13

Interactions among Species

Nearly 20 years before he published *On the Origin of Species*, Charles Darwin started to study orchids, intrigued by the extraordinary features of their flowers. He examined British species, and he grew tropical species, solicited from horticulturists, in his greenhouse. In 1862, in his first book after *On the Origin of Species*, he summarized his studies in *On the Various Contrivances by which British and Foreign Orchids are Fertilised by Insects, and on the Good Effects of Intercrossing*. It is a landmark work, in which Darwin put into practice his principles of natural selection and descent with modification. Parting with the prevailing theological interpretation, that flowers were shaped by God to inspire us with beauty, Darwin showed that the astonishingly diverse and peculiar features of orchid flowers increase the chance that they will attract insects and deposit pollen on them in so precise a way as to ensure cross-pollination. Among these remarkable plants was a species from Madagascar, *Angraecum sesquipedale*, with a nectar-bearing tube up to 30 cm long (**FIGURE 13.1**). Other plants with much shorter nectar spurs are visited by insects with tongues long enough to reach the nectar, so Darwin predicted that there must exist in Madagascar a moth with a similarly long proboscis. One reviewer ridiculed this idea, and indeed the very idea that the features of flowers are useful, but in 1903 a sphinx moth with a proboscis up to 30 cm long was described from Madagascar, and was fittingly named *Xanthopan morganii praedicta*. *Angraecum* and its moth perfectly illustrated Darwin's speculation (in *On the Origin of Species*) that both a flower and a pollinating insect "might slowly become, either simultaneously or one after the other, modified and adapted in the most perfect manner."

Red-billed oxpeckers (*Buphagus erythrorhynchus*) like the one shown here on a Cape buffalo (*Syncerus caffer*) spend most of their time on large African ungulates, where they eat mostly ticks, but also feed at open wounds. Their interaction with the mammals is on the border between mutualism and parasitism.

FIGURE 13.1 A coevolved interaction. The orchid *Angraecum sesquipedale* bears nectar in an exceedingly long spur and is pollinated by the long-tongued sphinx moth *Xanthopan morganii praedicta*. The moth was discovered about 40 years after Darwin predicted its existence. Each of the species in this mutualism is adapted to obtain something from the other.

Coevolution and Interactions among Species

Every species is subjected to natural selection from its biotic environment: the complex of other organisms with which it interacts. Most of these species can be classified as resources (used as nutrition or habitat), competitors (for resources such as food and space), enemies (predators or parasites), or mutualists. In mutualistic interactions, each species obtains a benefit from the other. (**Symbiosis**, meaning "living together," describes intimate associations between species that may be either mutualists or parasite and host. An endosymbiont lives within the other organism's body.) The community of other species with which a species interacts is complex and variable—both the identity and genetic composition of interacting species vary in time and place. Thus, a plant species may be pollinated or attacked by many species of insects, and be inhabited by any of hundreds of species of fungi and bacteria that live on or in its leaves and roots. Similarly, the natural environment of humans includes a variable "human microbiome": the trillions of bacteria, including thousands of species—mostly harmless and some even beneficial—that occupy the gut, skin, nostrils, and other microhabitats [15, 34, 55].

Some of the most familiar examples of natural selection, such as industrial melanism in the peppered moth and the sickle-cell polymorphism in human hemoglobin, entail biological agents (predaceous birds and malarial parasites, respectively) (see Chapter 5). In many such interactions, the evolution of one species has been affected by the other, but not vice versa. **Coevolution**, strictly defined, is reciprocal genetic change in interacting species, owing to natural selection imposed by each on the other. Not all adaptations of one species to other species are necessarily coevolved.

The nature and strength of an interaction between two species may vary depending on genotype, environmental conditions, and other species with which those species interact. For example, populations of the limber pine in areas where squirrels eat the seeds have cones that reduce squirrel depredation, but are also less favorable for the Clark's nutcracker, a bird that the pine depends on for seed dispersal (**FIGURE 13.2**). 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 [73].

The term "coevolution" includes several concepts [28, 72]. In its simplest form, called *specific coevolution*, two species evolve in response to each other (**FIGURE 13.3A**). Darwin's *Angraecum* orchid and its specialized pollinating moth are an example. *Diffuse coevolution* occurs when several species are involved and their effects are not independent (**FIGURE 13.3B**). For example, genetic variation in the resistance of a host to two different species of parasites might be correlated [35]. In *escape-and-radiate coevolution*, a species evolves a defense against enemies and is thereby enabled to radiate into diverse descendant species, to which different enemies may later adapt (**FIGURE 13.3C**).

A few cases have been described in which the phylogeny of a group of organisms matches the phylogeny of a group of its parasites or symbionts. An example is the association between aphids and endosymbiotic bacteria (*Buchnera*) that live in special aphid cells and supply the essential amino acid tryptophan to their hosts. The completely concordant phylogenies of the aphids and bacteria (**FIGURE 13.4**)

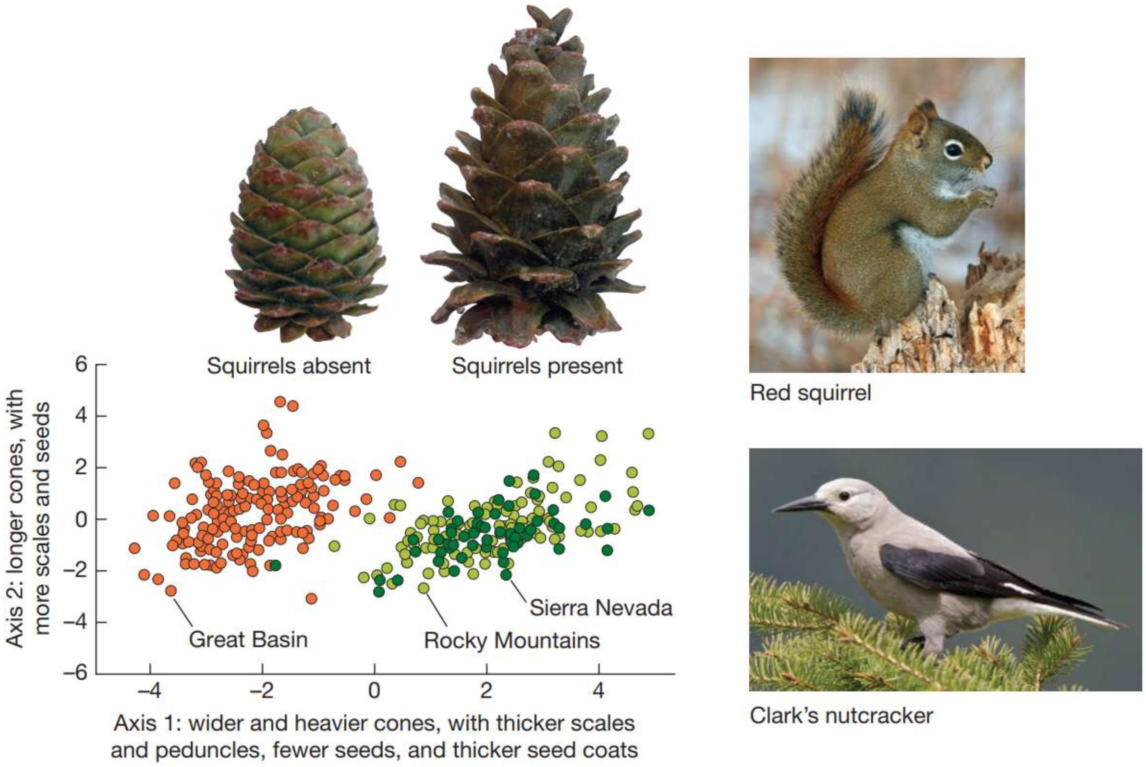


FIGURE 13.2 A geographic mosaic of interactions. Typical cones of limber pine (*Pinus flexilis*) populations that (at right) are adapted to resist seed-eating squirrels or (at left) are adapted for seed dispersal by Clark's nutcracker where squirrels are absent. The graph of two variables, each of which combines several measurements of cones and seeds, shows that pines in an area without squirrels (Great Basin, orange dots) differ from those in two areas with squirrels (Sierra Nevada and Rocky Mountains, dark and light green dots, respectively). Each dot represents one tree. (After [67]; pine cone photos from [67].)

show that this association dates from the origin of the aphids, and that the bacteria have diverged in concert with speciation in their hosts. The explanation is simple: the bacteria are transmitted from mother aphids to their offspring just as if they were mitochondria. By themselves, matching phylogenies should not be considered coevolution, because there need not have been any reciprocal adaptation. A match can arise simply because the parasite or endosymbiont has had little or no opportunity to be transmitted between different hosts. The phylogeny

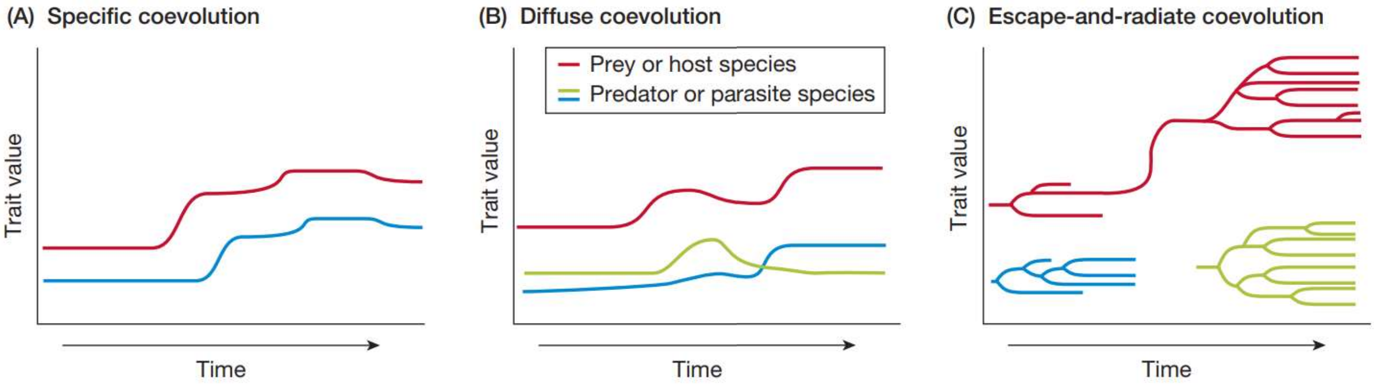
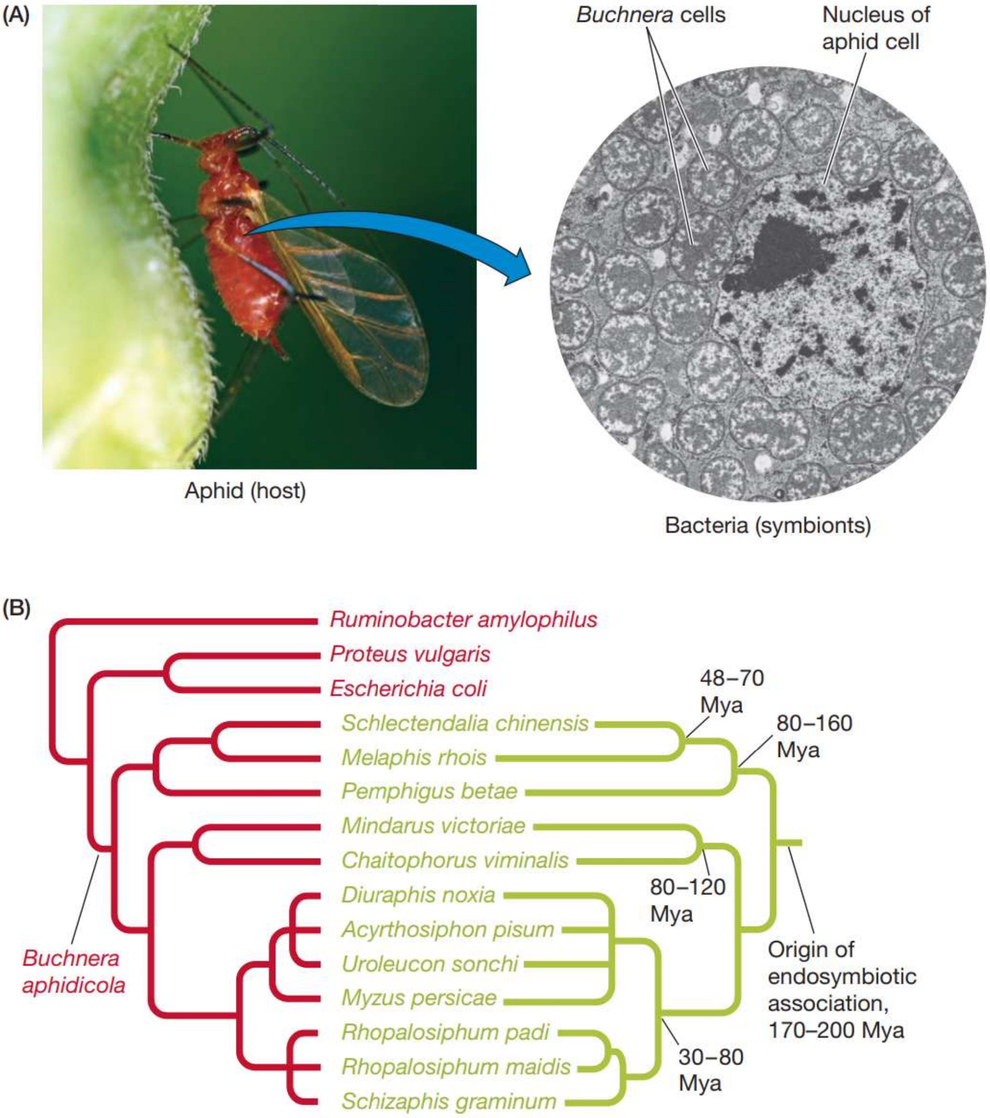


FIGURE 13.3 Three kinds of coevolution. In each graph, the horizontal axis represents evolutionary time, and the vertical axis shows the state of a character in a species of prey or host and one or more species of predators or parasites. (A) Specific coevolution. (B) Diffuse coevolution, in which a prey species interacts with two or more predators, can take many paths. In this case, a prey species becomes better defended against two predators, only one of which (blue curve) becomes better able to capture the prey. (C) Escape-and-radiate coevolution. A 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.

FIGURE 13.4 (A) *Buchnera aphidicola* bacteria are endosymbionts of aphids. The electron micrograph (at right) shows bacterial cells living inside a specialized aphid cell (bacteriocyte). (B) 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 green. The estimated ages of the aphid lineages are based on fossils and biogeography. These *Buchnera* lineages are as old as the aphid lineages that carry them. (After [53]; electron micrograph courtesy of N. Moran and J. White.)



of free-living parasites and mutualists seldom matches the host phylogeny very closely [29, 57, 82].

The Evolution of Enemies and Victims

Interactions between enemies and victims include predators and their prey, parasites and their hosts, and herbivores and their host plants. Such interactions are often unstable, because enemies can extinguish victim populations, or reduce them to the point that the enemy population becomes extinct for lack of food. Many species of Australian marsupials were driven to extinction by introduced foxes and feral cats [19]; a chytrid fungus has extinguished some species of frogs and threatens many other amphibians [12]. Because the future does not affect the action of natural selection (see Chapter 3), the possibility that the prey or host might be killed off does not cause enemies to evolve restraint that might preserve prey populations. Victims and their enemies coexist only if their interactions are stabilized by ecological and evolutionary factors, including adaptations to escape or resist enemies.

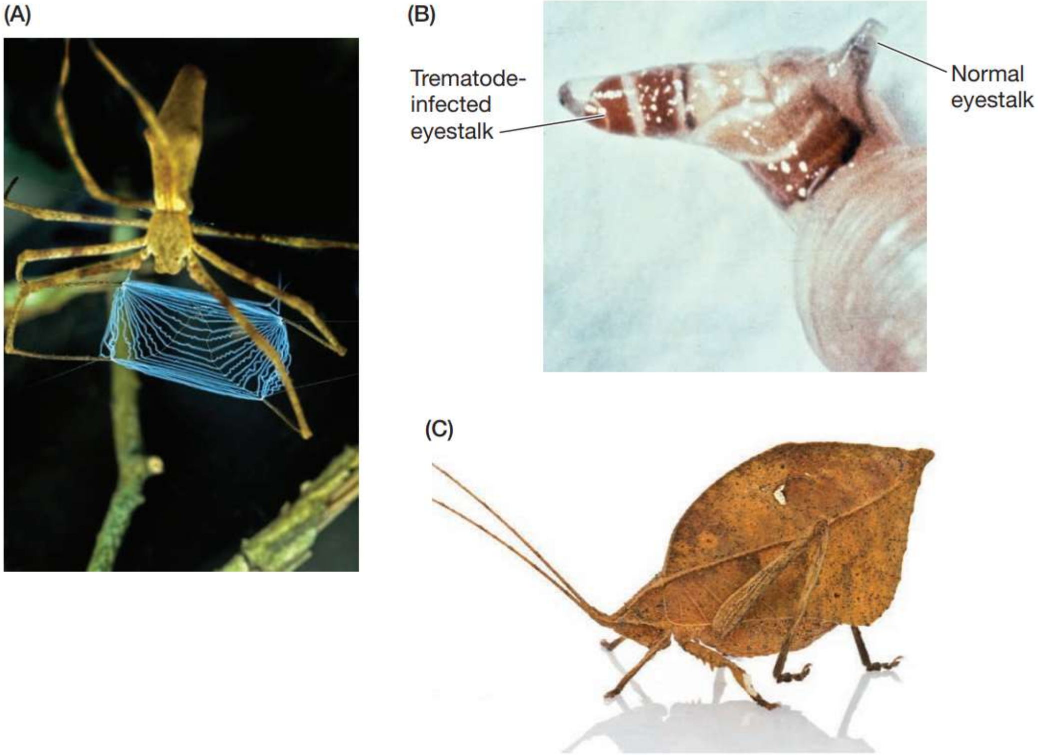


FIGURE 13.5 Predators and parasites have evolved many extraordinary adaptations to capture prey or infect hosts, and prey have elaborate counteradaptations. (A) This tropical net-casting spider (*Deinopis subrufa*) holds an expandable web that it uses to quickly envelope slowly flying insects that pass by. (B) The larva of a parasitic trematode (*Leucochloridium*) migrates to the eyestalk 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. (C) Katydids (Tettigoniidae) of the genus *Mimetica* have an extraordinary resemblance to leaves, including what looks like leaf venation and damage by herbivores. (B, photo by P. Lewis, courtesy of J. Moore.)

Predators and parasites have evolved some extraordinary adaptations for capturing, subduing, or infecting their victims (**FIGURE 13.5**). Defenses against predation and parasitism can be equally impressive, ranging from cryptic patterning to the most versatile of all defenses: the vertebrate immune system, which can generate antibodies against thousands of foreign compounds. The CRISPR-Cas mechanism in some bacteria is also an elaborate system of recognizing and defending against foreign invaders—that is, viruses. Many such adaptations appear to be directed at a variety of different enemies or prey species, so the coevolution, if any, has probably been diffuse.

R. A. Fisher, one of the founders of evolutionary genetics, suggested that a species' environment, such as the climate, is constantly changing, but "probably more important than the changes in climate will be the evolutionary changes in progress in associated organisms" [25]. This idea is expressed by the **Red Queen hypothesis**, named by paleontologist Leigh Van Valen [79] for the Red Queen whom Alice meets in Lewis Carroll's *Through the Looking-Glass*: each species has to run (i.e., evolve) as fast as possible just to stay in the same place (survive) because interacting species also continue to evolve. The dynamics of Red Queen coevolution may take several forms, including escalation and oscillation. In the long term, the dynamics may lead to indefinite coexistence of enemy and victim species, a switch by the enemy to a different victim species, or extinction of one or both species [1, 56].

An **evolutionary arms race**, also called escalation, may occur if the capture rate of the prey by the predator increases with the difference between the defensive trait of a prey species and a corresponding character in a predator. Then the characteristics of both species that affect their interaction evolve in one direction: for example, greater speed of gazelles and of pursuit predators such as cheetahs (**FIGURE 13.6**). This can lead to extinction or to a stable point when the costs of increasing the trait (e.g., speed, or a plant's defensive chemicals) become too great.

The Japanese camellia (*Camellia japonica*) and the camellia weevil (*Curculio camelliae*) present a dramatic example of escalatory coevolution. The camellia's

FIGURE 13.6 Evolutionary arms race between predator and prey. Selection by predators such as cheetahs has resulted in the evolution of high speed in prey such as the gazelle in this picture. Predators are therefore also under selection for greater speed.

seeds are enclosed by a woody fruit wall (pericarp) that is much thicker in southern than in northern populations (**FIGURE 13.7**). A high proportion of seeds are consumed by larvae of the weevil, which inserts eggs into the seed chamber through a hole that the female bores with her mandibles, located at the end of her long snout, or rostrum. Investigators showed that the weevils' success in boring through to the seed chamber depends on their rostrum length, relative to the thickness of a fruit's pericarp [76]. Although southern weevil populations have a much longer rostrum, the southern plant population is ahead in this conflict, with pericarps thick enough to reduce the weevils' success to less than 50 percent. In the north, weevil populations are ahead—their rostra are long enough to ensure a success rate well over 50 percent. These species may be engaged in an evolutionary arms race.

In some cases, prey species have evolved defenses that can make them as dangerous to predators as predators are to prey. The rough-skinned newt (*Taricha granulosa*) of northwestern North America has one of the most potent known defenses against predation: the neurotoxin tetrodotoxin (TTX). One newt can have enough TTX in its skin to kill 25,000 laboratory mice. The level of TTX varies greatly among geographic populations of the newt. Populations of the garter snake *Thamnophis sirtalis* from outside the range of the newt have almost no resistance to TTX [8, 31]. But snake populations that are sympatric with toxic newts feed on them, and those populations are resistant to TTX. The average level of snake resistance and newt toxicity is not perfectly matched, for some snake populations are resistant to much higher TTX concentrations than any newt possesses (**FIGURE 13.8**). There is no selection for increased resistance in these populations, for the snakes do not vary in survival from eating the highly toxic newts.

Theoretical models of quantitative traits show that in contrast to escalation, oscillations may occur if the capture rate of the prey by the predator depends on a close match between the predator and prey traits [1]. If the prey's trait will evolve in

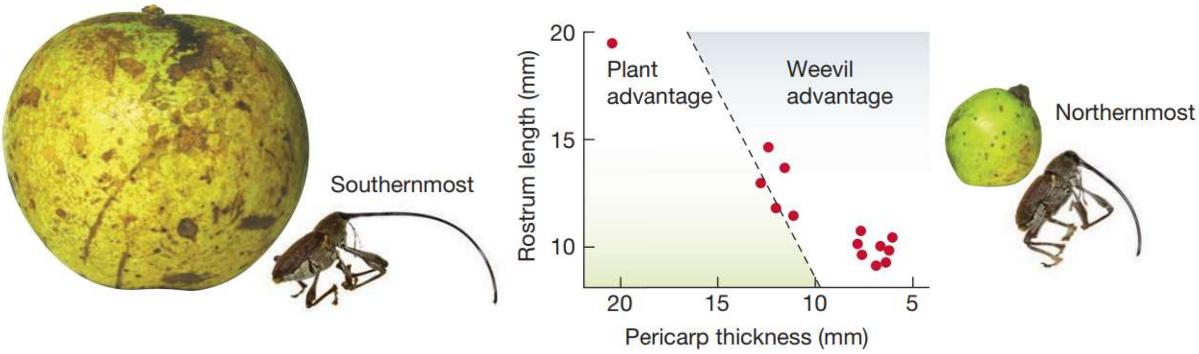


FIGURE 13.7 Imbalance in a coevolutionary conflict. The graph plots the thickness of the pericarp of the Japanese camellia against the rostrum length of the camellia weevil in several populations. To the left of the dashed line, plants are effectively defended against the weevils, while to the right of the line the weevil can effectively feed on the seeds. (After [76]; fruit photos from [76]; weevil photos courtesy of Hiro Toju.)

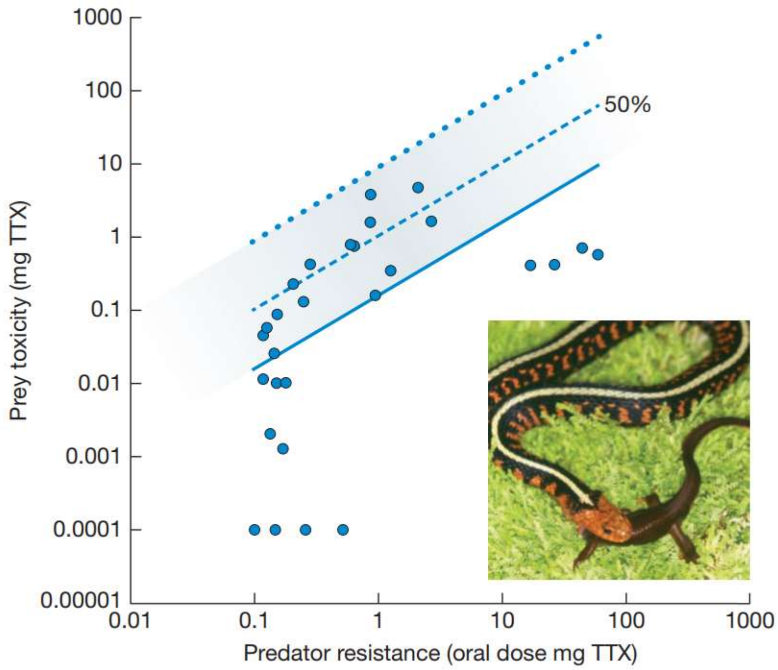


FIGURE 13.8 Toxicity of rough-skinned newts (*Taricha granulosa*) and resistance of garter snakes (*Thamnophis sirtalis*) in several localities. Prey toxicity is the amount of TTX (tetrodotoxin) in the newt; predator resistance is the oral dose of TTX required to reduce the speed of a garter snake by 50 percent. Below the lower boundary (solid blue line), snakes can consume co-occurring newts with no reduction in speed; above the upper boundary (dotted line), toxicity is so high that co-occurring snakes would be completely incapacitated. In general, populations of garter snakes are more resistant where more toxic newts are found, but there is some mismatch: almost half the snake populations fall below the lower boundary, and are therefore much more resistant than they need to be. (After [31]; photo courtesy of Edmund D. Brodie, Jr.)

one direction, the predator's trait will evolve to track it. Eventually, the prey's trait may evolve in the opposite direction as its cost becomes too great, and evolution of the predator's trait will follow. The result may be continuing cycles of change in the characteristics of both species, and these changes may contribute to cycles in population density. Parasite-host interactions can involve oscillations in gene frequencies (see below).

Phenotypic matching is important for some brood-parasitic birds, such as certain species of cuckoos, that lay eggs only in the nests of 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 13.9A**). Adults of host species treat parasite

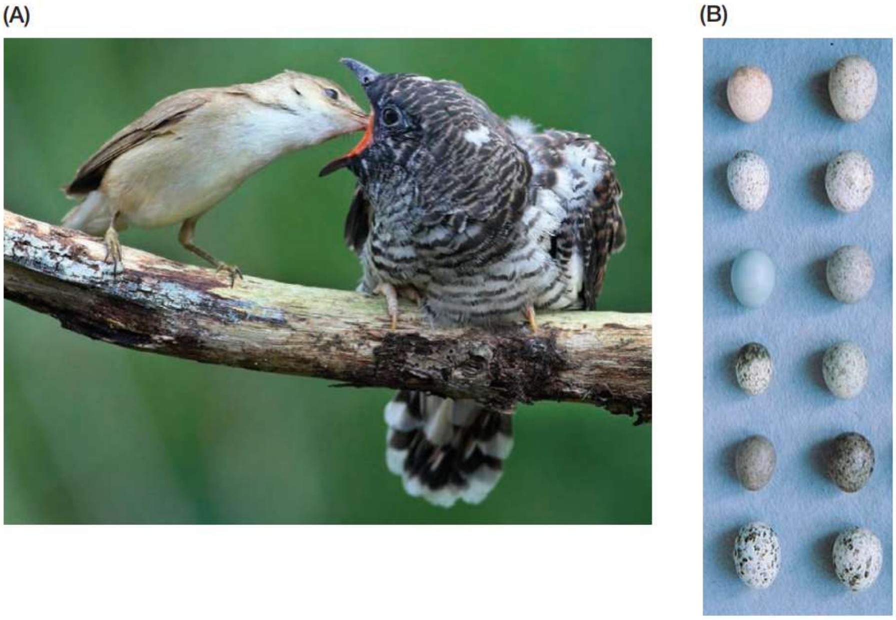


FIGURE 13.9 Adaptations for and against brood parasitism. (A) A fledgling common cuckoo (*Cuculus canorus*) being fed by its foster parent, a much smaller reed warbler (*Acrocephalus scirpaceus*). (B) Mimetic egg polymorphism in the common cuckoo. The left column shows eggs of six species parasitized by the cuckoo (from top: European robin, pied wagtail, dunnock, reed warbler, meadow pipit, great reed warbler). The right column shows a cuckoo egg laid in the corresponding host's nest. The match is quite close except in the dunnock nest. (B, photo by M. Brooke, courtesy of N. B. Davies.)

nestlings like 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. Many brood parasites have counteradapted by laying mimetic eggs [65]. Each population of the common cuckoo (*Cuculus canorus*) contains several different genotypes, which prefer different hosts and lay eggs closely resembling those of their preferred hosts (**FIGURE 13.9B**). Nick Davies and Michael Brooke traced the fate of artificial cuckoo eggs placed in the nests of various host species [16]. Bird species that are not parasitized by cuckoos tend not to eject cuckoo eggs. But among the cuckoos' preferred hosts, those species whose eggs are mimicked by cuckoos reject artificial eggs more often than those whose eggs are not mimicked. These species have adapted to brood parasitism by evolving greater discrimination. Moreover, populations of two host species that reject artificial cuckoo eggs in Britain accept them in Iceland, where cuckoos are absent. Thus two evolving traits, host discrimination and cuckoo egg pattern, shape the evolution of this interaction.

Aposematism and mimicry

Diverse animals, such as bees and coral snakes, have evolved warning, or **aposematic**, coloration: bright colors that signal to a potential predator that they are distasteful or dangerous. Predators learn to avoid the color pattern, and so both the predator and the aposematically colored prey benefit. The warning pattern is subject to positive frequency-dependent selection because individuals that deviate from the common pattern, which predators have learned, are likely to be attacked (see Figure 5.24). Thus, a mutation that confers a new aposematic pattern is likely to be disadvantageous. How new aposematic phenotypes evolve is therefore a puzzle. They might be caused by genetic drift in places or at times when selection by predators is relaxed (see p. 130 in Chapter 5) [48].

Mimicry is a form of convergent evolution in which resemblance between different species has evolved because it is advantageous for members of one species to resemble another. The species, then, do not owe their resemblance to common ancestry, but in some cases are so similar that experts have to look very carefully to distinguish them. The most common kind of mimicry is defensive mimicry, which often is based on the aposematic coloration of other species [49]. Two common forms of defensive mimicry are named for the naturalists who first recognized them. In **Batesian mimicry**, a palatable species (a mimic) resembles an unpalatable species (a model). 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 that can learn is more likely to avoid eating a butterfly that looks like an unpalatable model if it has had a recent reinforcing experience (e.g., vomiting after eating a butterfly with that pattern). If the predator 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 negative frequency-dependent selection, as is seen in the African swallowtail *Papilio dardanus* (**FIGURE 13.10**).

The other major form of defensive mimicry is **Müllerian mimicry**, in which two or more unpalatable species are co-mimics (or co-models) and jointly reinforce aversion learning by predators. This hypothesis was proposed by Fritz Müller in 1879 and has been confirmed by experiments in which the survival of distasteful mimetic butterflies was shown to be higher if they closely matched an abundant co-mimic species (**FIGURE 13.11**). This form of mimicry causes positive

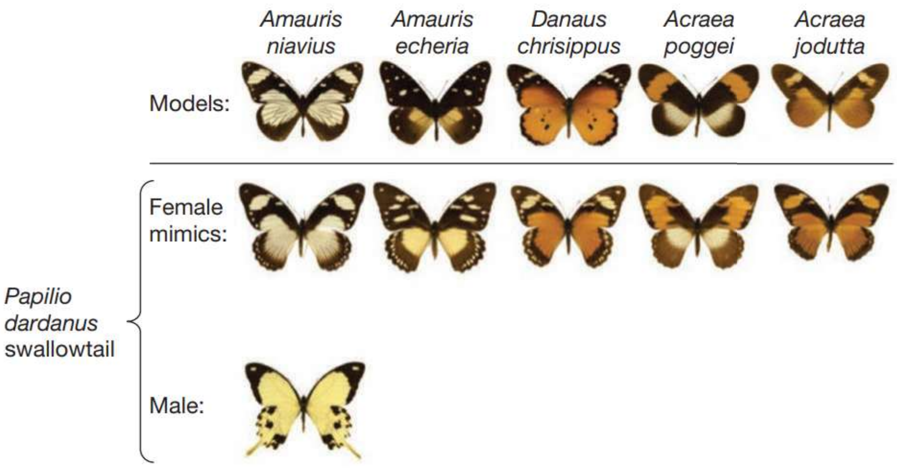


FIGURE 13.10 Mimetic polymorphism in the African swallowtail butterfly *Papilio dardanus*. Males have only one color form (at bottom), but populations contain several color forms of females (mimics, in the middle row), each of which closely resembles a distantly related distasteful species (models, in the top row). Predators that have attacked a distasteful model learn to avoid butterflies with that color pattern. As the abundance of any specific color morph of *P. dardanus* increases, its fitness tends to decline, because predators are increasingly likely to associate the pattern with a tasty meal rather than a foul taste. (From [75].)

frequency-dependent selection, since common phenotypes will be better recognized and avoided, and deviants from the common pattern will be less likely to survive.

Plants and herbivores

Almost all plants synthesize a variety of secondary compounds (so called because they play little or no role in primary metabolism). Thousands of such compounds have been described, including many that humans have found useful as drugs (e.g., salicylic acid, the active ingredient of aspirin), stimulants (caffeine), condiments (capsaicin, the "hot" element in chili peppers), and in other ways (cannabinol, in marijuana). Families of plants are often characterized by particular groups of similar compounds, such as cardiac glycosides in milkweeds (Apocynaceae) and glucosinolates in mustards (Brassicaceae). Many of these compounds are known to be toxic or repellent to animals, and there is plentiful evidence that insects and other herbivores impose selection for chemical and other defenses.

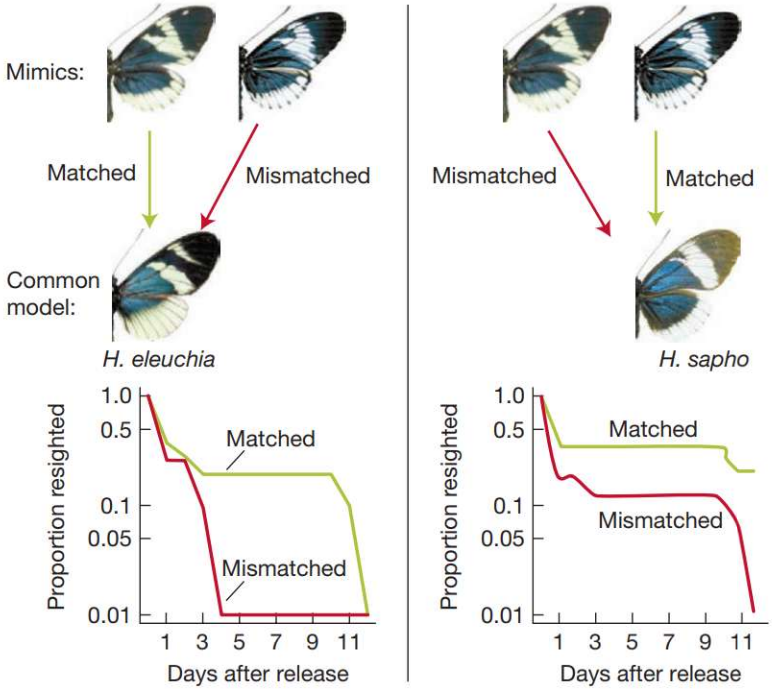
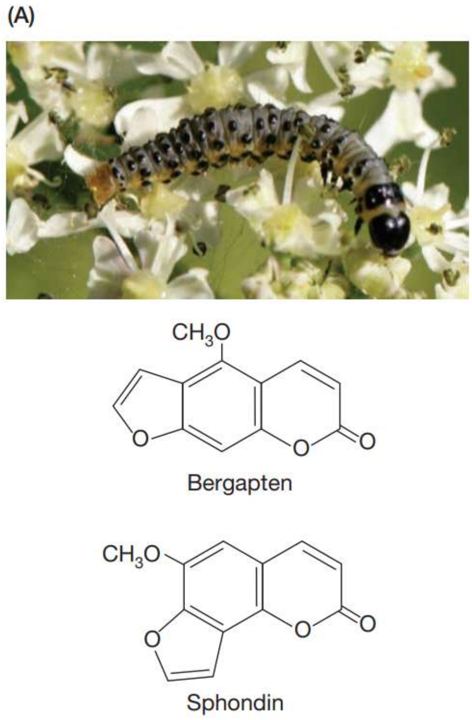


FIGURE 13.11 Müllerian mimicry protects *Heliconius* butterflies. Two color morphs of *Heliconius cydno* mimic two different species of models (*H. sapho* and *H. eleuchia*). The models vary in abundance between localities, and the mimic that matches the common model survives best. Left: In one locality, the model species *H. eleuchia* is most common. Both morphs of the mimic species were marked and released, and their survival was monitored in the following days. The mimic that matched the common model survived best. Right: In another locality, the model species *H. sapho* is more common. The same procedure used in the first experiment showed that again the mimic that matched the locally abundant model survived best. This second experiment confirms that a mimic's survival rate was determined by whether it matched the model that was most frequent, not by an intrinsic advantage of one mimic color pattern over the other. (From [38].)



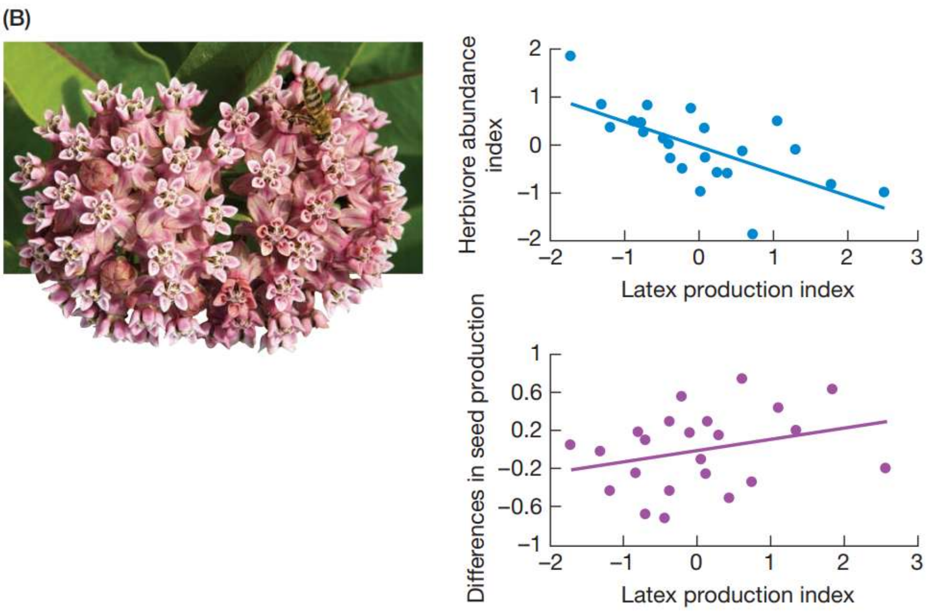


FIGURE 13.12 Secondary chemicals can defend plants against herbivores. (A) The furanocoumarins bergapten and sphondin are among the defensive secondary compounds of wild parsnip (*Pastinaca sativa*), the host plant of a moth larva, the parsnip webworm (*Depressaria pastinacella*). (B) Common milkweed (*Asclepias syriaca*) is genetically variable for latex production. Families of plants with greater latex levels had fewer herbivorous insects and higher fitness, measured by seed production relative to a control without herbivory. (B after [3].)

For example, seed production in wild parsnip (*Pastinaca sativa*) is correlated with genetically variable resistance to the seed-eating parsnip webworm (*Depressaria pastinacella*), based on the concentrations of two furanocoumarin compounds in the seeds (**FIGURE 13.12A**) [5]. Similarly, the fitness of common milkweed (*Asclepias syriaca*) is strongly affected by genetic variation in the production of latex, a gummy white fluid that reduces the abundance and impact of insects on the plant (**FIGURE 13.12B**) [3].

Paul Ehrlich and Peter Raven proposed a scenario of escape-and-radiate coevolution (see Figure 13.3C), 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 [23]. Eventually, though, some insect species from other hosts shift to these plants, adapt to their defense, and give rise to a clade of adapted herbivores.

Subsequent research has provided evidence for this idea [27]. For example, the plant order Brassicales (mustards and relatives) evolved about 92 million years ago (Mya), with the ability to synthesize glucosinolates, the precursors of toxic mustard oils, from certain amino acids. These plants are the almost exclusive larval food of the butterfly subfamily Pierinae, which adapted to Brassicales about 68 Mya by evolving an enzyme that breaks down glucosinolates. Later, new kinds of glucosinolates evolved in one lineage of Brassicales. Soon afterward, two lineages of the butterflies adapted to these novel glucosinolates. In these lineages, different duplications (see Chapter 14) of the gene that encodes the glucosinolate-degrading enzyme led to evolution of enzymes with new functions. These evolutionary innovations were associated with increased proliferation of new species in both the plant and butterfly lineages [22].

Parasite-host interactions and infectious disease

Evolutionary biologists include most pathogenic bacteria and other disease-causing microorganisms among parasites. The two greatest challenges a parasite faces are overcoming the host's defenses and moving from one host to another by vertical transmission from a host parent to its offspring or by horizontal transmission via the environment (see Chapter 12, Figure 12.15). Parasites that reduce the survival or reproduction of their hosts are considered **virulent**. Many parasites are virulent not because it is to their advantage to kill their host, but because their own survival and reproduction require that they consume part of the host, to obtain energy and protein. Some parasites actually prolong the life of their host (and enhance their own reproduction) by interfering with its hormones and effectively castrating it.

Several models of the coevolution of parasites (including pathogens) and their hosts are based on genetic evidence from empirical studies [4, 20]. *Gene-for-gene models* (**FIGURE 13.13A**) are based on interactions between some plants and fungal pathogens [39]. The host has several loci at which an allele encodes a receptor protein that recognizes a cell-surface protein (ligand) of a pathogen and confers resistance. Resistance to pathogens with different ligands depends on the plant's different recognition (receptor) genes. A pathogen can infect (is virulent) if it lacks the ligand or if the plant lacks the corresponding receptor protein. In a population of resistant plants, selection may fix the pathogen genotype that lacks the ligand. In contrast, *matching allele models* (**FIGURE 13.13B**) may assume that a pathogen can infect a host only if it has a protein that matches a cell surface receptor protein of the host, like a key and a lock. In this case, any particular resistance allele will decline in frequency when the pathogen's corresponding infectivity allele has high frequency. As a different resistance allele increases in frequency in the host population, the corresponding infectivity allele increases in the pathogen population. Such frequency-dependent selection can cause cycles or irregular fluctuations in allele frequencies. A matching allele model describes variation in resistance of a freshwater crustacean, the water-flea *Daphnia magna*, to genotypes of the bacterium *Pasteuria ramosa* [45].

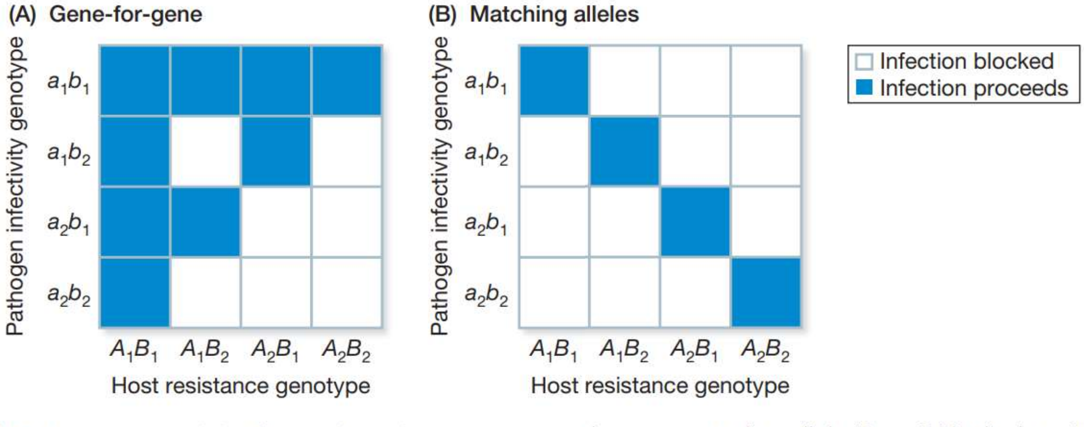


FIGURE 13.13 Two genetic models of coevolution between pathogens and their hosts. The filled cells indicate combinations of host and pathogen genotypes in which the pathogen is able to infect. For simplicity, both a haploid host and a haploid pathogen are assumed. (A) In the gene-for-gene model, the host has two loci at which alleles A_2 and B_2 encode receptor proteins that bind pathogens with surface proteins (ligands) produced by corresponding alleles a_2 and b_2. The plant is resistant, and infection fails, only if either a_2 or b_2 in the pathogen is counteracted by the corresponding allele (A_2 or B_2) in the host. Thus, the pathogen genotype $a_1 b_1$ can infect any host because it lacks ligands to which host proteins can bind. The host genotype A_1B_1 is susceptible to all pathogens because it lacks both binding proteins. In the matching alleles model, both alleles at each locus (A_1 and A_2, B_1 and B_2) are resistance alleles that encode "locks" that can be opened only by the matching "keys" of the pathogen. The pathogen can infect only if it has the matching allele at both the *A* and *B* loci. (A after [39]; B after [4].)

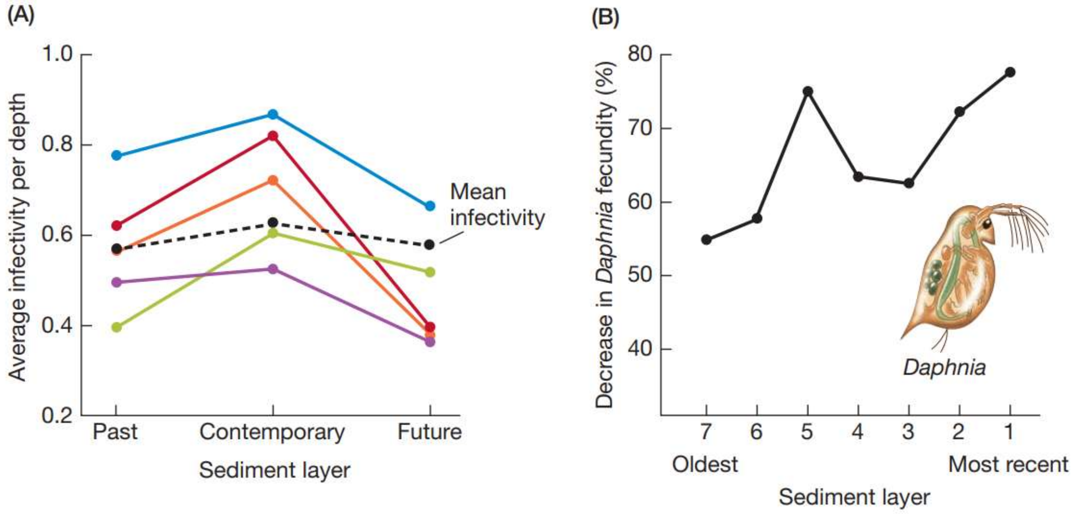


FIGURE 13.14 Parasite-host coevolution. (A) *Daphnia* were hatched from eggs from several layers of pond sediment, dating from different years, and were experimentally exposed to *Pasteuria* from the same ("contemporary"), previous ("past"), or following ("future") sediment layers. The bacteria were generally most successful in infecting contemporary *Daphnia*. Each line presents results for *Daphnia* from a particular sediment layer; the dashed line is the mean infectivity of all trials, some of which, for simplicity, are not shown here. (B) Even though bacteria at any one time were best able to infect contemporary *Daphnia*, their virulence increased over time. The graph shows that bacteria taken from more recent sediment layers were more harmful than bacteria from older layers when they were tested on a standard laboratory strain of *Daphnia*. (After [18].)

Ellen Decaestecker and colleagues described an ingenious "resurrection study" that revealed cycles of genetic change in the freshwater crustacean *Daphnia* and pathogenic *Pasteuria* bacteria [18]. *Daphnia* can produce eggs that remain dormant in pond sediments for many years, and the eggs may harbor *Pasteuria* spores. Decaestecker and colleagues revived eggs and bacteria from different layers of lake sediment, then experimentally cross-infected *Daphnia* from several different years with bacteria from the same ("contemporary") year, a preceding ("past") year, and a subsequent ("future") year. They discovered that the hosts were more frequently infected by contemporary than by past or future bacteria (**FIGURE 13.14A**). These observations indicate that the *Daphnia* population underwent genetic change from year to year and that the bacteria evolved in concert, as in matching allele models of coevolution. The *Daphnia* changed so that they were no longer as easily infected by past bacteria, and the bacteria changed and were able to infect contemporary *Daphnia*. Even though both host and parasite underwent continual cyclic coevolution, the average virulence of the parasite (measured by how much it reduces the host's fecundity) increased over time (**FIGURE 13.14B**).

THE EVOLUTION OF VIRULENCE In a different study of *Daphnia magna*, Dieter Ebert found that microsporidian parasites (*Pleistophora intestinalis*) that reproduce in the gut 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 13.15**) [21]. Thus populations of this parasite are best adapted to their local host population, and have a more virulent effect on sympatric than on allopatric host populations. Like the increasing virulence of the *Pasteuria* bacteria that Decaestecker's group studied, this pattern contradicts the widely held, naïve hypothesis that parasites always evolve to be more benign (also see Chapter 12).

In Chapter 12 we described evolutionary changes in the myxoma virus that was used to control the European rabbit in Australia. In that case, the virus evolved

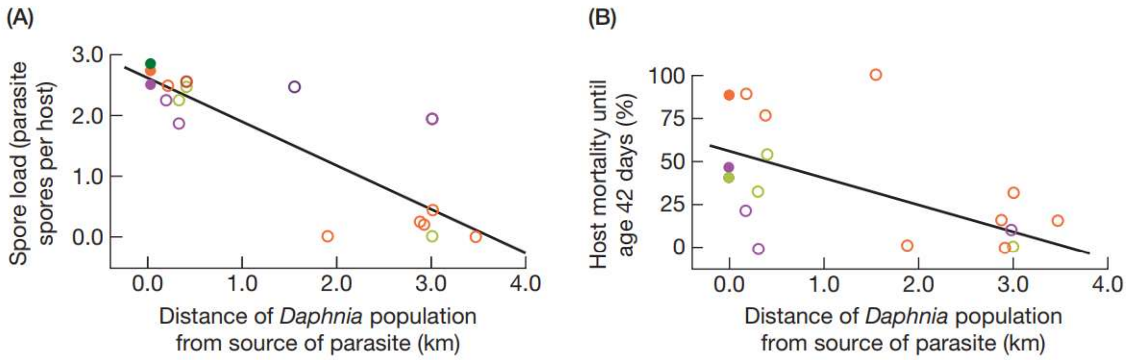


FIGURE 13.15 Fitnesses of three strains of a microsporidian parasite and their effects on various populations of their host species, the water flea *Daphnia magna*. Each strain, represented by a different color, was tested in hosts from its locality of origin (solid symbols) and from localities at various 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 locality, 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 [21].)

a lower level of virulence. This happened by group selection: rabbits harboring a group of highly virulent viruses tended to die before the virus could be transmitted to new hosts. But this is by no means the only possible outcome. Other factors can also determine whether a parasite evolves to be more benign or more virulent [9, 24, 26]. If multiple, unrelated genotypes of parasites occur together within hosts, selection favors the genotype with the highest reproductive rate, which may be highly virulent. This may outweigh group selection for lower virulence. Selection is likely to favor more virulent genotypes in horizontally transmitted parasites than in those that are vertically transmitted from parent hosts to offspring. 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 [11]. Another factor is that if the host can sustain parasite reproduction for only a short time, selection favors rapid parasite reproduction, which may entail greater virulence. For example, an effective immune system (or medical treatment that rapidly kills the parasite) may sometimes induce the evolution of higher virulence [61]. When chickens were immunized against a virus by a vaccine that did not prevent transmission from infected birds, the virus evolved a higher transmission rate and higher virulence [62].

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. Genetic diversity in host populations is important for maintaining resistance to pathogens. Conversely, populations that are inbred or have low genetic diversity may be at risk of infection. 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 susceptibility 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 [78]. 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. Phylogenetic analyses are routinely used to trace the origins of new pathogens, such as Ebola virus and the human immunodeficiency viruses (HIV-1 and HIV-2) (see Chapter 16). In some cases, evolutionary change in the pathogen plays a role in its transition to humans [83]. When the origins of a new pathogen can be discovered, it may be possible to determine the genetic basis of the pathogen's adaptation 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 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 [36].

Mutualisms

Mutualisms are interactions between species that benefit individuals of both species. However, they exemplify not altruism, but reciprocal exploitation, in which each species obtains something from the other. In *On 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.

Some mutualisms have arisen from parasitic or other exploitative relationships. Yuccas (*Yucca*), 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 13.16A**). 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 13.16B**).

As with intraspecific cooperation (see Chapter 12), 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. Several possible factors can reduce the fitness of cheater genotypes, and thus maintain a mutualistic relationship. One is simply punishment of cheaters ("sanctions"), to prevent overexploitation [10]. Another possibility is that one or both partner species may be able to choose to reward the most cooperative or beneficial individuals of the other species, or exclude cheaters. Yet another possibility is that selection will favor honest genotypes if the individual's genetic self-interest depends on the fitness of its host or partner [33]. This will be the case if there is a long-term or permanent association between individuals, restricted opportunities to switch to other partners or to use other resources, or vertical transmission of endosymbionts from parents to offspring. For example, the *Buchnera* bacteria that live in the cells of aphids and are vertically transmitted are beneficial mutualists.

The factors that discourage the evolution of cheating have been most studied in legumes and their associated rhizobial bacteria, which convert (fix) atmospheric nitrogen (N_2) to ammonium (NH_4^+) that the plant can use. (Legumes and their rhizobia are extremely important for soil fertility in some regions.) Legumes reward rhizobia by housing them in root nodules and providing them with photosynthate (sugars). In one experiment [40], researchers mimicked cheating rhizobia by replacing normal N_2-containing air with atmosphere that lacked N_2, so that the rhizobia provided less ammonium to soybean plants. The rhizobia on these plants increased far less than in plants that had normal, N_2-fixing rhizobia, because the N_2-deprived plants "punished" their rhizobia, depriving them of oxygen. Other investigators found that plants supplied greater benefits to more beneficial strains

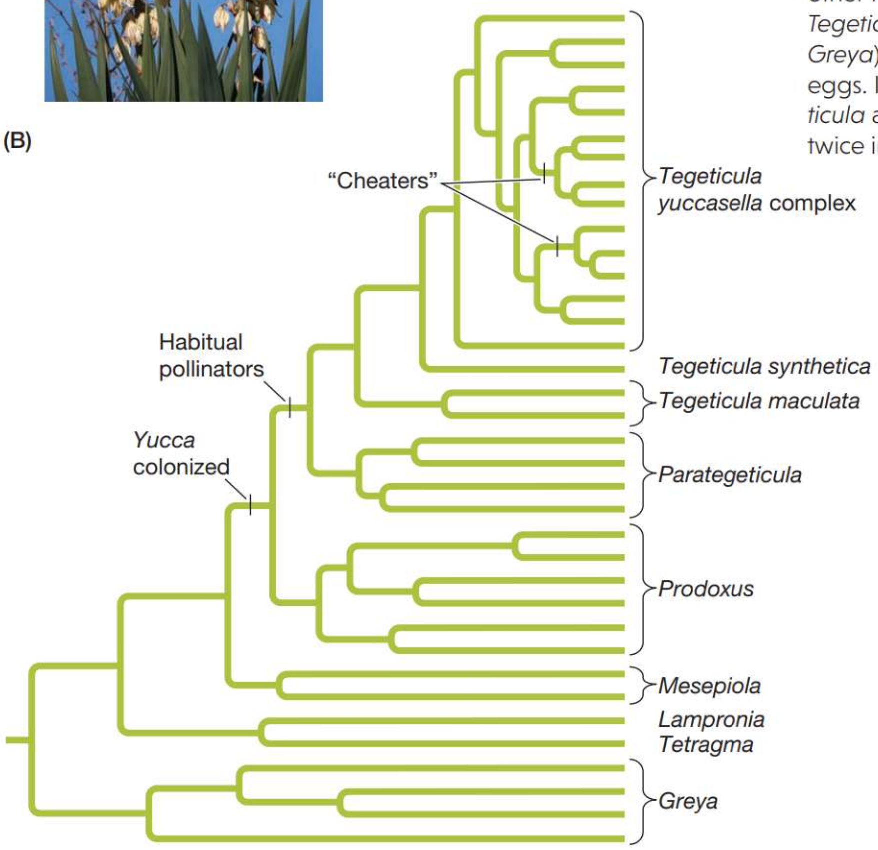
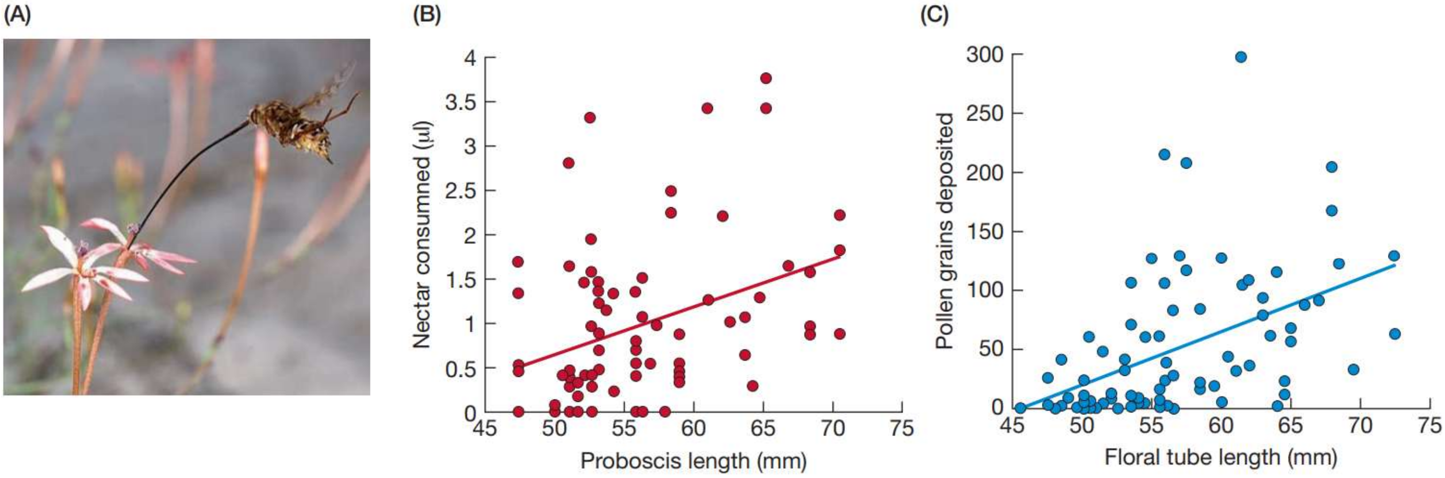


FIGURE 13.16 Mutualisms may result in extreme adaptations. (A) Yucca moths of the genus *Tegeticula* not only lay eggs in yucca flowers, but also use specialized mouthparts to actively pollinate the flowers—as the gray moth clinging to the flower's pistil is doing. The moth then inserts eggs into the flower's ovary. (B) A phylogeny of the yucca moth family, showing major evolutionary changes. The genera other than the "habitual pollinators" *Parategeticula* and *Tegeticula* are seed predators, some species of which (in *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*. (B after [59].)

of rhizobia, illustrating adaptive "partner choice" [32]. Thus, legume-rhizobia mutualisms may be stable for more than one reason. These mechanisms suggest that if the plants were supplied with excess ammonium and became less dependent on their rhizobial partners, the system might break down. To test this hypothesis, a research team took advantage of an ecological experiment in which some plots were fertilized with nitrogen for 22 years. As they predicted, test plants inoculated with rhizobia from the fertilized plots produced much less biomass than those inoculated from unfertilized plots [81]. The evolution of less beneficial rhizobia may have occurred because fertilized plants relieved sanctions against cheaters or no longer rewarded beneficial strains.

Mutualisms are not always stable over evolutionary time: many species cheat. For instance, many orchids secrete no nectar for their pollinators; some of them, in fact, deceive male insects that accomplish pollination while "copulating" with the flower (see Figure 3.23 in Chapter 3). 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 13.16B) [59].

Let's return to Darwin's extraordinary orchid, and its predicted sphinx moth, with which we began this chapter. Why did the orchid's nectar tube and the moth's proboscis become so long? The answer is that mutualism often is permeated with conflict. Darwin argued that natural selection would cause the insect species to



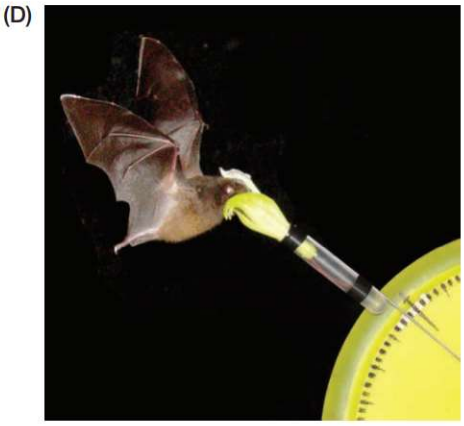


FIGURE 13.17 (A) The extraordinarily long proboscis of the fly *Moegistorhynchus longirostris* as it approaches the long, tubular flower of the iris *Lapeirousia anceps*. Flies with longer tongues consume more nectar (B) and plants with longer floral tubes receive more pollen (C). (D) An apparatus used to obtain similar data on the nectar-feeding bat *Anoura fistulata*, which can extend its tongue twice as far as any other nectar-feeding bat. (A courtesy of A. Pauw; B and C after [58]; D from [54], courtesy of Nathan Muchhala.)

evolve a proboscis long enough to reach the nectar. But why would a very long nectar tube be advantageous to the plant? Because, Darwin suggested, it would force the insect to press its head deeply into the flower and necessarily pick up and deposit pollen. If the insect's proboscis were longer than the tube, its head would not contact the pollen and the plant would not achieve reproduction. So, Darwin suggested, there may be an ongoing "race," in which the plant matches any elongation of the proboscis with an equal or greater elongation of the nectar tube.

One hundred forty-seven years after Darwin presented this hypothesis, two research teams tested and confirmed it,[1] using other plant-pollinator associations that are similarly extreme. In South Africa, Anton Pauw and collaborators, studying an iris with a long corolla tube and a fly with an equally long proboscis, found that flies with longer proboscises consume more nectar and that longer-tubed plants receive more pollen (**FIGURE 13.17A–C**) [58]. In Ecuador, Nathan Muchhala and James Thomson offered long-tongued bats experimentally altered flowers of another long-tubed plant, as well as tubes with sugar water [54]. They found that long-tongued bats delivered and received more pollen when they fed in longer tubes (**FIGURE 13.17D**). Both groups documented an advantage to the plant, and one showed an advantage to the pollinator as well.

Partly because of genomic studies, mutualism is increasingly recognized as an important basis for adaptation and the evolution of biochemical complexity [52]. The best-known examples are the evolution of mitochondria from purple bacteria and of chloroplasts from cyanobacteria (see Figure 2.5). When a new, "compound"

---

[1] Almost all of Darwin's many hypotheses have been fully or partly confirmed by later scientists. The major exception is his theory of heredity.

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. These genes may account for as many as 18 percent of the protein-coding genes of *Arabidopsis* [50].

Some mutualistic symbioses provide one or both partners with new capabilities [52]. For example, many features of bacteria are encoded by phage-borne genes. Bacteria and other microbes have formed intimate mutualisms with diverse multicellular organisms, especially animals, which lack the ability to synthesize essential amino acids and vitamins but can obtain some of these nutrients from their microbial partners. Some extreme associations are in sap-sucking homopteran insects (aphids, leafhoppers, cicadas, and relatives), which derive different amino acids from as many as eight different types of coexisting symbionts. Almost all plants and animals, including humans, harbor many kinds of symbionts, whose effects are largely unknown but are the subject of increasing research.

The Evolution of Competitive Interactions

Competition between species plays a huge role in evolutionary theory. In *On the Origin of Species*, Darwin spoke of "divergence of character," explaining that although species arising from a common ancestor will at first be very similar, natural selection will make them more different, because "the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers." (By analogy, if a city has more than enough surgeons but few pharmacists, a student might do better to go to pharmacy school.)

Darwin based his hypothesis on his perception that 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 the same resources (interspecific competition). Interspecific competition has two major effects. First, two (or more) competing species that use exactly the same resources cannot coexist indefinitely: one will be driven to extinction. Second, competition can impose selection on one or both species. One of the possible results is divergence in resource use. If this happens repeatedly as new species arise in a clade, the result may be adaptive radiation [66].

If two species feed on a variety of food types, those individuals that are most prone to eat the same food as members of the other species may suffer lower fitness because they are competing for a limited supply (**FIGURE 13.18**). Individuals that use other food types, for which they do not compete with the other species, are likely to have higher fitness. Consequently, one or both species may evolve to use somewhat different food types from the other species, and come to overlap less in diet [68, 70]. Such divergence in response to competition between species is called **ecological character displacement**.

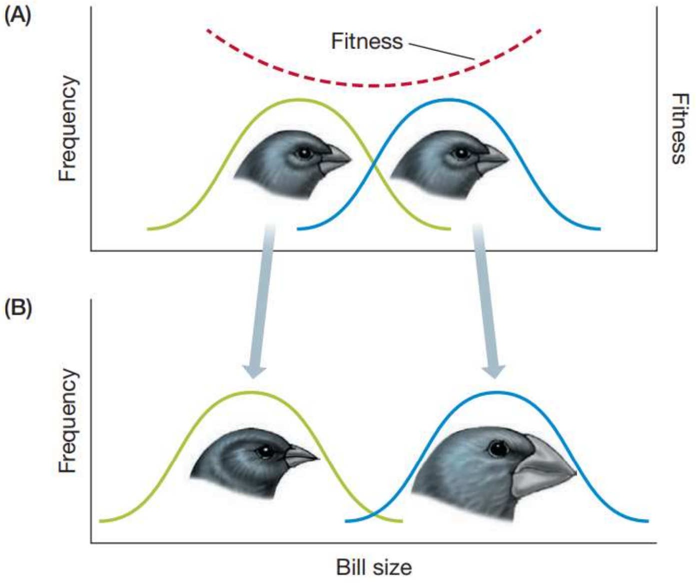


FIGURE 13.18 A model of ecological character displacement in response to competition between two species. The *x*-axis represents a quantitative phenotypic character, in this case bill size, that is closely correlated with some quality of a resource, such as the average size of the seeds eaten by that phenotype. (A) The frequency distributions of bill size of two species (blue and green) overlap. The dashed curve is the fitness function; fitness is lowest for those in the overlap area, representing individuals of both species that compete for the same resources. (B) Because of selection within each species against phenotypes that compete with the other species, the species undergo divergent evolution. The overlap in their resource use is reduced, and the character they use for processing the resources (bill size) diverges.

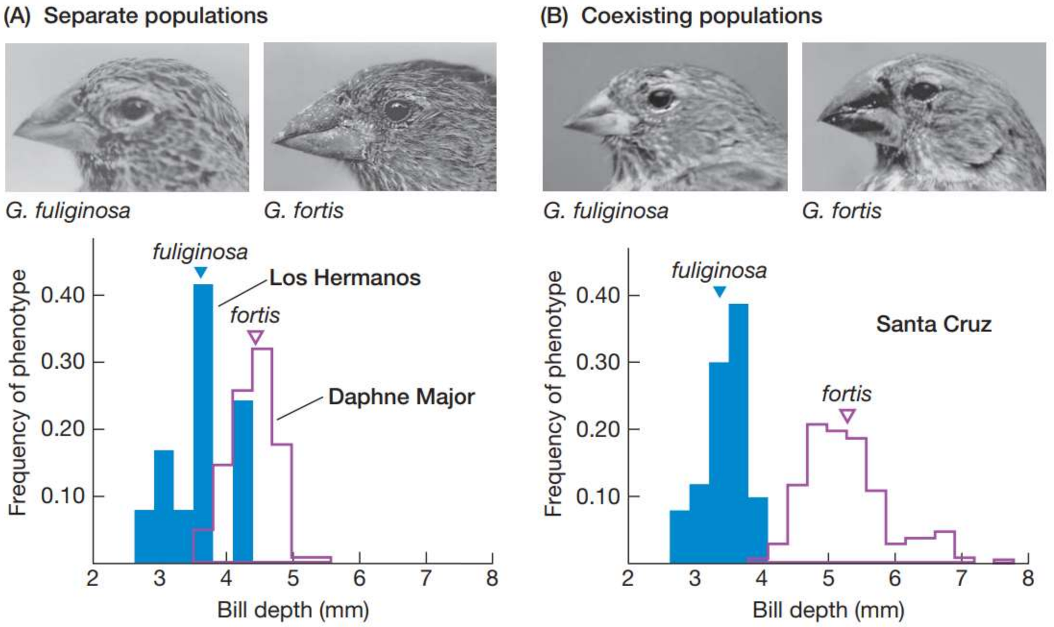


FIGURE 13.19 Character displacement in bill size in seed-eating ground finches of the Galápagos Islands. Bill depth is correlated with the size and hardness of the seeds most used by each population; arrowheads show average bill depths. (A) Only *Geospiza fuliginosa* occurs on Los Hermanos, and only *G. fortis* occurs on Daphne Major. (B) The two species coexist on Santa Cruz, where they differ more in bill depth. (After [30]; photos courtesy of Peter R. Grant.)

A famous example of this pattern is the Galápagos finches *Geospiza fortis* and *G. fuliginosa*, which differ more in bill size where they coexist than where they occur singly (**FIGURE 13.19**) [30]. The process of character displacement was experimentally demonstrated by Jonathan Losos and his colleagues in the green anole (*Anolis carolinensis*), which is native to the southeastern United States, and the brown anole (*A. sagrei*), a West Indian species that has invaded many islands in southern Florida. Although the two species overlap in perch height, brown anoles typically perch closer to the ground than the more arboreal green anoles. Losos and colleagues experimentally introduced brown anoles to several small islands, but not to others, and discovered that green anoles soon shifted to higher perches [69]. They also found that within 15 years after brown anoles invaded islands, green anoles evolved a higher number of specialized toe scales that enhance their ability to climb trees (**FIGURE 13.20**). Extensive previous research has shown that anoles compete for food and that competition is reduced between species that occupy different structural sites in forested habitats.

Competition for resources can sustain diversity both of species and of genotypes within species [7, 60]. This is the basis of a pattern called **ecological release**, 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. For example, pumpkinseed sunfish (*Lepomis gibbosus*) are found in both shallow water and open water in lakes where they are the only species of sunfish, but they are limited to shallow water if another species of sunfish occupies the open water. Pumpkinseeds collected in open versus shallow water have heritable, functionally adaptive differences in body shape and a feeding structure, and differ in diet [64].

Some species compete not only by depleting resources, but also by **interference competition**, whereby individuals suppress competitors by behavioral dominance [2] or by other means, such as poisoning them (as do some plants, fungi, and bacteria). Chinese populations of an unintentionally introduced American goldenrod (*Solidago canadensis*) have evolved enhanced production of a chemical that inhibits the growth of a Chinese plant species more than native American goldenrod populations do [84]. A possible reason for this evolutionary change is that introduced plants may be able to allocate more energy to competitive ability because they have become freed from many of their natural enemies, and can reduce their defenses against herbivores [6]. Some evidence for this hypothesis was found in a natural American population of this goldenrod, in which some plots were kept herbivore-free by insecticide. After 12 years, plants from these plots were more susceptible to

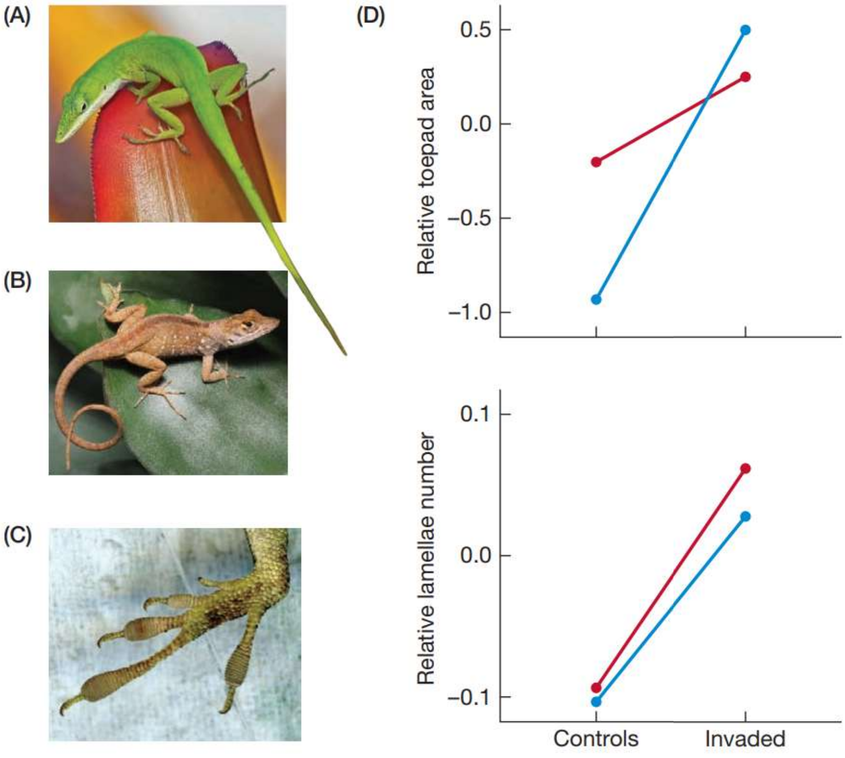


FIGURE 13.20 Results of an experiment in which indigenous green anoles (A) were confined with invasive brown anoles (B) on a small, a medium, and a relatively large island in Florida, and on control islands without the competing species. Evolutionary changes in the size of the toepads and scales (lamellae) specialized for climbing, seen in (C), were monitored over 15 years. (D) Both traits increased significantly on the invaded islands, compared to the controls (circles). The difference persisted when lizards from invaded and control islands were reared under controlled conditions (diamonds), showing that the change is genetic. (D after [69], C courtesy of Yoel Stuart.)

herbivorous beetles than were those from unsprayed plots, and they produced more polyacetylenes, which inhibit growth of competing plants [77]. Competition can result in the exclusion or extinction of some species, a special concern when species are introduced to new areas and may become "invasive" [46].

Evolution and Community Structure

The assemblage of species in a local habitat, such as a lake or forest, is often called a community. The field of community ecology is concerned with questions such as what determines how many species occur together in a local community, how food webs and other interactions among species are structured, and why the number of species differs among habitats and geographic regions. We describe here a few of the many ways in which an evolutionary perspective contributes to answering these questions [13, 51].

Phylogenetic information can cast light on the role of evolutionary history in the species richness and interaction web of a community [13, 63, 74]. The species in a large region (e.g., southeastern North America) belong to clades that, perhaps in the remote past, originated in the region or dispersed into it (see Chapter 18). Phylogenetically conservative traits may affect which clades could, and which could not, persist in a new ecological setting. For example, all species of *Heliconius* butterflies (see Figure 13.11) require passionflowers (Passifloraceae) as food plants for their larvae, and do not exist in places that lack these plants. Because of their previously evolved characteristics, members of some clades, but not others, can succeed in any particular habitat or local area (**FIGURE 13.21**). In a forest in Borneo, the trees that occur together in small plots are more closely related than a random sample of the trees in the entire forest would be, which suggests that closely related species share features that suit them to the particular environmental factors that differ among plots [80]. However, the opposite effect may be seen if specialized enemies destroy seeds and seedlings that are close to adult trees of the same or closely related species, leaving the space available for other species to grow in [42, 71]. Among the 31 species of *Inga* trees studied in a forest in Peru, trees found

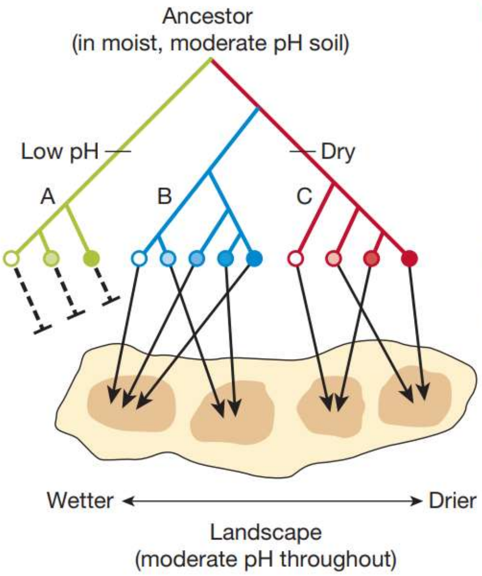


FIGURE 13.21 Factors that may affect phylogenetic relationships among the members of an ecological community. The phylogeny depicts a hypothetical plant clade, the ancestor of which was adapted to moist soils with intermediate pH. Among its current descendants, one clade (A) has become adapted to, and is now found in, acidic soils, and another (C) is associated with dry soils. In a landscape that includes wetter and drier sites but lacks acidic soils, clade A is not found. Drier sites will generally have species in clade C, and wetter sites species in clade B; the environment acts as a filter, resulting in phylogenetic clustering by habitat. But variation among species in each clade leads to stronger competition and exclusion between the closest relatives, so the closest neighbors are phylogenetically overdispersed: they are not as closely related as might be found in random samples of the species.

growing close to each other were more different in defense characteristics than if they had been sampled at random [41]. The evolution of different defenses that cause each species to be attacked by different enemies has contributed to the great diversity of tree species in tropical forests [14, 37].

The diversity of species in a community also results from evolutionary divergence that reduces competition among multiple species [66]. For example, among sympatric members of the weasel family in both North America and Israel, the spacing of the size of the canine teeth is more regular among species and sexes than expected by chance. The canine teeth are used to kill prey, and the differences in their size are thought to reflect differences in the average size of prey taken by these carnivores (**FIGURE 13.22**) [17].

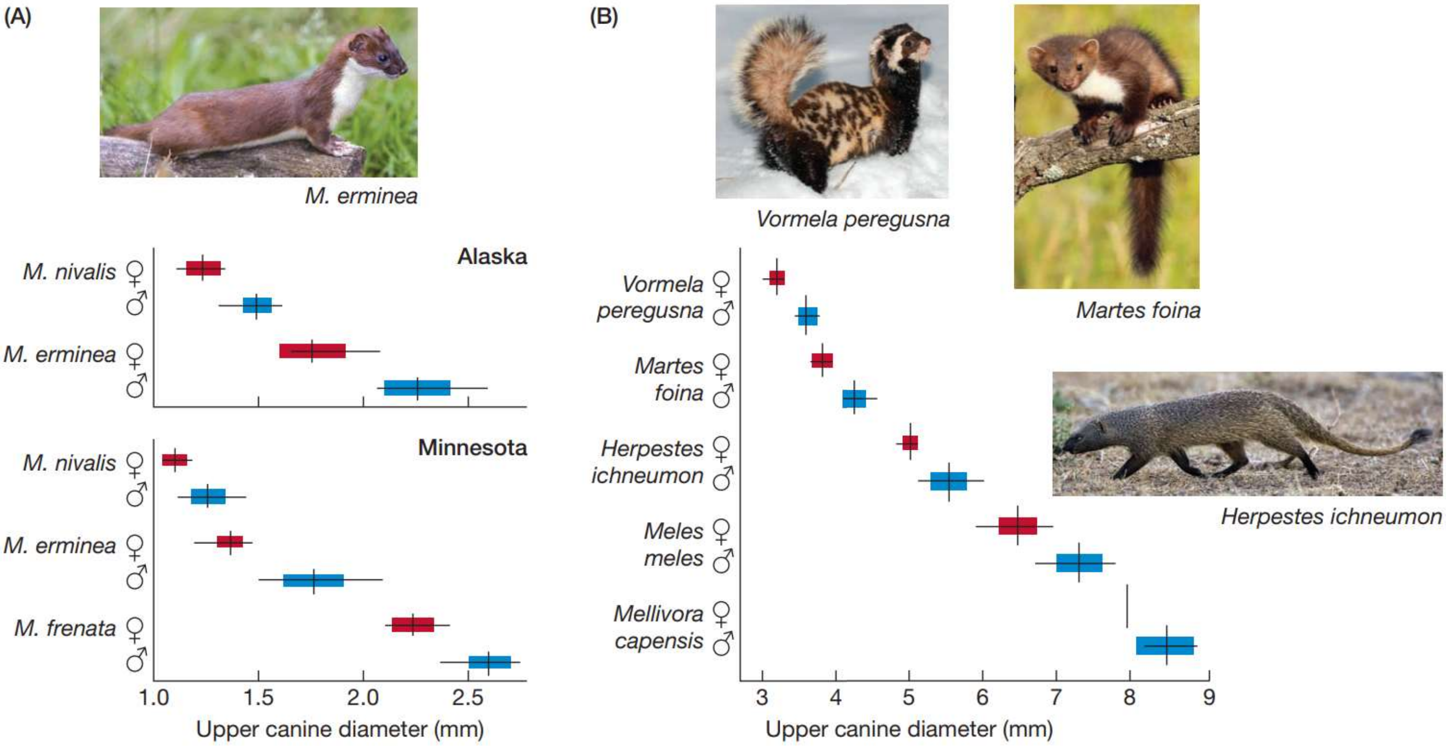


FIGURE 13.22 Size of the canine teeth differs among sympatric species of the weasel family (Mustelidae), and between the sexes in each species, in (A) Alaska and Minnesota and (B) Israel. In all sites, the spacing is more regular than would be expected at random. These differences are thought to be adaptations to feeding on prey that differ in average size. *Herpestes ichneumon*, the Egyptian mongoose, is a member of another family of Carnivora but is ecologically similar to the mustelids. Vertical lines are means, horizontal bars represent ± 1 standard deviation, and horizontal lines are range. (After [17].)

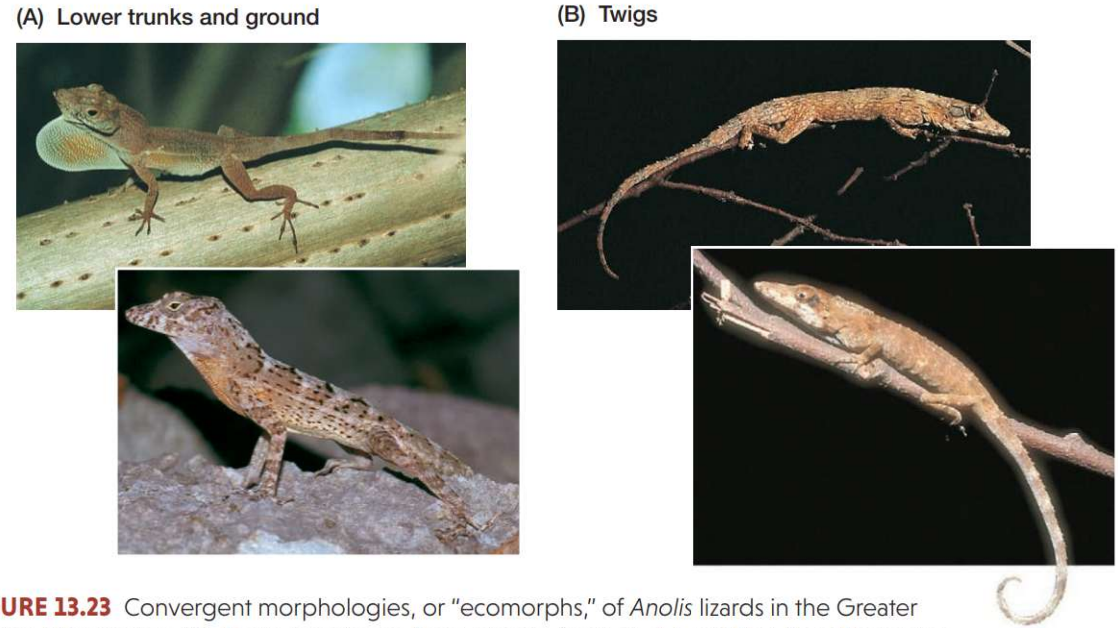


FIGURE 13.23 Convergent morphologies, or "ecomorphs," of *Anolis* lizards in the Greater Antilles, West Indies. (A) *Anolis lineatopus*, from Jamaica (top), and *A. strahmi*, from Hispaniola (bottom), have independently evolved the stout head and body, long hind legs, and short tail associated with living on lower tree trunks and on the ground. (B) *Anolis valencienni*, from Jamaica (top), and *A. insolitus*, from Hispaniola (bottom), are both twig-living anoles that have convergently evolved a more slender head and body, shorter legs, and a longer tail. (Photos by K. de Queiroz and R. Glor, courtesy of J. Losos.)

If two regions have similar environments, we might expect to see convergent evolution not only of individual species but of assemblages of species. For example, communities of plants that have evolved independently in similar environments have similar characteristics. Tropical rainforests throughout the world have tall canopy trees, festooned with ferns and other epiphytes; warm deserts throughout the world have small-leaved or leafless shrubs and cactus-like succulents. Each of these growth forms includes species in diverse phylogenetic lineages.

Convergence is also seen in parallel adaptive radiations, such as the cichlid fishes of the several African Rift Valley lakes (see Figure 9.1). The most extreme example of community-level convergence has been described in the anoles (*Anolis*) of the West Indies [43, 47]. As we noted in the previous section, these insectivorous, mostly arboreal lizards are known to compete for food. Each of the large islands of the Greater Antilles (Cuba, Hispaniola, Jamaica, Puerto Rico) has a monophyletic group of species that have evolved within the island. Many of the species on each island are ecologically and morphologically similar to those on the other islands. They occupy certain microhabitats, such as tree crown, twig, and trunk, and have consistent adaptive morphologies that have evolved independently on each island (**FIGURE 13.23**). However, evolution is not always so repeatable or predictable [44]; the largest of the Greater Antilles (Cuba and Hispaniola) have some ecologically and morphologically unique species of *Anolis*. Ecological niches that are occupied in one region often seem unoccupied in other, climatically similar regions. Blood-feeding (vampire) bats occur in the New World tropics, but not in Africa despite abundant ungulate prey; sea snakes occur in the Indian and Pacific oceans, but are absent from the Atlantic.

Go to the
Evolution Companion Website
EVOLUTION4E.SINAUER.COM
for data analysis and simulation exercises, quizzes, and more.

SUMMARY

- 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.
- The phylogenies of certain symbionts and parasites are congruent with the phylogenies of their hosts. This may imply that they diverged in parallel because the symbionts did not disperse between different host lineages. It does not necessarily imply that they coevolved, in the sense of reciprocal adaptation to each other.
- The Red Queen hypothesis states that species may continue to evolve indefinitely because of changes in interacting species. For example, coevolution in predator-prey and parasite-host interactions can theoretically result in a stable genetic equilibrium under some conditions, but often involves an ongoing evolutionary arms race, indefinite fluctuations in genetic composition, or even extinction. Among the many interesting adaptations in predator-prey interactions are aposematism (warning coloration) and mimicry.
- Parasites (including pathogenic microorganisms) may evolve to be more or less virulent depending on the correlation between virulence and the parasite's reproductive rate, the parasite's mode of transmission between hosts (vertical versus horizontal), infection of hosts by single versus multiple parasite genotypes, and group selection. Parasites do not necessarily evolve to be benign. New pathogens sometimes emerge by evolutionary change that enables them to infect new hosts (e.g., humans).
- In mutualism, each species obtains some benefit from the other. This does not entail altruism, and it often involves some conflict. 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.
- Evolutionary responses to competition among species may lead to divergence in resource use and sometimes in morphology (character displacement). Thus, competition is a cause of ecological diversification. However, selection for greater ability to compete can also result in greater aggression, and competitive exclusion of less competitive species.
- Both ongoing evolution and phylogenetic legacies can influence which species coexist in local ecological communities. Phylogenetically conservative characters may be subject to environmental filtering, so that the species in a habitat are phylogenetically clustered; conversely, very closely related species tend to be spatially separated. Because evolutionary history determines the features of species that affect their interactions, it helps explain the networks of interactions among species in a community.

TERMS AND CONCEPTS

aposematic
Batesian mimicry
coevolution
ecological character displacement
ecological release
evolutionary arms race
interference competition
matching allele model
mimicry
Müllerian mimicry
mutualism
Red Queen hypothesis
symbiosis
virulent

SUGGESTIONS FOR FURTHER READING

J. N. Thompson reviews many aspects of coevolution and provides numerous examples in *The Geographic Mosaic of Coevolution* (University of Chicago Press, Chicago, 2004), and in *Relentless Evolution* (University of Chicago Press, Chicago, 2013), which includes discussion of how interaction networks evolve. 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).

M. E. J. Woolhouse and colleagues provide an outstanding overview of parasite-host coevolution in "Biological and biomedical implications of the co-evolution of pathogens and their hosts" (*Nat. Genet.* 32: 569–577, 2002). "Models of parasite virulence" by S. A. Frank (*Q. Rev. Biol.* 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. "The merging of community ecology and phylogenetic biology" by J. Cavender-Bares and colleagues (*Ecol. Lett.* 12: 693–715, 2009), is an excellent overview of the subject.

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 determine whether or not there has been an evolutionary 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 a tree's 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 a hypothetical experiment to determine whether greater virulence is advantageous in a horizontally transmitted parasite or in a vertically transmitted parasite.
5. Do you expect that an infectious pathogen such as the bacterium *Staphylococcus aureus* or the HIV virus that causes AIDS will evolve to become more or less virulent? What do you need to know in order to make your best projection? You may want to read about the biology of one such pathogen in order to arrive at an answer.
6. Some authors have suggested that selection by predators may have favored host specialization in herbivorous insects (e.g., Bernays and Graham, 1988, *Ecology* 69(4): 886–892). How might this occur?
7. It seems surprising that certain orchids successfully deceive insects into "copulating" with their flowers. Have these species of insects, evidently failing to perceive the difference between a flower and a female of their own species, failed to adapt? If so, what might account for this failure?
8. 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 or exclusion, 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, *Systematic Biology* 41: 403–420, for example.)
9. Suppose that, among related host species that carry related symbionts, the relationship is mutualistic in some pairs and parasitic in others. How would you determine (a) which relationship is mutualistic and which is parasitic, (b) what the direction of evolutionary change has been, and (c) whether the change from one to the other kind of interaction has been a result of evolutionary change in the symbiont, in the host, or both?