than to chemically different plants.

Coevolution of Enemies and Victims

In considering the *processes* of evolutionary change in interacting species, we will begin with interactions between enemies and victims: predators and their prey, parasites and their hosts, herbivores and their host plants. Predators and parasites have evolved some extraordinary adaptations for capturing, subduing, or infecting their victims (Figure 19.5). Defenses against predation and parasitism can be equally impressive, ranging from cryptic patterning (see Figure 12.5), to the highly toxic chemical defenses of both plants and animals (see Figure 19.8), to the most versatile of all defenses: the vertebrate immune system, which can generate antibodies against thousands of foreign compounds. Many such adaptations appear to be directed at a variety of different enemies or prey species, so

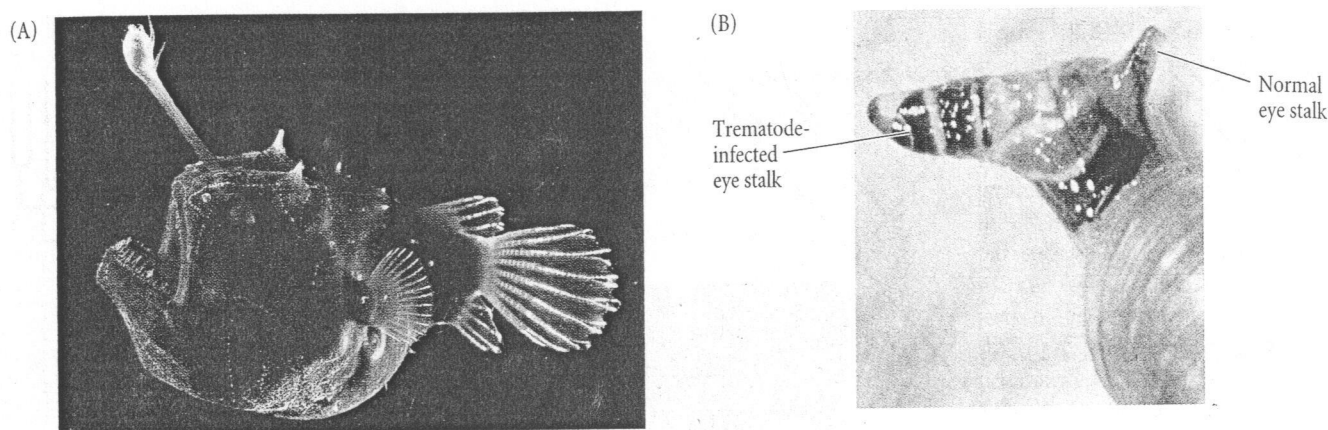


Figure 19.5 Predators and parasites have evolved many extraordinary adaptations to capture prey or infect hosts. (A) The dorsal fin spine of a deep-sea anglerfish (*Himantolophus*) is situated above the mouth and modified into a luminescent fishing lure. (B) The larva of a parasitic trematode (*Leucochloridium*) migrates to the eye stalk of its intermediate host, a land snail, and turns it a bright color to make the snail more visible to the next host in the parasite's life cycle, a snail-eating bird such as a thrush. (A © David Shale/naturepl.com; B photo by P. Lewis, courtesy of J. Moore.)

although it is easy to demonstrate adaptations in a predator or a prey species, it is usually difficult to show how any one species has coevolved with another.

Theoretically, the coevolution of predator and prey might take any of several courses (Abrams 2000): it might continue indefinitely in an unending escalation of an evolutionary arms race (Dawkins and Krebs 1979); it might result in a stable genetic equilibrium; it might cause continual cycles (or irregular fluctuations) in the genetic composition of both species; or it might even lead to the extinction of one or both species.

An unending arms race is unlikely because adaptations that increase the offensive capacity of the predator or the defensive capacity of the prey entail allocations of energy and other costs that at some point outweigh their benefits. Consequently, a stable equilibrium may occur when costs equal benefits. For example, the toxic SECONDARY COMPOUNDS that plants use as defenses against herbivores, such as the tannins of oaks and the terpenes of pines and of *Bursera*, can account for more than 10 percent of a plant's energy budget. Such high levels of chemical defense are especially typical of slowly growing plant species that inhabit nutrient-poor environments (Coley et al. 1985). Genetic lines of wild parsnip (*Pastinaca sativa*) containing high levels of toxic furanocoumarins suffered less attack from webworms, and matured more seeds, than lines with lower levels when grown outdoors; in the greenhouse, however, where they were free from insect attack, the lines with higher levels of furanocoumarins had lower seed production (Berenbaum and Zangerl 1988). Costs of this kind may explain why plants are not more strongly defended than they are, and thus why they are still subject to insect attack.

Another kind of cost arises if a defense against one enemy makes the prey more vulnerable to another enemy. For example, terpenoid compounds called cucurbitacins enhance the resistance of cucumber plants (*Cucumis sativus*) to spider mites, but they attract certain cucumber-feeding leaf beetles (Dacosta and Jones 1971).

Table 19.1 Gene-for-gene interactions between a parasite and its host

Parasite genotype	Host genotype			
	R_1 — R_2 —	R_1 — r_2r_2	r_1r_1 R_2 —	r_1r_1 r_2r_2
V_1 — V_2 —	—	—	—	+
V_1 — v_2v_2	—	—	+	+
v_1v_1 V_2 —	—	+	—	+
v_1v_1 v_2v_2	+	+	+	+

Source: After Frank 1992.

Note: In each species, two loci, with dominant and recessive alleles at each locus, control resistance (of the host) and infectivity (of the parasite). A + sign indicates that the parasite genotype can grow on a host of a given genotype (i.e., the parasite is infective and the host is susceptible); the — signs indicate that the host genotype is resistant to the parasite genotype.

Models of enemy-victim coevolution

GENE-FOR-GENE MODELS. Coevolution of enemies and victims has been modeled in several ways, appropriate to different kinds of characters. For example, models of evolution at one or a few loci are appropriate for **gene-for-gene interactions**, which were first described in cultivated flax (*Linum usitatissimum*) and in flax rust (*Melampsora lini*), a basidiomycete fungus. Similar systems have been described or inferred in several dozen other pairs of plants and fungi, and in the interaction between cultivated wheat (*Triticum*) and a major pest, the Hessian fly (*Mayetiola destructor*). In each such system, the host has several loci at which a dominant allele (R) confers resistance to the parasite. At each of several corresponding loci in the parasite, a recessive allele (v) confers infectivity—the ability to infect and grow in a host with a particular R allele (Table 19.1). If resistance has a cost, any particular resistance allele (R_i) will

Figure 19.6 A computer simulation of genetic changes at (A) a resistance locus in a host and (B) an infectivity locus in a parasite. The host is diploid and has three resistance alleles; the parasite is haploid and has six infectivity alleles. Each parasite genotype can overcome the defenses of one of the six host genotypes (e.g., parasite P_1 can attack host H_1H_1). Both populations remain polymorphic and fluctuate irregularly in genetic composition. (After Seger 1992.)

decline in frequency when the parasite's corresponding infectivity allele (v_i) has high frequency, because R_i is then ineffective. As a different R allele (R_j) increases in frequency in the host population, the corresponding infectivity allele v_j increases in the parasite population.

According to computer simulations, such frequency-dependent selection can cause cycles or irregular fluctuations in allele frequencies (Figure 19.6). In populations of Australian flax (*Linum marginale*), the frequencies of different rust genotypes fluctuated from year to year. On the whole, highly infective genotypes—those that could attack the greatest number of flax genotypes—occurred in highly resistant flax populations, and less infective rusts were found in less resistant flax populations (Thrall and Burdon 2003). Resistance genes are now the subject of intense study at the molecular level (Stahl and Bishop 2000). The pattern of sequence variation in the resistance genes of *Arabidopsis*, a flowering plant in the mustard family (Brassicaceae), suggests that polymorphism has been maintained by balancing selection, as the frequency-dependent gene-for-gene model predicts (Bakker et al. 2006).

QUANTITATIVE TRAITS. Coevolutionary models of a defensive polygenic character (y) in a prey species and a corresponding polygenic character (x) in a predator are mathematically complex and include many variables that can affect the outcome (Abrams 2000). An important distinction is whether the capture rate of the prey by the predator increases with the difference $x - y$ (e.g., when the predator's speed is greater than the prey's), or decreases (e.g., if it depends on a close match between the size of the prey and the size of the predator's mouth). In the first case, mathematical analyses suggest that both species will often evolve in the same direction (e.g., toward greater speed), arriving at an equilibrium point that is determined by physiological limits or excessive investment costs. However, suppose the capture rate depends on a close match between x and y , that deviation too great in either direction increases the cost of x (or y), and that $\bar{x} = \bar{y}$. Then either increasing or decreasing y will improve prey survival. In this case, y will evolve in one or the other direction, and x will evolve to track y . Eventually y may evolve in the opposite direction as its cost becomes too great, and x will evolve likewise. The result might be continuing cycles of change in the characteristics of both species, and these genetic changes may contribute to cycles in population density (Figure 19.7).

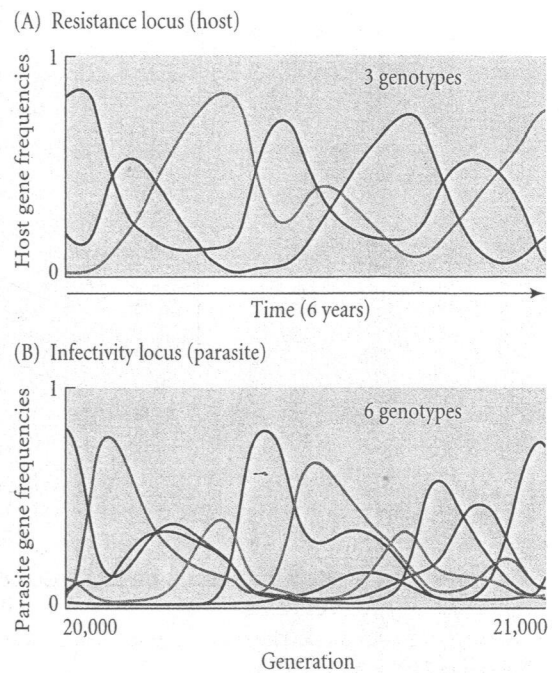
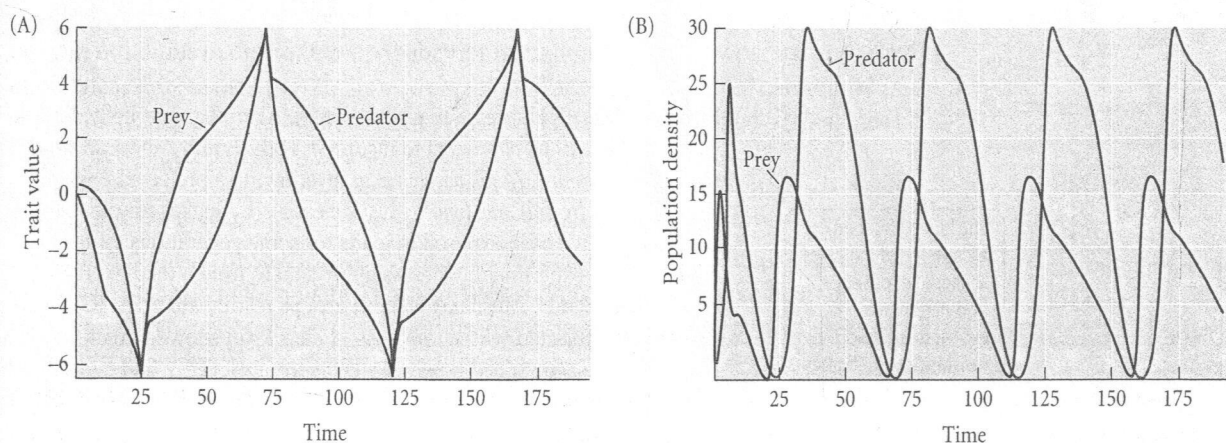


Figure 19.7 Computer simulation of coevolution between prey and predator in which the optimal predator phenotype (e.g., mouth size) matches a prey phenotype (e.g., size). (A) Evolution of character state means. As a character state diverges from a reference value, its fitness cost prevents it from evolving indefinitely in either direction. The evolution of the predator's character state lags behind the prey's. (B) Changes in character state means may be paralleled by cycles in population density, arising partly from changes in the match between the predator's character and the prey's. (After Abrams and Matsuda 1997.)



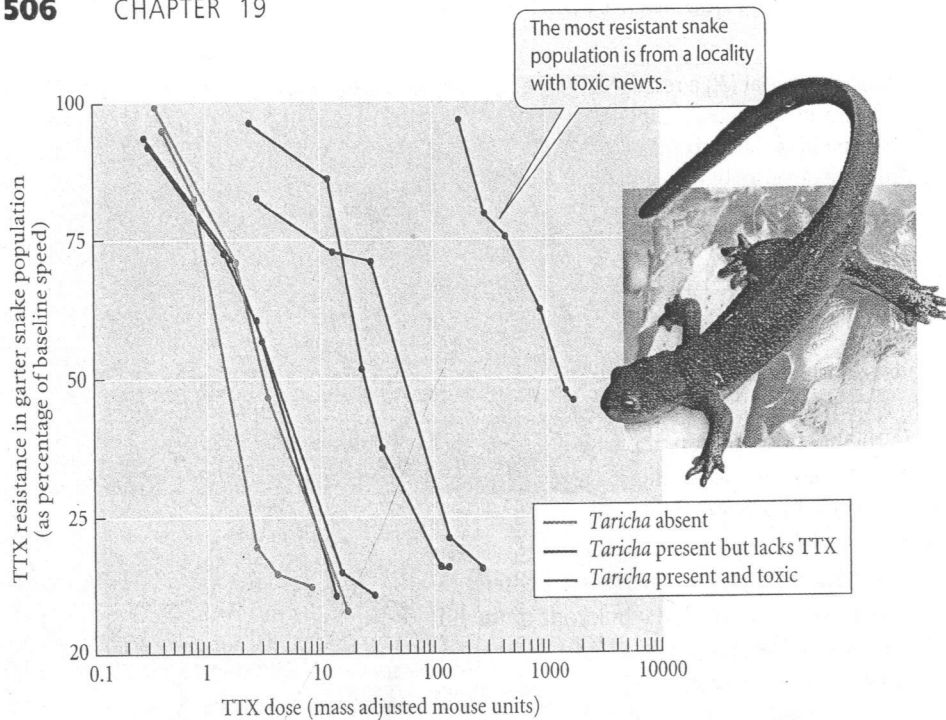


Figure 19.8 Variation in TTX resistance, measured by crawling speed after injection in relation to dose, in garter snakes (*Thamnophis sirtalis*) from several localities. The least resistant population is from Maine, where the toxic rough-skinned newt (*Taricha granulosa*) does not occur. Two of the other nonresistant populations coexist with newt populations that lack TTX. The three most resistant populations are sympatric with toxic newt populations. (After Brodie and Brodie 1999; photo © Mike Anich/Photolibary.com.)

Examples of predator-prey coevolution

The rough-skinned newt (*Taricha granulosa*) of northwestern North America has one of the most potent known defenses against predation: the neurotoxin tetrodotoxin (TTX). Most populations have high levels of TTX in the skin (one newt has enough to kill 25,000 laboratory mice), but a few populations, such as the one on Vancouver Island, British Columbia, have almost none (Brodie and Brodie 1999; Brodie et al. 2002). Populations of the garter snake *Thamnophis sirtalis* from outside the range of this newt have almost no resistance to TTX. But populations that are sympatric with toxic newts feed on them, and can be as much as a hundred times more resistant to TTX than are allopatric populations (Figure 19.8). Resistance to toxic prey has evolved rapidly in the red-bellied black snake (*Pseudechis porphyriacus*), one of many Australian snake species that have been endangered by feeding on the South American cane toad (*Bufo marinus*), a highly toxic amphibian that was introduced into Australia in 1935 on the misguided presumption that it would control insect pests of sugar cane. (It did not.) Populations of several species of Australian snakes, which have never before been exposed to toxic prey, have declined greatly in abundance because they eat cane toads. Ben Phillips and Richard Shine (2004, 2006) determined that black snake populations that have been exposed to cane toads for about 23 generations have evolved several counteradaptations (Figure 19.9): they are physiolog-

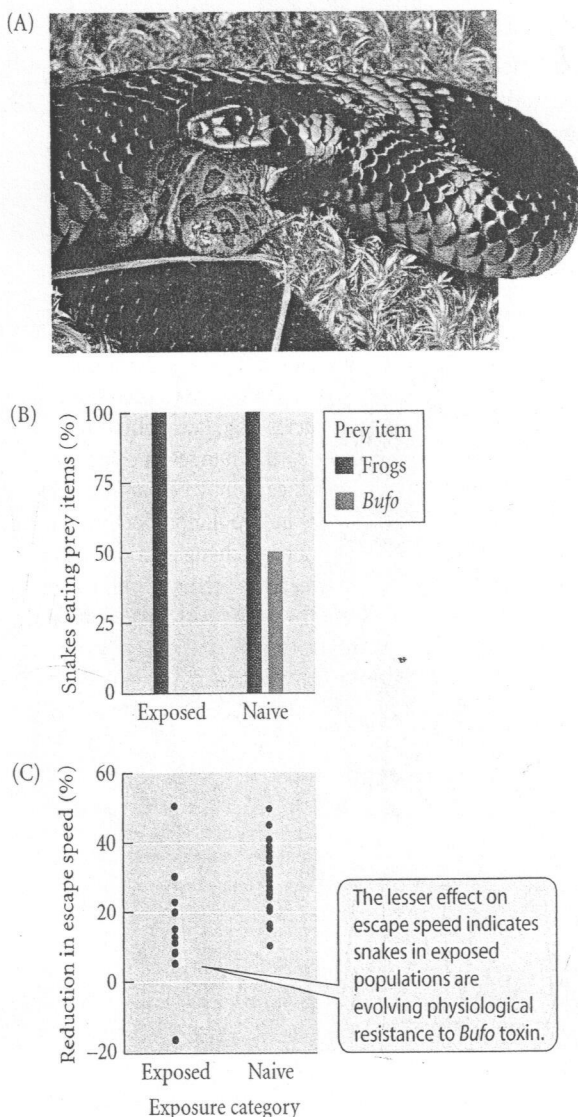
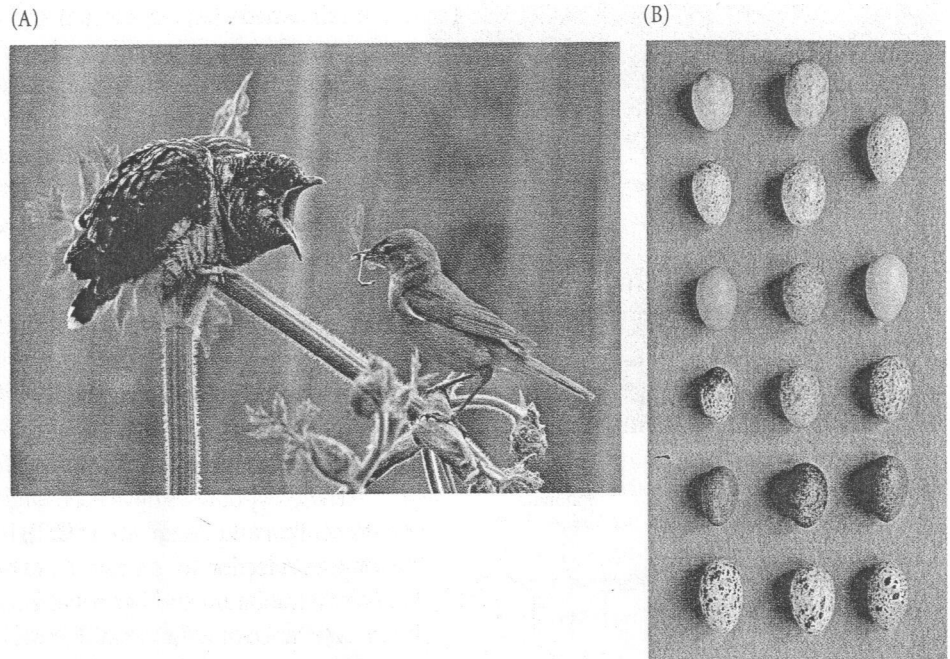


Figure 19.9 Evidence of adaptation of the Australian red-bellied black snake (*Pseudechis porphyriacus*) to incursion of the South American cane toad (*Bufo marinus*). (A) *P. porphyriacus* swallowing a preferred prey, the spotted grass frog (*Limnodynastes tasmaniensis*). (B) Snakes from a region where they have been exposed to toads for some generations refused to eat *Bufo* in an experiment, whereas many snakes from a toadless region ("naive") ate toads. All snakes in both groups readily ate frogs. (C) Toad-naïve snakes injected with a low dose of toad toxin showed greater reduction in escape speed than did snakes from a locality that had been exposed to toads. (A © Robert Valentic/Naturepl.com; B, C after Phillips and Shine 2006.)

Figure 19.10 (A) A fledgling common cuckoo (*Cuculus canorus*) being fed by its foster parent, a much smaller reed warbler (*Acrocephalus scirpaceus*). (B) Mimetic egg polymorphism in the European cuckoo. The left column shows eggs of six species parasitized by the cuckoo (from top: robin, pied wagtail, dunnock, reed warbler, meadow pipit, great reed warbler). The middle column shows a cuckoo egg laid in the corresponding host's nest. The match is quite close except in the dunnock nest. The right column shows artificial eggs used by researchers to test rejection responses. (A © David Kjaer/naturepl.com; B photo by M. Brooke, courtesy of N. B. Davies.)



ically more resistant to toad toxin, they avoid eating toads, and they have evolved a narrower mouth, so they are less capable of swallowing large toads than toad-naïve populations of black snakes far from the range of the cane toad.

Brood-parasitic birds, such as cowbirds and some species of cuckoos, lay eggs only in the nests of certain other bird species. Cuckoo nestlings hatch first and eject their host's eggs from the nest, so the host ends up rearing only the parasite (Figure 19.10A). Adults of host species do not treat parasite nestlings any differently from their own young, but some host species do recognize parasite eggs and either eject them or desert the nest and start a new nest and clutch.

The most striking counteradaptation among brood parasites is egg mimicry (Rothstein and Robinson 1998). Each population of the common cuckoo (*Cuculus canorus*) contains several different genotypes that prefer different hosts and lay eggs closely resembling those of their preferred hosts (Figure 19.10B). Some other individuals lay non-mimetic eggs. Some host species accept cuckoo eggs, some frequently eject them, and others desert parasitized nests. By tracing the fate of artificial cuckoo eggs placed in the nests of various bird species, Nicholas Davies and Michael Brooke (1998) found that species that are not parasitized by cuckoos (because of unsuitable nest sites or feeding habits) tend not to eject cuckoo eggs, whereas among the cuckoos' preferred hosts, those species whose eggs are mimicked by cuckoos rejected artificial eggs more often than those whose eggs are not mimicked. These species have evidently adapted to brood parasitism. Moreover, populations of two host species in Iceland, where cuckoos are absent, accepted artificial cuckoo eggs, whereas in Britain, where those two species are favored hosts, they rejected such eggs. Surprisingly, among suitable host species, those that are rarely parasitized by cuckoos did not differ in discriminatory behavior from those commonly parasitized. Davies and colleagues suspect that the rarely parasitized species were more commonly parasitized in the past, and that their ability to reject cuckoo eggs has selected against the cuckoo genotypes that parasitized these species.

Plants and herbivores

Almost all plants synthesize a variety of so-called secondary compounds that play little or no role in basic metabolism. Thousands of such compounds have been described, including many that humans have found useful as drugs (e.g., salicylic acid, the ingredient of aspirin), stimulants (caffeine), condiments (capsaicin, the "hot" element in chili peppers), and in other applications (e.g., cannabidiol, in marijuana). Higher taxa of plants are often characterized by particular groups of similar compounds, such as cardiac glycosides

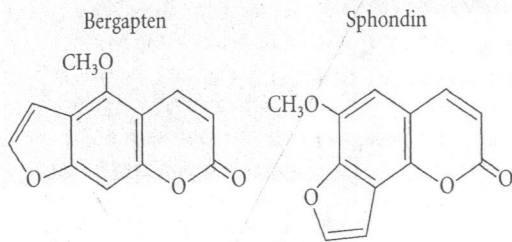


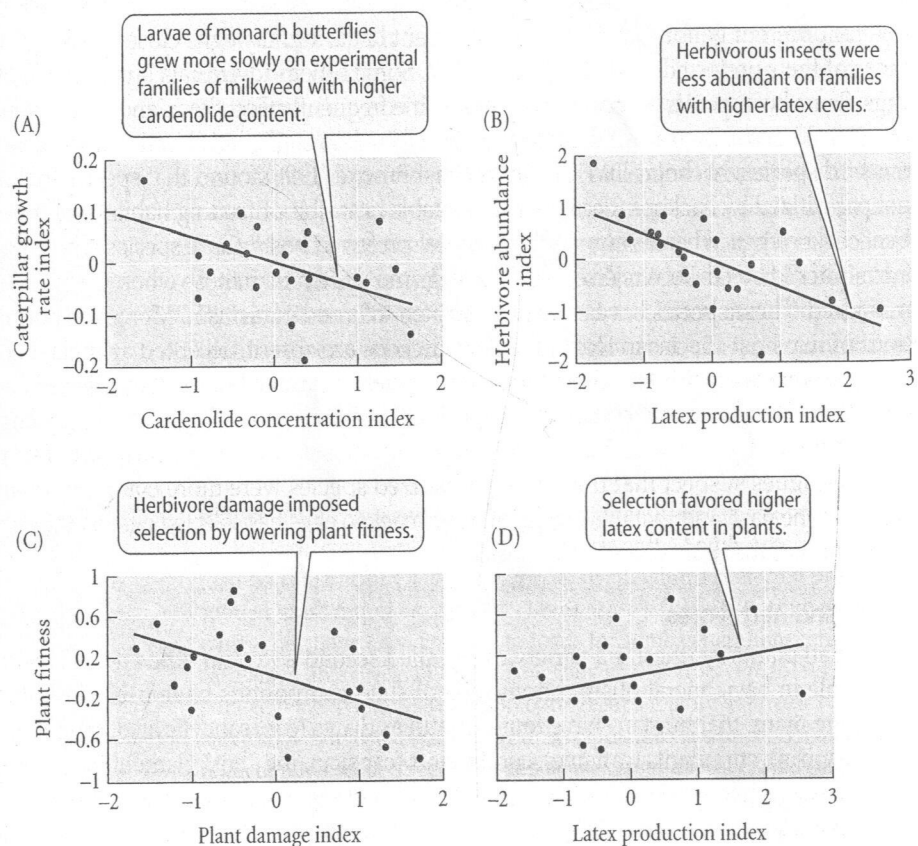
Figure 19.11 The furanocoumarins bergapten and sphondin are among the defensive compounds of wild parsnip (*Pastinaca sativa*), the host plant of a moth larva, the parsnip webworm (*Depressaria pastinacella*). (After Berenbaum et al. 1986; photo courtesy of May Berenbaum.)

in milkweeds (Apocynaceae) and glucosinolates in mustards (Brassicaceae). Some compounds are known to be toxic to animals, and some to be repellant, and so the hypothesis was posed that these features, as well as physical features such as spines, evolved as defenses against herbivores, especially insects (e.g., Fraenkel 1959). Paul Ehrlich and Peter Raven (1964) proposed a scenario of “escape and radiate” coevolution, in which a plant species that evolves a new and highly effective chemical defense may escape many of its associated herbivores, and give rise to a clade of species that share the novel defense. Eventually, though, some insect species from other hosts shift to these plants, adapt to them, and give rise to a clade of adapted herbivores. The association of the diverse species of *Blepharida* leaf beetles with the many species of *Bursera* (see Figure 19.4) is one of many examples of adaptive radiations of plants and associated insects that may have arisen in this way. —

These hypotheses have been largely supported by subsequent research (Rosenthal and Berenbaum 1992). Insects and other herbivores certainly impose selection for chemical and other defenses in plants. For example, May Berenbaum and her colleagues (1986) found that genetic variation in resistance of wild parsnip (*Pastinaca sativa*) to its major herbivore, the seed-eating parsnip webworm (*Depressaria pastinacella*), is mostly attributable to the level of two furanocoumarin compounds in the seeds (Figure 19.11). Anurag Agrawal (2005) planted multiple families of the milkweed *Asclepias syriaca* in a common garden and measured a fitness component—seed production—in relation to the density of herbivorous insects on the plants, the damage they inflicted, and several putative defenses such as cardenolide content and production of the gummy white fluid (latex) for which the plant is named. He found protective effects of cardenolides, which reduced insect growth (Figure 19.12A), and latex, which reduced the abundance and impact of insects on a plant (Figure



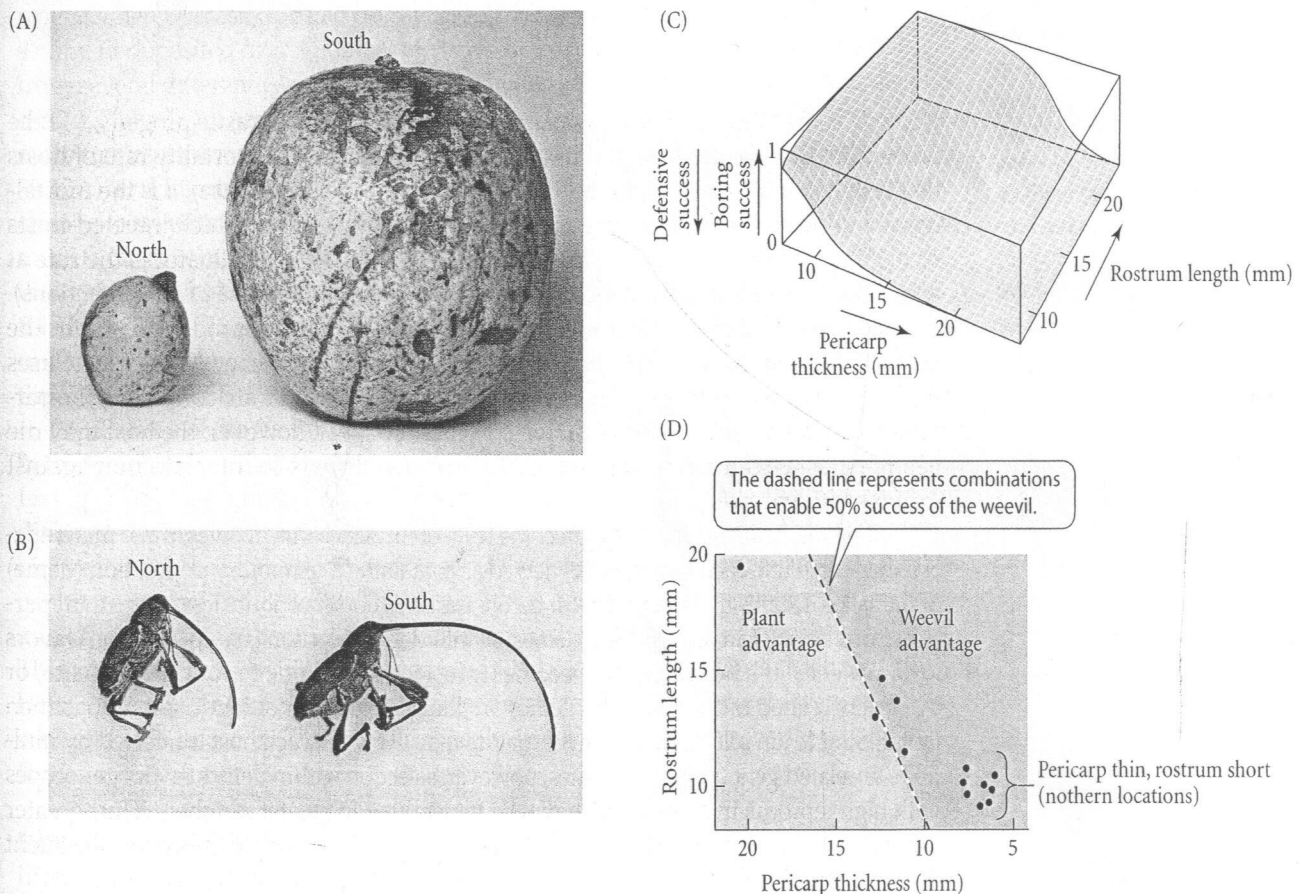
Figure 19.12 Evidence of selection for defensive traits in the common milkweed (*Asclepias syriaca*). (After Agrawal 2005; photo © Nancy Nehring/istockphoto.com.)



19.12B). Because plant fitness is significantly lowered by insect damage (Figure 19.12C), genetically higher levels of latex and other defenses improve fitness (Figure 19.12D). Thus natural selection by herbivores favors the evolution of these defenses.

Not surprisingly, herbivores often adapt to plant defenses (Bernays and Chapman 1994; Tilmon 2008). For example, among populations of parsnip webworms, resistance to the toxic effects of furanocoumarins is correlated with differences in the level of these compounds among populations of the host plant (Zangerl and Berenbaum 2003). A dramatic example of local adaptation involves a physical rather than chemical plant defense: the thick, woody fruit wall (pericarp) that encloses the seeds of the Japanese camellia (*Camellia japonica*; Figure 19.13A). A high proportion of seeds are consumed by larvae of the camellia weevil (*Curculio camelliae*) which feeds exclusively on this plant. The adult weevil inserts eggs into the seed chamber through a hole she bores with her mandibles, located at the end of her long snout, or rostrum (Figure 19.13B). Hirokazu Toju and Teiji Sota (2006) determined weevils' success in boring through to the seed chamber as a function of their rostrum length, relative to the thickness of a fruit's pericarp (Figure 19.13C), and determined the relation between these that would result in a 50 percent success rate for the weevil (or 50 percent seed mortality for the plant). They related these calculations to wild populations. Southern populations of the camellia have much thicker pericarps than do northern populations, and the rostrum length of the weevil likewise shows a strong cline. However, the clines differ in slope, so that northern weevil populations are "ahead" in this conflict—their rostra are long enough to ensure a success rate well over 50 percent—whereas in the south the plant population is "ahead," with pericarps thick enough to reduce the weevils' success (Figure 19.13D). These species may be engaged in an "arms race," although the reason for the thinner pericarp in northern camellia populations is not clear.

Figure 19.13 Imbalance in a coevolutionary conflict. (A) Fruits of the Japanese camellia (*Camellia japonica*) have a much thicker pericarp in the south than in the north. (B) The rostrum of the camellia weevil (*Curculio camelliae*) is much longer in southern than in northern populations. (C) The average boring success of the weevils as a function of their rostrum length and the pericarp thickness of a fruit, based on experimental data. The success of the plant in defense of its seeds is the opposite of the weevil's success in reaching the seeds. (D) Average rostrum length and pericarp thickness of associated populations of weevil and camellia in various localities in Japan are plotted as points relative to the line representing combinations of these variables that enable 50 percent success of the weevil. In populations to the right of the dashed line, the weevil is favored because its rostrum is long relative to the plant's pericarp thickness. In the population left of the line, the plant has the advantage. Points at the lower right represent more northern localities, in which the pericarp is thin and the rostrum short. (After Toju and Sota 2006; photos courtesy of Hiro Toju.)



Infectious disease and the evolution of parasite virulence

The two greatest challenges a parasite faces are moving itself or its progeny from one host to another (transmission) and overcoming the host's defenses. Some parasites are transmitted **vertically**, from a host parent to her offspring, as in the case of *Wolbachia* bacteria, which are transmitted in insects' eggs. Other parasites are transmitted **horizontally** among hosts via the external environment (e.g., human rhinoviruses, the cause of the common cold, which are discharged by sneezing), via contact between hosts (e.g., the gonorrhea bacterium and other venereal disease agents), or via carriers (VECTORS, such as the mosquitoes that transmit the yellow fever virus and the malaria-causing protist *Plasmodium*).

The effects of parasites on their hosts vary greatly. Those that reduce the survival or reproduction of their hosts are considered VIRULENT. We are concerned here with understanding the evolutionary factors that affect the degree of virulence. This topic has immense medical implications because the evolution of virulence can be rapid in "microparasites" such as viruses and bacteria (Bull 1994; Ewald 1994). The level of virulence depends on the evolution of both host and parasite. For example (Fenner and Ratcliffe 1965), after the European rabbit (*Oryctolagus cuniculus*) became a severe rangeland pest in Australia, the myxoma virus, from a South American rabbit, was introduced to control it. Periodically after the introduction, wild rabbits were tested for resistance to a standard strain of the virus, and virus samples from wild rabbits were tested for virulence in a standard laboratory strain of rabbits. Over time, the rabbits evolved greater resistance to the virus, and the virus evolved a lower level of virulence. Although some almost avirulent strains were detected, the virus population did not become completely avirulent.

THEORY OF THE EVOLUTION OF VIRULENCE. Many people imagine that parasites generally evolve to be benign (avirulent) because the parasite's survival depends on that of the host population. However, a parasite may evolve to be more benign or more virulent depending on many factors (May and Anderson 1983; Bull 1994; Frank 1996).

The fitness of a parasite genotype is proportional to the number of hosts its progeny infect and may be measured by R_0 , the number of new infections produced by an infected host:

$$R_0 = \frac{bN}{v + d + r}$$

where N is the number of hosts available for infection by the parasite progeny, b is the probability that the progeny will infect each such host, v is the mortality rate of hosts that is due to parasitism (and is a function of the parasite's virulence), d is the mortality rate of hosts that is due to other causes, and r is the rate at which infected hosts recover and become immune to further infection. Thus the denominator is the rate at which hosts move out of the infected class (and thus are not a source of new infections). In many cases, b depends on the number of parasite offspring produced within the host—but this variable is often proportional to host mortality v , since the parasite uses the host's resources (energy, protein, etc.) to reproduce. If b and v are correlated, the parasite may evolve greater virulence. If v becomes too great, however, the host may die before parasites can be transmitted to new hosts, so there is counterselection against extreme virulence.

Among many factors that may affect the level of virulence that evolves, three merit special mention. First, each host may be viewed as containing a temporary population (deme) of parasites. Demes that kill their host before transmission contribute less to the total parasite population than more benign demes, so interdemic selection (group selection) favors low virulence. If a host typically becomes infected by only one individual parasite, or by closely related individuals, the demes are kin groups, so interdemic selection is then tantamount to kin selection, and low virulence may evolve. If each host is infected by multiple, unrelated genotypes of parasites, however, selection within demes favors genotypes with high reproductive rates, which will be transmitted in greater numbers. Thus greater virulence is expected to evolve in parasite species in which multiple infection is frequent (Frank 1996).

Second, if hosts rapidly become immune to the parasite (i.e., if r in the above equation is large), selection favors rapid reproduction—that is, outrunning the host's immune system—by the parasite. Because this may entail greater virulence, an effective immune system (or a drug that rapidly kills the parasite) may sometimes induce the evolution of higher virulence.

A third factor affecting the level of virulence is whether parasites are transmitted horizontally or vertically. The transmission (and thus fitness) of horizontally transmitted parasites does not depend on the reproduction of their host (or, therefore, on its long-term survival). In contrast, the progeny of a vertically transmitted parasite are “inherited” directly, so b depends on the host's reproductive success. Hence we may expect evolution toward a relatively less virulent state in vertically transmitted parasites. This hypothesis was supported by an experiment with bacteriophage, in which a phage genotype that reduces its host's growth declined in frequency, and a more “benevolent” genotype increased, when horizontal transmission was prevented (Bull et al. 1991).

VIRULENCE AND RESISTANCE IN NATURAL POPULATIONS. *Daphnia magna*, a planktonic crustacean, is parasitized by a microsporidian protist (*Pleistophora intestinalis*) that reproduces in the gut epithelium and releases daughter spores in the host's feces. In experimental pairs of infected and uninfected *Daphnia*, the greater the number of parasites in the infected individual, the more likely the other was to become infected. Moreover, the parasites produced more spores, and caused greater mortality, when they infected *Daphnia* from their own or nearby populations than when they infected hosts from distant populations (Figure 19.14). Thus populations of this parasite are best adapted to their local host population, and their more virulent effect on sympatric than on allopatric host populations contradicts the naive hypothesis that parasites necessarily evolve to be benign.

Daphnia magna can produce eggs that remain dormant in pond sediments for many years. The eggs may harbor resting spores of another parasite, the bacterium *Pasteuria ramosa*. Ellen Decaestecker and colleagues (2007) revived eggs and bacteria from layers of sediment deposited over a number of years, then experimentally cross-infected *Daphnia* from several different years with bacteria from the same (“contemporary”) year, the preceding (“past”) year, and the subsequent (“future”) year. They discovered that hosts were more frequently infected by “contemporary” than by “past” or “future” bacteria (Figure 19.15A), and interpreted this to indicate that the *Daphnia* population underwent genetic change from year to year and that the bacteria evolved in concert, as in gene-for-gene models of coevolution (see Figure 19.6). The same research group had previously found that genotypes of *Daphnia* vary in their resistance to different genotypes of *Pasteuria*, as this hypothesis requires (Decaestecker et al. 2003). Even though both host and parasite underwent continual coevolution, the average virulence of the parasite increased over time (Figure 19.15B).

Populations of the freshwater snail *Potamopyrgus antipodarum* in New Zealand include both sexual and parthenogenetic genotypes (see Figure 15.7). Mark Dybdahl and Curtis Lively (1998) found that in a lake populated mostly by asexual snails, the frequencies of different clonal genotypes (distinguished by allozyme markers) changed over the course of 5 years, and the rate of infection of most of the genotypes peaked about a year after the genotype peaked in frequency. This observation suggests that rare snail genotypes have a selective advantage because they are resistant to the most prevalent parasite genotypes. This hypothesis was confirmed by exposing 40 rare clones and 4 clones that had recently been common to infection by parasites from the same lake: the rare clones were much less susceptible to infection. These results, like those with *Daphnia*, are consistent with gene-for-gene coevolution.

EVOLUTION AND EPIDEMICS. The genetics and evolution of parasite-host interactions are highly relevant to human health, as well as that of other species of concern. First, the

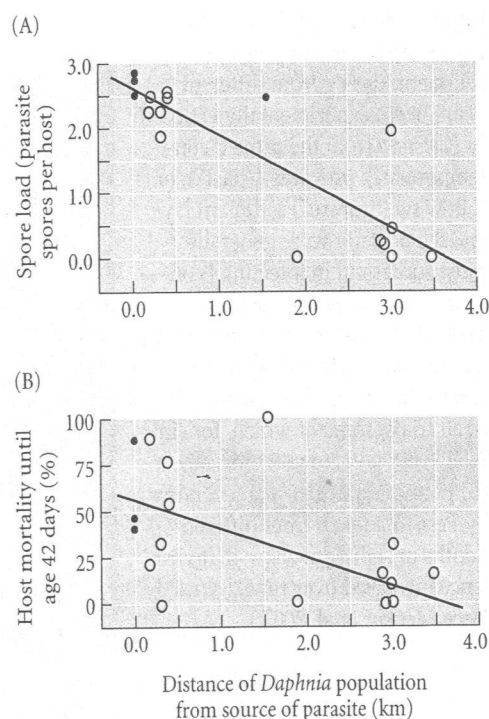
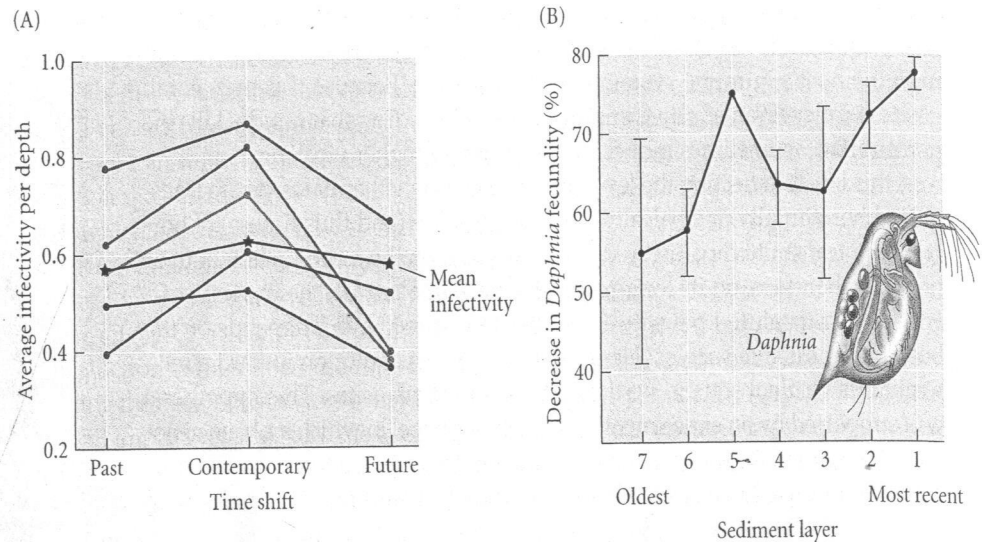


Figure 19.14 The fitnesses of three strains of a microsporidian parasite and their effects on various populations of the host species, the water flea *Daphnia magna*. Each strain, represented by a different color, was tested in hosts from its locality of origin (solid symbols) and from localities at various distances away (open symbols). (A) The number of parasite spores produced per host (spore load) was greatest when the parasite infected individuals from its own location, showing that parasites are best adapted to local host populations. (B) Host mortality was greatest in the parasite's own or nearby host populations, showing that the parasite is most virulent in the host population with which it has coevolved. (After Ebert 1994.)

Figure 19.15 (A) When *Daphnia* eggs from several depths in pond sediment, dating from different years, were experimentally exposed to *Pasteuria* from the same ("contemporary"), previous ("past"), or following ("future") sediment layers, the bacteria were generally most successful in infecting "contemporary" *Daphnia*. Each line presents results from *Daphnia* from a particular sediment layer; the starred line is the mean infectivity of all trials, some of which, for simplicity, are not shown here. (B) Reduction of *Daphnia* fecundity by *Pasteuria* taken from different depths of sediment show that virulence increased over time. (After Decaestecker et al. 2007.)



examples we have considered suggest that genetic diversity in a host population may be important for maintaining resistance to pathogens. Conversely, populations that are inbred or have low genetic diversity may be at risk. For example, in 1970, 85 percent of the hybrid seed corn planted in the United States carried a cytoplasmic genetic factor for male sterility that was considered useful for preventing unintended cross-pollination. Unfortunately, this genetic factor also caused hypersusceptibility to the southern corn leaf blight (*Helminthosporium maydis*), and about 30 percent of the country's corn crop—and up to 100 percent in some places—was lost to this fungus (Ullstrup 1972). Widely planting a genetically uniform crop is a prescription for disaster.

Among the greatest threats to human health are "emerging pathogens," many of which enter the human population from other species. Some such events may occur entirely because of environmental changes that, for example, increase the likelihood of transmission from an animal "reservoir" to a human population, but in other cases, evolutionary change of the pathogen plays a role (Woolhouse et al. 2005). Phylogenetic analyses are routinely used to trace the origins of new pathogens, such as the evolution of human immunodeficiency viruses (HIV-1 and HIV-2) from chimpanzees and African monkeys (see Figure 3.4). Comparisons of the phylogeny of clades of RNA viruses with the phylogeny of their hosts show that some families of viruses have shifted to new host species much more frequently than others have (Jackson and Charleston 2004).

When the origins of a new pathogen can be discovered, it may be possible to determine the genetic basis by which the pathogen adapted to its new host. For instance, canine parvovirus arose and became pandemic in dogs throughout the world in 1978. Phylogenetic analysis showed that it arose from a feline panleukopenia virus that infects cats and several other carnivores. Six amino acid changes in the capsid protein of the virus enable it to infect dog cells, by specifically binding the canine transferrin receptor. After the virus first entered the dog population, several additional evolutionary changes made it more effective at binding the dog receptor, and unable to bind that of its original feline host (Hueffer et al. 2003).

Recombination plays a role in host shifts by influenza A viruses, which are major threats to human health. In 1918, the "Spanish flu" killed about 675,000 people in the United States (of whom about half were young adults) and 20 to 40 million worldwide. This was the most devastating of many influenza A pandemics. Influenza A viruses are widespread in birds, especially ducks and other aquatic species, and are thought to enter the human population usually through intermediate vehicles such as pigs, but sometimes directly from birds (Hay et al. 2001). Once the virus has established a population in humans, new antigenic variants continually evolve in response to immune suppression by human hosts. However, the shift from birds to mammals seems usually to be based, at least in part, on major genetic changes caused by recombination among fairly different

strains. There is some evidence that recombination played a role in the emergence of the Spanish flu (Gibbs et al. 2001), and of the avian flu (H5N1) that arose in China and other eastern Asian countries in 2003 and 2004 and which caused disease in domestic poultry and several human deaths (Li et al. 2004). There is concern that H5N1 or a related strain could evolve further and become another pandemic (Longini et al. 2005).

Mutualisms

Mutualisms are interactions between species that benefit individuals of both species. In **SYMBIOTIC MUTUALISMS**, individuals are intimately associated for much of their lifetimes. Some mutualisms have promoted the evolution of extreme adaptations. Flowers that are pollinated by long-tongued moths usually have a long, tubular, white corolla and are fragrant at dusk or at night. Darwin, having seen the Madagascan orchid *Angraecum sesquipedale* in a London greenhouse, with a nectar spur up to 30 cm long, predicted that somewhere in Madagascar there must exist a moth with a similarly long proboscis, capable of pollinating it. More than a century later, such sphinx moths, with tongues more than 24 cm long, were found, and they do indeed pollinate this orchid and its relatives (Figure 19.16; Nilsson et al. 1985).

In *The Origin of Species*, Darwin challenged his readers to find an instance of a species having been modified solely for the benefit of another species, “for such could not have been produced through natural selection.” No one has met Darwin’s challenge. Mutualisms exemplify not altruism but reciprocal exploitation, in which each species obtains something from the other. Some mutualisms, in fact, have arisen from parasitic or other exploitative relationships. Yuccas (*Yucca*, Agavaceae), for example, are pollinated only by female yucca moths (*Tegeticula* and *Parategeticula*), which carefully pollinate a yucca flower and then lay eggs in it (Figure 19.17A). The larvae consume some of the many seeds that develop. Some of the closest relatives of *Tegeticula* simply feed on developing seeds, and one of these species incidentally pollinates the flowers in which it lays its eggs, illustrating what may have been a transitional step from seed predation to mutualism (Figure 19.17B).

The theoretical bases for the evolution of mutualism between species are much the same as those governing the evolution of reciprocity between conspecific individuals, as described in Chapter 16. As in the case of intraspecific cooperation, there is always the potential for conflict within mutualisms because a genotype that “cheats” by exploiting its partner without paying the cost of providing a benefit in exchange is likely to have a selective advantage. Thus selection will always favor protective mechanisms, including punishing cheaters, to prevent overexploitation (Bull and Rice 1991). Moreover, selection will favor “honest” genotypes if the individual’s genetic self-interest depends on the fitness of its host or partner (Herre et al. 1999). Thus the factors that should favor evolutionary stability of mutualisms include vertical transmission of endosymbionts from parents to offspring, repeated or lifelong association with the same individual host or partner, and restricted opportunities to switch to other partners or to use other resources. Some mutualisms indeed appear to conform to these principles. For example, the *Buchnera* bacteria that live in the cells of aphids and are vertically transmitted are all mutualistic, as far as is known. However, this is not an invariable rule, and some vertically transmitted symbionts are harmful to their hosts.

An example of how evolutionary stability can be achieved by punishment is provided by the interaction between yucca species and the moths that are their sole pollinators (Pellmyr and Huth 1994). Typically, the moth lays only a few eggs in each flower, so that only a few of the flower’s many developing seeds are consumed by the larvae. The moth could lay more eggs per flower—indeed, she distributes eggs among many flowers—so

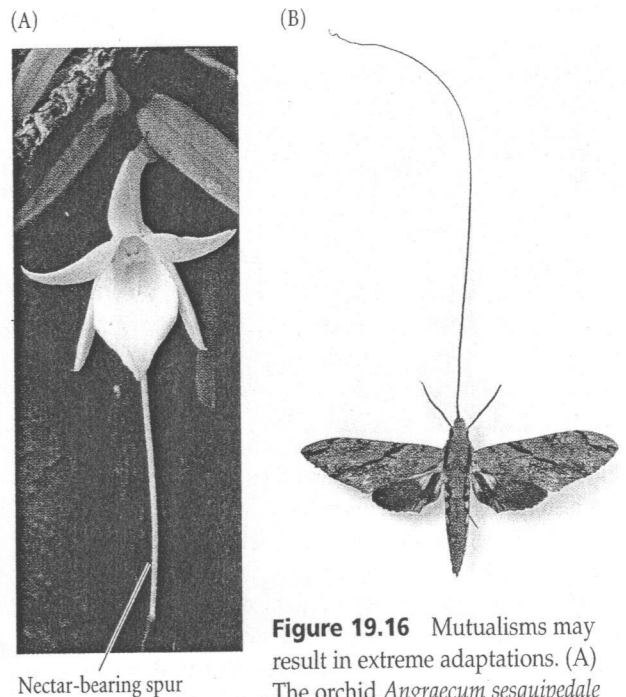
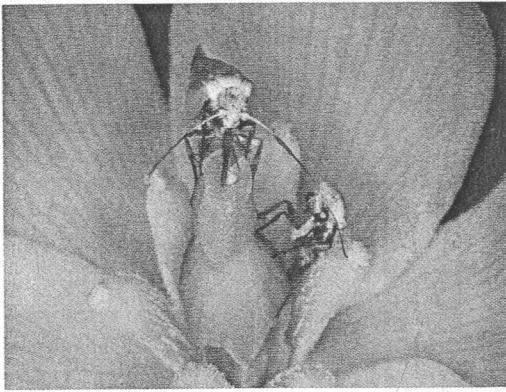


Figure 19.16 Mutualisms may result in extreme adaptations. (A) The orchid *Angraecum sesquipedale* bears nectar in an exceedingly long spur. (B) The long-tongued sphinx moth *Xanthopan morgani praedicta* pollinates *A. sesquipedale*. Darwin predicted the existence of such a pollinator based on seeing the orchid in a London greenhouse. (A © Pete Oxford/Naturepl.com; B © The Natural History Museum, London.)

(A)



(B)

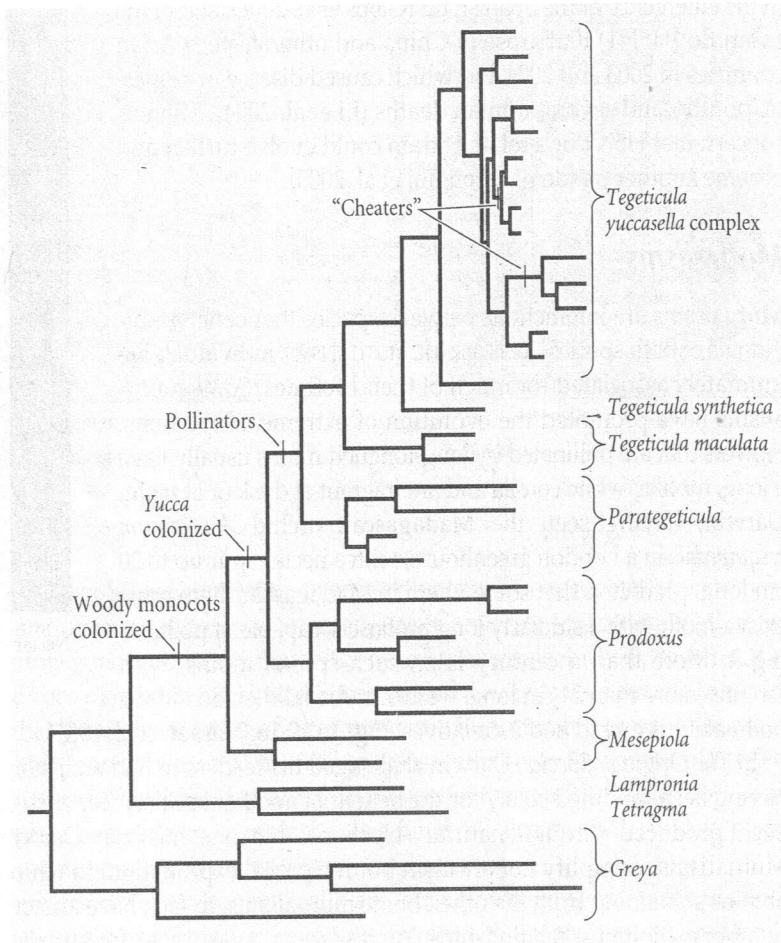


Figure 19.17 Yucca moths and their evolutionary history. (A) Yucca moths of the genus *Tegeticula* not only lay eggs in yucca flowers but use specialized mouthparts to actively pollinate the flowers in which they oviposit. (B) A phylogeny of the yucca moth family, showing major evolutionary changes. Some species in basal genera such as *Greya* incidentally pollinate the flowers in which they lay eggs. Intimate mutualism evolved in the ancestor of *Tegeticula* and *Parategeticula*, and “cheating” later evolved twice in *Tegeticula*. (A courtesy of O. Pellmyr; B after Pellmyr and Leebens-Mack 1999.)

why does she lay so few in each? The answer lies, in part, in the fact that the plant does not have enough resources to mature all of its many (often 500–1500) flowers into fruits. Pellmyr and Huth hand-pollinated all the flowers on some plants and found that only about 15 percent of the flowers yielded mature seed-bearing fruits; the rest were aborted and dropped from the plant. In the field, Pellmyr and Huth found more moth eggs, on average, in aborted than in maturing fruits, suggesting that the plant is more likely to abort a fruit if many eggs have been laid in it. Fruit abortion imposes strong selection on moths that lay too many eggs in a flower because the larvae in an aborted flower or fruit perish. Thus the moth has evolved restraint by individual selection and self-interest.

Mutualisms are not always stable over evolutionary time: many species cheat. For instance, many orchids secrete no nectar for their pollinators, and some practice downright deceit: they release a scent that mimics a female insect’s sex pheromone, attracting male insects that accomplish pollination while “copulating” with the flower (see Figure 11.2). Two lineages of yucca moths that have evolved from mutualistic ancestors do not pollinate, and they lay so many eggs that the larvae consume most or all of the yucca seeds (see Figure 19.17B). These “cheaters” circumvent the plant’s abortion response to high numbers of eggs by laying their eggs after the critical period in which fruit abortion occurs (Pellmyr and Leebens-Mack 1999).

Evolutionary shifts between mutualism and antagonism can sometimes occur rapidly. Many insects carry a maternally transmitted intracellular bacterium, *Wolbachia*, that in various insects causes parthenogenesis, cytoplasmic incompatibility, or death of male offspring. In the 1980s, *Wolbachia* invaded and swept through California populations of *Drosophila simulans*, reducing female fecundity by 15 to 20 percent. Recent tests show that the fecundity of *Wolbachia*-infected females from these populations is now 10 percent greater than that of uninfected females, suggesting that *Wolbachia* has evolved into a mutu-

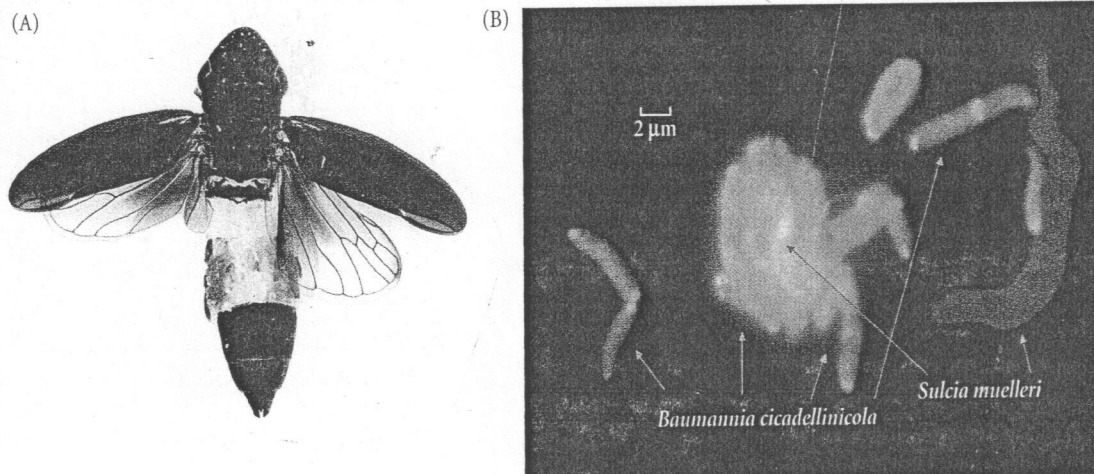
alist (Weeks et al. 2007). In the parasitoid wasp *Asobara tabida*, *Wolbachia* is actually required for the formation of eggs, because it regulates the apoptosis (cell death) of nurse cells in the ovary (Pannebakker et al. 2007).

MUTUALISM AND ADAPTATION. Partly because of genome studies, mutualism is increasingly recognized as an important basis for adaptation and the evolution of biochemical complexity (Moran 2007). The best-known examples are the evolution of mitochondria from purple bacteria and chloroplasts from cyanobacteria (see Figure 5.4). When a new, "compound" organism is formed from an intimate symbiosis, the subsequent evolution of both genomes is affected. For example, chloroplasts have fewer than 10 percent as many genes as free-living cyanobacteria, but many of the original cyanobacterial genes have been transferred to the plant nuclear genome. As many as 4500 of the protein-coding genes of *Arabidopsis*, or about 18 percent of the total, may have been acquired by transfer from the cyanobacterial ancestor early in plant evolution (Martin et al. 2002).

Mutualistic symbiosis often provides one or both partners with new capabilities. For example, many of the features of bacteria—including characteristics that make some bacteria pathogenic—are encoded by phage-borne genes. Some prokaryotes form mutualistic consortia, such as an association between methanogenic archaea and bacteria capable of fermentation. Bacteria and other microbes have formed intimate mutualisms with diverse multicellular organisms, especially animals, which are exceptional among eukaryotes in the extent to which they have lost the ability to synthesize essential amino acids and vitamins—probably because animals can often obtain these compounds from their food. Among the many animals that harbor symbiotic bacteria, the most extreme associations have been found in sap-sucking homopteran insects (aphids, leafhoppers, cicadas, and relatives), which have been extensively studied by Nancy Moran and her collaborators (Moran 2007). Plant sap lacks many nutrients, including essential amino acids, which in all homopterans are supplied by bacteria that are harbored in specialized cells (bacteriocytes). The phylogeny of these vertically transmitted bacteria closely matches the phylogeny of their hosts, denoting ancient associations. However, diverse groups of bacteria have formed such associations, and new endosymbionts have replaced ancestral ones in some homopteran lineages. Some individual insects carry up to six types of symbionts.

The phylogeny of a major group of homopterans that includes leafhoppers and cicadas matches that of a bacterial symbiont, *Sulcia*, indicating (together with the insects' fossil record) that this association has persisted since the late Permian, 270 Mya. In one subfamily of leafhoppers, known as sharpshooters, *Sulcia* was joined by another bacterium, *Baumannia*, in the Eocene (Figure 19.18). Like most endosymbionts, both mutualistic and parasitic, these bacteria have lost great numbers of genes, especially those whose function is supplied by their host's genome. The remarkable feature of *Sulcia* and *Baumannia* in the sharpshooters is that they have retained complementary functions: *Sulcia* can synthesize most of the essential amino acids required by its host, whereas *Baumannia* has lost

Figure 19.18 The members of an extraordinary mutualism. (A) A sharpshooter (*Cuerna sayi*), one of a large clade of sap-feeding homopteran insects that are nutritionally dependent on endosymbiotic bacteria. The bacteriocytes, revealed by dissecting away the exoskeleton, are the brightly colored masses on both sides of the abdomen. (B) Sharpshooters contain two endosymbionts, *Sulcia* (red) and *Baumannia* (green), here visualized by fluorescent probes for taxon-specific 16S rRNA sequences. The two bacteria and their host insect are codependent, and together can subsist on a diet of xylem sap, perhaps the least nutritionally adequate diet of any animal. (A courtesy of D. M. Takiya and R. Rakitov; B courtesy of N. A. Moran.)



most of these biosynthetic pathways but has retained a feature that *Sulcia* has lost: biosynthesis of vitamins (Wu et al. 2006). More remarkable still, *Baumannia* has retained the ability to synthesize a single essential amino acid, histidine—precisely the one that *Sulcia* cannot synthesize. The two endosymbionts and their host are codependent, and together can subsist on a diet of xylem sap, perhaps the least nutritionally adequate diet of any animal.

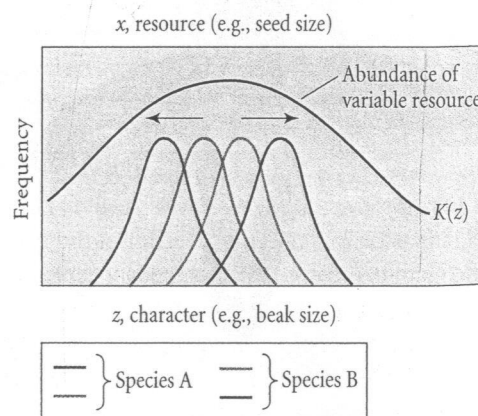
The Evolution of Competitive Interactions

The population densities of many species are limited, at least at times, by resources such as food, space, or nesting sites. Consequently, competition for resources occurs within many species (intraspecific competition) and between different species if they use some or all of the same resources (interspecific competition). Darwin postulated that competition would impose selection for divergence in resource use and viewed it as a major reason for the origin and divergence of species. There is now considerable evidence that evolution in response to competition is one of the major causes of adaptive radiation (Schluter 2000).

Ecologists have shown that sympatric animal species characteristically differ in resource use; for instance, species of Darwin's finches in the Galápagos Islands differ in diet and, accordingly, in bill shape (see Figure 3.23). It is plausible that such differences have evolved, at least in part, to avoid competition. Suppose individuals that differ in a phenotypic trait (e.g., bill depth in seed-eating birds) differ in the resource they use (e.g., seed size), that two species are both variable in this character, and that the frequency distributions of the two species overlap greatly, so that most individuals compete both with members of their own species and with the other species (Figure 19.19). Then, as long as there is a broad range of resource types, the individuals with the most extreme phenotypes (e.g., extremely small or large bills) will experience less intraspecific competition than more "central" phenotypes because they are less abundant, and they will experience less interspecific competition because they tend not to use the same resources as the other species. Therefore, the most extreme genotypes will have higher fitness. Such density-dependent diversifying selection can result in the two species evolving less overlap in their use of resources and in a shift of their phenotype distributions away from each other (Slatkin 1980; Taper and Case 1992). Divergence in response to competition between species is often called ecological **character displacement**, a term coined by William L. Brown and Edward O. Wilson (1956) to describe a pattern of geographic variation wherein sympatric populations of two species differ more greatly in a characteristic than do allopatric populations. The term is also used to mean the process of divergence that is due to competition.

The kind of geographic pattern that Brown and Wilson described has provided some of the best evidence for evolutionary divergence in response to competition (Taper and Case 1992; Schluter 2000). In northwestern North America, for example, several lakes have reproductively isolated open-water and bottom-dwelling forms of the three-spined stickleback fish (*Gasterosteus aculeatus*; see Figure 18.9). They differ in body shape (an adaptation to their habitat) and in mouth morphology and the number and length of the gill rakers (adaptations to feeding on different prey). Other lakes have only a single form of this

Figure 19.19 A model of evolutionary divergence in response to competition. The x -axis represents a quantitative phenotypic character (z), such as bill size, that is closely correlated with some quality of a resource (x), such as the average size of the food items eaten by that phenotype. The curve $K(z)$ represents the frequency distribution of food items that vary in size, and consequently the density that pure populations of various phenotypes, z , could attain. Two variable species (orange and green) initially overlap greatly in z , and therefore in the food items they depend on. Those phenotypes in each species that overlap with the fewest members of the other species experience less competition, and so may have higher fitness. Divergent selection on the two species is expected to shift their character distributions (red, dark green) so that they overlap less.



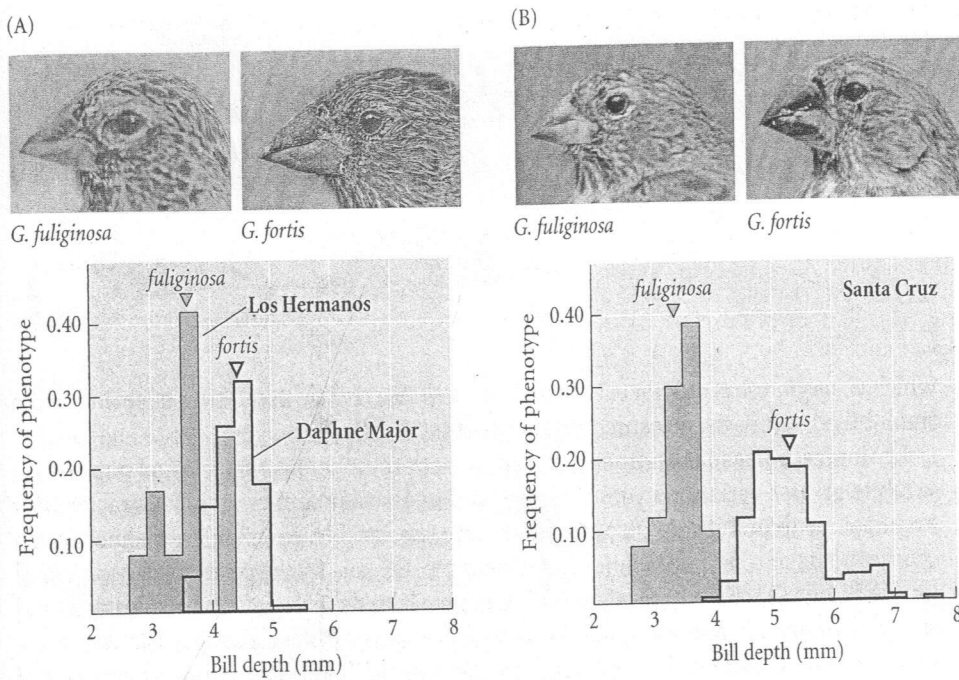


Figure 19.20 Character displacement in bill size in seed-eating ground finches of the Galápagos Islands. Bill depth is correlated with the size and hardness of seeds most used by each population; arrows show average bill depths. (A) Only *Geospiza fuliginosa* occurs on Los Hermanos, and only *G. fortis* occurs on Daphne Major. (B) The two species coexist on Santa Cruz, where they differ more in bill depth. (After Grant 1986; photos courtesy of Peter R. Grant.)

stickleback, with intermediate morphology (Schluter and McPhail 1992). Illustrating a famous case of character displacement, the Galápagos ground finches *Geospiza fortis* and *G. fuliginosa* differ more in bill size where they coexist than where they occur singly (Figure 19.20). Differences in bill size are correlated with the efficiency with which the birds process seeds that differ in size and hardness, and the population size of these finch species is often food-limited, resulting in competition (Grant 1986). Peter Grant and Rosemary Grant (2006) observed the process of character displacement in the population of *G. fortis* on the island of Daphne Major, where this species faced no competitors until *G. magnirostris*, a larger-billed species, colonized and built up a large population (Figure 19.21; see Figure 2.3B). Before *G. magnirostris* became abundant, a severe drought in 1977 that reduced seed availability caused the *G. fortis* population to evolve larger bills, because only larger-billed birds could eat the large, hard seeds of *Tribulus* plants after most smaller seeds had been consumed. When normal conditions returned, average bill size declined to its previous value. But by the time another drought occurred, in 2004, *G. magnirostris* had become abundant; it consumed most of the *Tribulus* seeds, and the *G. fortis* population evolved a smaller bill, for survival depended on eating the smallest available seeds,

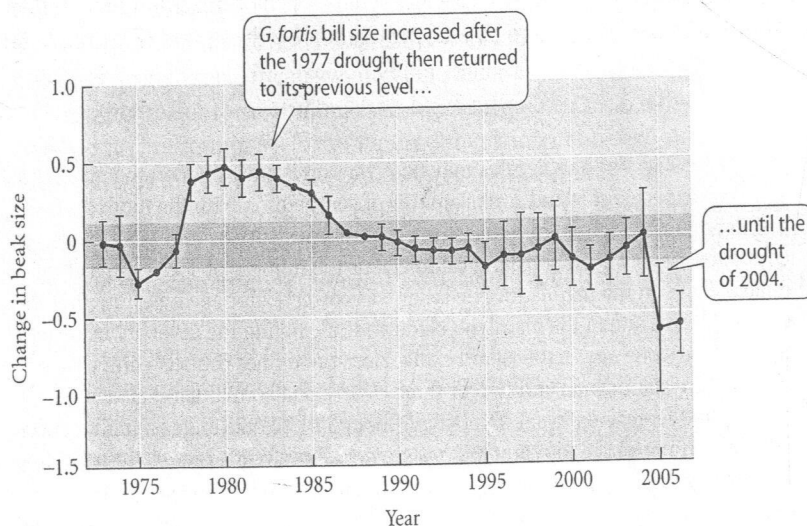
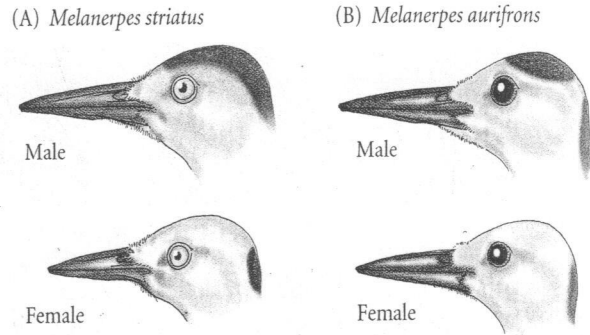


Figure 19.21 A history of change in mean beak size in the ground finch *Geospiza fortis* on the island of Daphne Major. Bill size increased after the 1977 drought and slowly returned to its previous level, until the drought of 2004, when bill size decreased because of character displacement from *G. magnirostris*, which has a larger bill and depleted the supply of large seeds. The darker shaded bar marks the range of mean beak size in 1973, with significant deviation showing up above and below that range. (After Grant and Grant 2006.)

Figure 19.22 Ecological release. The difference in bill size between the sexes is greater in *Melanerpes striatus* (A), the only species of woodpecker on the island of Hispaniola, than in continental species such as *M. aurifrons* (B), which is sympatric with other woodpecker species. Bill size is correlated with differences in feeding behavior, so greater sexual dimorphism results in broader resource use in *M. striatus*. (After Selander 1966.)



which *G. magnirostris* did not eat. This was a heritable change in bill size: offspring of the small-billed survivors, measured in 2006, had small bills.

Ecological release is another geographic pattern, wherein a species or population exhibits greater variation in resource use and in associated phenotypic characters if it occurs alone than if it coexists with competing species. Ecological release is most often characteristic of island populations. For example, the sole finch species on Cocos Island (in the Pacific Ocean, northeast of the Galápagos Islands) has a much broader diet, and forages in more different ways, than do any of its relatives in the Galápagos Islands, where there are many more species (Werner and Sherry 1987). Similarly, the only species of woodpecker on the Caribbean island of Hispaniola exhibits greater sexual dimorphism in the length of the bill and tongue than do related continental species that coexist with other woodpeckers, and the sexes differ in where and how they forage (Figure 19.22).

Competition among species is a cause of ecological diversification, as character displacement shows. On the other hand, alleviation of competition, resulting in ecological release, may enhance rates of speciation and diversification (Figure 19.23). The fossil record of diversity suggests that when incumbent taxa have become extinct, ecological opportunity has sometimes allowed diversification of other clades on a macroevolutionary scale (see Figure 7.19).

Multispecies interactions and community structure

The concept of character displacement between two competing species can readily be extended to “community-wide character displacement” among greater numbers of species that might evolve to partition resources (NICHE PARTITIONING). Using mathematical models, the pioneering evolutionary ecologists Robert MacArthur and Richard Levins (1967) predicted that coexisting species might be expected to be evenly spaced with respect to their average resources, such as the size of seeds or prey items. Morphological adaptations might reflect these ecological differences. Many examples fit this prediction (Schluter 2000). For example, among sympatric cats in Israel, differences between sexes and species in the size of the canine teeth, which are used to kill prey, are more nearly equal than expected by chance, and are thought to reflect differences in the average size of prey taken by these cats (Figure 19.24; Dayan et al. 1990).

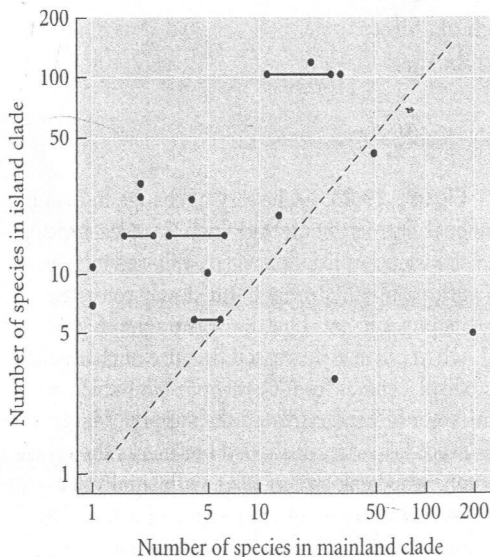


Figure 19.23 Speciation rates may be higher on islands than on the mainland, a pattern expected if island forms are free of competition with the more diverse mainland biota. Each point represents the number of species (of plants, birds, *Drosophila*, or *Anolis*) in an island clade versus the number of species in a closely related clade on the mainland. The latter was corrected for age by estimating the diversification rate in the mainland clade and calculating the diversity expected if it had the same age as the island clade. Horizontal lines connect comparisons between an island clade and two or three closely related mainland clades. The dashed line represents equal diversity. Although these data suggest higher speciation rates on islands, the comparisons are not all between sister clades, and the sample of island taxa may be biased toward those with high diversity. Thus more research is needed. (After Schluter 2000.)

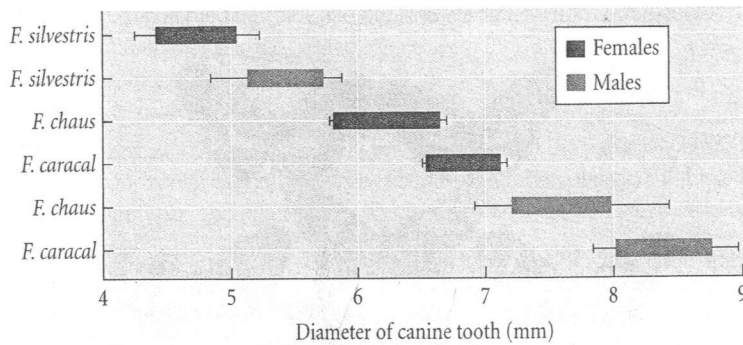


Figure 19.24 A nonrandom pattern of “equal spacing” among related predators may have evolved to minimize competition for food. The size of the canine teeth differs among three sympatric species of cats in Israel, and between the sexes in each species. These differences are thought to be adaptations to feeding on prey that differ in average size. The species are the wildcat (*Felis silvestris*), jungle cat (*F. chaus*), and caracal (*F. caracal*). (After Dayan et al. 1990.)

Several kinds of evolutionary outcomes may result from interactions between a predator species and multiple species of prey. If a predator’s abundance increases with the abundance of one prey, a second species of prey may suffer heavier predation and so decline—a phenomenon called “apparent competition” (Holt 1977). One or both prey species may then be selected to diverge from the other in characteristics that affect susceptibility to the predator, such as defense features. No examples of this possibility have yet been well documented, but many lineages have diverged because of trade-offs in adaptation to different predators. For example, *Enallagma* damselfly larvae with large tail fans that enable them to swim rapidly are adapted to escape dragonfly larvae, but they cannot escape fish, which move more rapidly and cue in on moving prey. *Enallagma* species that inhabit ponds with fish are cryptic, have small tail fans, and move slowly—but they are easier prey for dragonfly larvae (McPeck 1995).

Models of such interactions show that prey species subjected to a common predator are likely to diverge in some cases, but to converge if that lowers the risk of predation (Abrams 2000). The most dramatic examples of convergence are cases of defensive mimicry (Turner 1977; Joron and Mallet 1998; Mallet and Joron 1999). Traditionally, two forms of defensive mimicry have been recognized. In BATESIAN MIMICRY, a palatable species (a mimic) resembles an unpalatable species (a model). Mimicry works because predators learn, from unpleasant experience, to avoid potential prey that look like the unpalatable species. Often, although not always, the models and mimics display conspicuous aposematic (warning) patterns. Selection on a mimetic phenotype can depend on both its density, relative to that of a model species, and the degree of unpalatability of the model. A predator is more likely to avoid eating a butterfly that looks like an unpalatable model if it has had a recent reinforcing experience (e.g., swallowing a butterfly with that pattern and then vomiting). If it has recently swallowed a tasty butterfly, however, it will be more, not less, inclined to eat the next butterfly with the same phenotype. Thus the rarer a palatable Batesian mimic is relative to an unpalatable model, the more likely predators are to associate its color pattern with unpalatability, and so the greater the advantage of resembling the model will be. If a rare new phenotype arises that mimics a different model species, it will have higher fitness, and so a mimetic polymorphism can be maintained by frequency-dependent selection, as is seen in the African swallowtail *Papilio dardanus* (see Figure 9.1B).

The other major form of mimicry is MÜLLERIAN MIMICRY, in which two or more unpalatable species are co-mimics (or co-models) that jointly reinforce aversion learning by predators. Groups of species that benefit from defensive mimicry are known as MIMICRY RINGS. In many cases, mimicry rings include strongly unpalatable species, mildly unpalatable species that may be “quasi-Batesian” mimics of the more unpalatable species, and fully palatable Batesian mimics (Figure 19.25). Müllerian mimics are almost never polymorphic within populations, but different geographic races of certain species may have different aposematic color patterns and may belong to different mimicry rings (e.g., the geographic races of *Heliconius erato* and *H. melpomene*; see Figures 12.19 and 19.25).

Convergent evolution of similar adaptations to similar environmental conditions is a common phenomenon (Chapter 3). Ecologists have speculated that the structure of ecological communities—the number of species, their niche partitioning, the pattern of links between trophic levels—might likewise converge, and become similar in similar abiotic

Figure 19.25 A mimicry ring. *Heliconius melpomene* and *H. erato* have a very different color pattern in the Mayo and upper Huallaga rivers, in eastern Peru, than in the lower Huallaga basin, where they join a mimicry ring with a "rayed" pattern. This ring of unpalatable species includes four other species of *Heliconius*, three other genera of butterflies (the top three species in the center column), and a moth (center column, bottom). (Courtesy of J. Mallet.)



environments. If species could usually adapt rapidly to the other species they encounter, the structure of local assemblages of species might be predictable. Phylogenetic niche conservatism, the retention of ancestral physiological and ecological properties, however, suggests limitations on the degree to which species are free to coevolve (Chapter 6). In that case, local communities are formed largely by processes of ECOLOGICAL SORTING: species with evolved features that enable them to coexist, without adaptive adjustment, do so, while others are excluded by competition or predation.

As we saw in Chapter 6, some examples of convergent assemblages arising from parallel multispecies evolution have been described, such as the ecomorphs of *Anolis* lizards that have independently evolved to use similar microhabitats on the several islands of the Greater Antilles (see Figures 6.22 and 6.23). However, the history of evolution has seldom been so predictable, and convergence of community structure can be hard to discern. Nevertheless, evolutionary history has left its imprint on ecological communities (Ricklefs and Schluter 1993; Webb et al. 2002). For example, Campbell Webb (2000) found that locally co-occurring species of trees in a Bornean rainforest are phylogenetically more closely related than if they had been randomly sampled from all the available species, evidently because they have similar (phylogenetically conservative) habitat requirements. Conversely, Jeannine Cavender-Bares and collaborators (2004) found that co-occurring oaks (*Quercus*) consistently are members of two different clades that have convergently adapted to each of several habitats. These two examples show the effects of ecological sorting versus local evolution on local species assemblages. Similarly, each of the small islands of the Lesser Antilles has either one or two species of *Anolis*. On each two-species island, the species differ in size, but the large and small species form two different clades; thus the two-species communities have been formed by ecological sorting of species that could coexist without coevolutionary adjustment (Losos 1992). This contrasts with the parallel adaptive radiations of *Anolis* that have occurred on the large islands of the Greater Antilles.

Summary

1. Coevolution is reciprocal evolutionary change in two or more species resulting from the interaction among them. Species also display many adaptations to interspecific interactions that appear one-sided rather than reciprocal.
2. Phylogenetic studies can provide information on the age of associations among species and on whether or not they have codiversified or acquired adaptations to each other. The phylogenies of certain symbionts and parasites are congruent with the phylogenies of their hosts, implying cospeciation, but in other cases such phylogenies are incongruent and imply shifts between host lineages.

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3. Coevolution in predator-prey and parasite-host interactions can theoretically result in an ongoing evolutionary arms race, a stable genetic equilibrium, indefinite fluctuations in genetic composition, or even extinction.
4. Parasites (including pathogenic microorganisms) may evolve to be more or less virulent, depending on the correlation between virulence and the parasite's reproductive rate, vertical versus horizontal transmission between hosts, infection of hosts by single versus multiple parasite genotypes, and other factors. Parasites do not necessarily evolve to be benign.
5. Mutualism is best viewed as reciprocal exploitation. Selection favors genotypes that provide benefits to another species if this action yields benefits to the individual in return. Thus the conditions that favor low virulence in parasites, such as vertical transmission, can also favor the evolution of mutualisms. Mutualisms may be unstable if "cheating" is advantageous, or stable if it is individually advantageous for each partner to provide a benefit to the other.
6. Evolutionary responses to competition among species may lead to divergence in resource use and sometimes in morphology (character displacement). Competition has caused ecological diversification, whereas alleviation of competition can enhance the rate of increase in the number of species.
7. Character displacement between species that are subjected to a common predator may occur, but not many examples have as yet been reported. Convergence of prey species, as illustrated by defensive mimicry, occurs if it reduces predation.
8. The structure of ecological communities is affected by evolutionary adjustment of coexisting species to each other and by ecological sorting of species on the basis of characteristics that affect the likelihood of coexistence. Convergence of the structure of independently formed ecological communities can occur by both processes, but differences among communities may exceed similarities.

Terms and Concepts

character displacement

coevolution

ecological release

escape-and-radiate coevolution

gene-for-gene interactions

guild coevolution (= diffuse coevolution)

horizontal transmission

mutualism

specific coevolution

vertical transmission

Suggestions for Further Reading

J. N. Thompson, in *The Coevolutionary Process* (University of Chicago Press, 1994), discusses the evolution and ecology of many interactions, especially among plants and their herbivores and pollinators. He develops one of that book's themes further in *The Geographic Mosaic of Coevolution* (University of Chicago Press, 2004).

Plant-animal interactions are the focus of essays by prominent researchers in *Plant-Animal Interactions: An Evolutionary Approach*, edited by C. M. Herrera and O. Pellmyr (Blackwell Science, Oxford, 2002). "Models of parasite virulence" by S. A. Frank (*Quarterly Review of Biology* 71: 37-78, 1996) is an excellent entry into this subject. *The Ecology of Adaptive Radiation* by D. Schluter (Oxford University Press, Oxford, 2000) includes extensive treatment of the evolution of ecological interactions and their role in diversification. "Supplement on phylogenetic approaches to community ecology" appeared in the journal *Ecology* (vol. 87, July 2006).

Problems and Discussion Topics

1. How might coevolution between a specialized parasite and a host be affected by the occurrence of other species of parasites?
2. How might phylogenetic analyses of predators and prey, or of parasites and hosts, help to determine whether or not there has been a coevolutionary arms race?
3. The generation time of a tree species is likely to be 50 to 100 times longer than that of many species of herbivorous insects and parasitic fungi, so its potential rate of evolution should be slower. Why have trees, or other organisms with long generation times, not become extinct as a result of the potentially more rapid evolution of their natural enemies?
4. Design experiments to determine whether greater virulence is advantageous in a horizontally transmitted parasite and in a vertically transmitted parasite.

5. Some authors have suggested that selection by predators may have favored host specialization in herbivorous insects (e.g., Bernays and Graham 1988). How might this occur? Compare the pattern of niche differences among species that might diverge as a result of predation with the pattern that might evolve because of competition for resources.
6. Provide a hypothesis to account for the extremely long nectar spur of the orchid *Angraecum sesquipedale* (see Figure 19.16) and the long proboscis of its pollinator. How would you test your hypothesis?
7. In simple ecological models, two resource-limited species cannot coexist stably if they use the same resources. Hence coexisting species are expected to differ in resource use because of the extinction, by competition, of species that are too similar. Therefore, coexisting species could differ either because of this purely ecological process of "sorting" or because of evolutionary divergence in response to competition. How might one distinguish which process has caused an observed pattern? (See Losos 1992.)
8. Suppose that among related host species that carry related symbionts, the relationship is mutualistic in some pairs and parasitic in others. How would you (a) tell which is which, (b) determine what the direction of evolutionary change has been, and (c) determine whether the change from one to the other kind of interaction was a result of evolutionary change in the symbiont, in the host, or both?