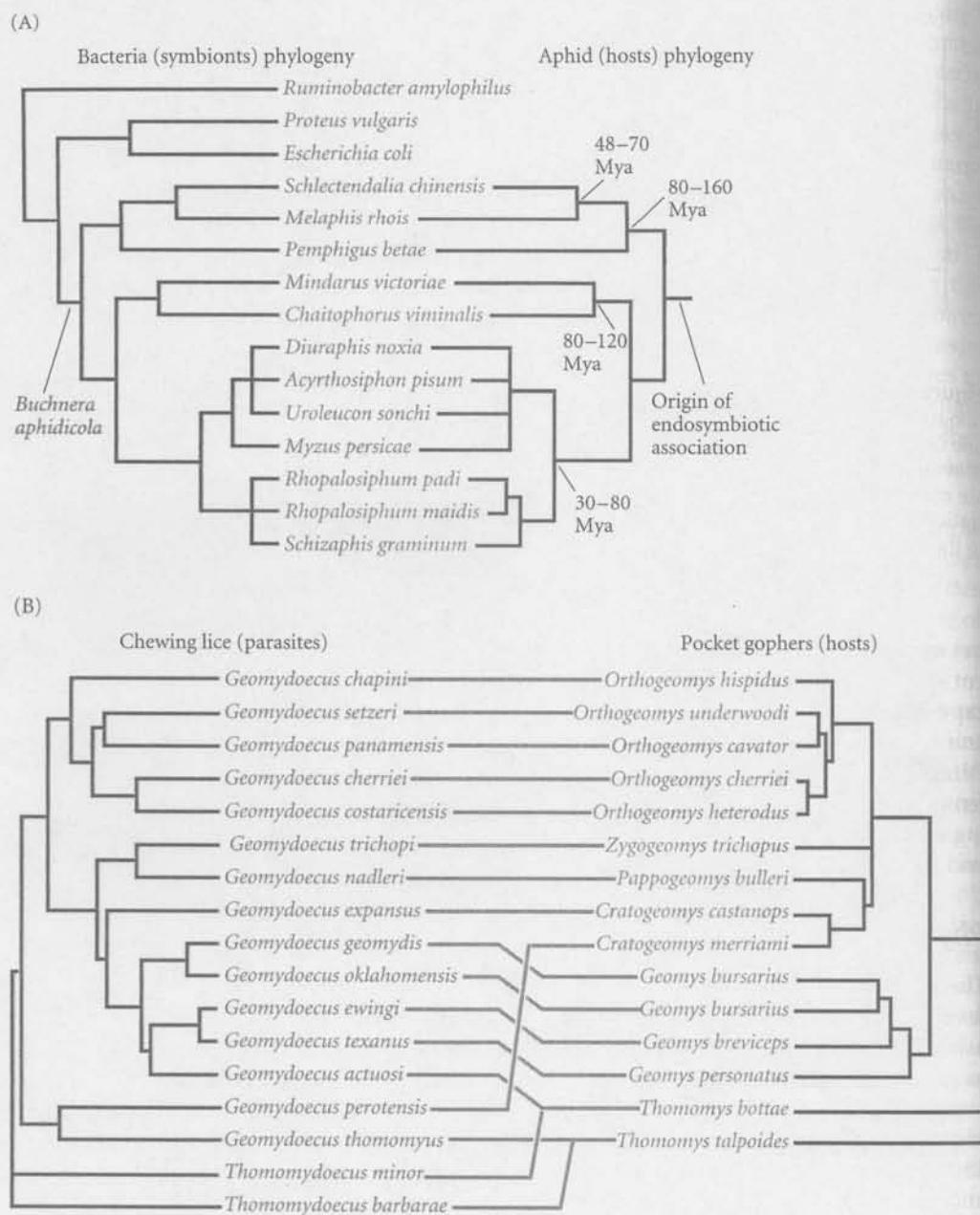


**Figure 18.3** Congruent and incongruent phylogenies of hosts and host-specific endosymbionts or parasites. Each parasite lineage is specialized on the host to which it is connected in the diagram. (A) The phylogeny of bacteria included under the name *Buchnera aphidicola* is perfectly congruent with 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. (B) Phylogenies of pocket gophers and their chewing lice. Note areas of both congruence (e.g., the uppermost five gopher/louse pairs) and incongruence (e.g., the gopher *C. merriami* and its louse *G. perotensis*). (A after Moran and Baumann 1994; B after Hafner et al. 2003.)



plants show exactly the same distinctive damage that is inflicted on living gingers by certain leaf beetles (subfamily Hispinae) today (Labandeira 2002).

### 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 18.4). Defenses against predation and parasitism can be equally impressive, ranging from cryptic patterning (Figure 18.5A; see also Figure 12.5), to the highly toxic chemical defenses of both plants and animals (Figure 18.5B), to the most versatile of all defenses—the vertebrate immune system, which can generate antibodies against thousands of foreign com-

**Figure 18.4** 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.)

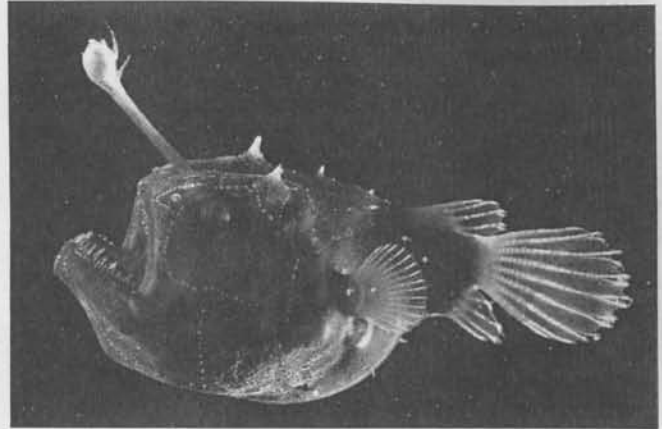
pounds (see Figure 19.9). Many such adaptations appear to be directed at a variety of different enemies or prey species, so although it is easy to demonstrate adaptations in a predator or a prey species, it is usually difficult to show how any one species has coevolved with another.

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.

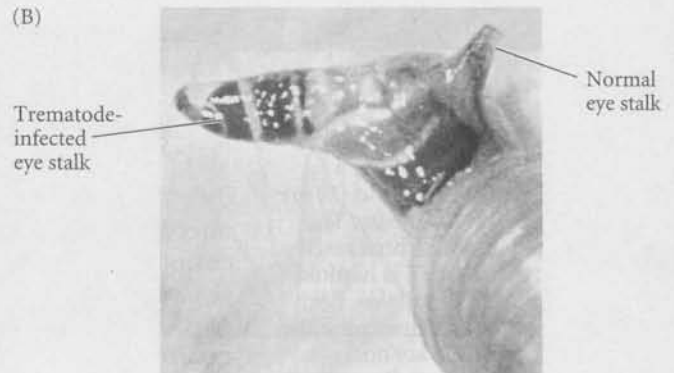
An unending arms race is unlikely because adaptations that increase the offensive capacity of the predator or the defensive capacity of the prey entail allocations of energy and other costs that at some point outweigh their benefits. Consequently, a stable equilibrium may occur when costs equal benefits. For example, the toxic SECONDARY COMPOUNDS that plants use as defenses against herbivores, such as the tannins of oaks and the terpenes of pines, 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, suggesting that they impose economic costs (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. 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).

(A)



(B)



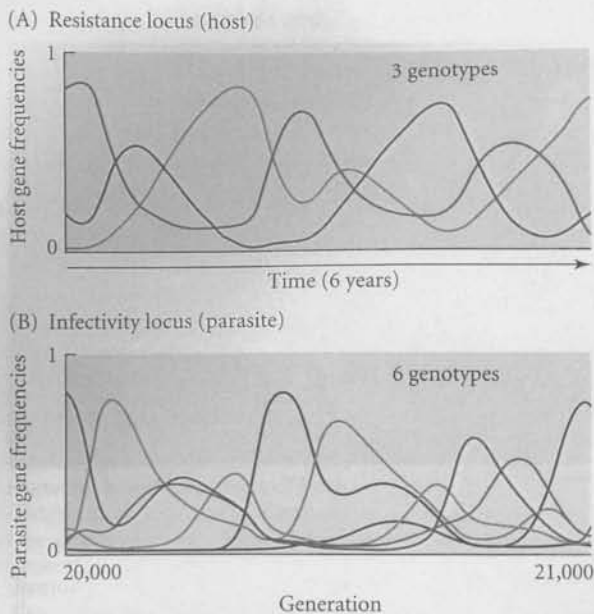
**Figure 18.5** Examples of defenses against predation. (A) The cryptically colored leaf-tailed gecko (*Uroplatus phantasticus*) blends with the floor of its dry forest home in Madagascar. (B) The toxins in the brilliant blue skin of *Dendrobates azureus* have been put to human use, as its common name of "poison dart frog" implies. Its color warns potential predators away. (A © Nick Garbutt/naturepl.com; B © Barry Mansell/naturepl.com)

(A)



(B)





**Figure 18.6** 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.)

different rust genotypes fluctuated from year to year (Figure 18.7). 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).

**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 as the difference ( $x - y$ ) increases (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 former case, mathematical analyses suggest that both

## Models of enemy-victim coevolution

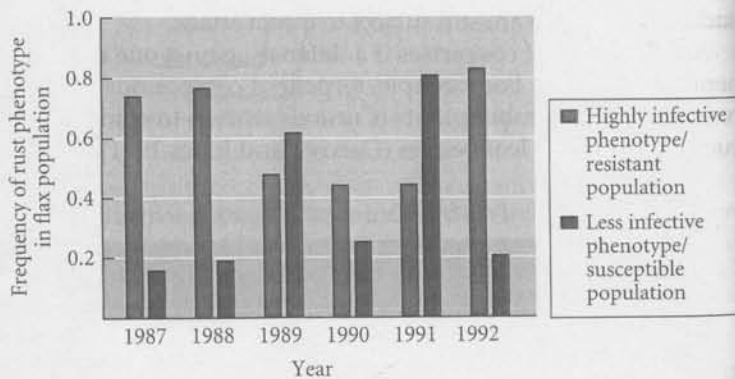
**GENE-FOR-GENE MODELS.** Coevolution of enemies and victims has been modeled in several ways, appropriate to different kinds of characters. For example, models of evolution at one or a few loci are appropriate for **gene-for-gene interactions**, which were first described in cultivated flax (*Linum usitatissimum*) and flax rust (*Melampsora lini*), a basidiomycete fungus. Similar systems have been described or inferred in several dozen other pairs of plants and fungi, as well as in cultivated wheat (*Triticum*) and one of its major pests, 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 18.1). If resistance has a cost, any particular resistance allele ( $R_i$ ) will 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 18.6). In wild populations of Australian flax, the frequencies of

**TABLE 18.1** 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.



**Figure 18.7** Changes in the frequencies of two phenotypes of flax rust over the course of 6 years in Australian populations of wild flax. A rust phenotype capable of infecting most resistant phenotypes of flax had high frequencies in a population of plants that were resistant to most other rust phenotypes. In a nearby flax population, in which 80 percent of plants were susceptible to the highly infective rusts, a less infective rust had fairly or very high frequencies. (After Thrall and Burdon 2003.)



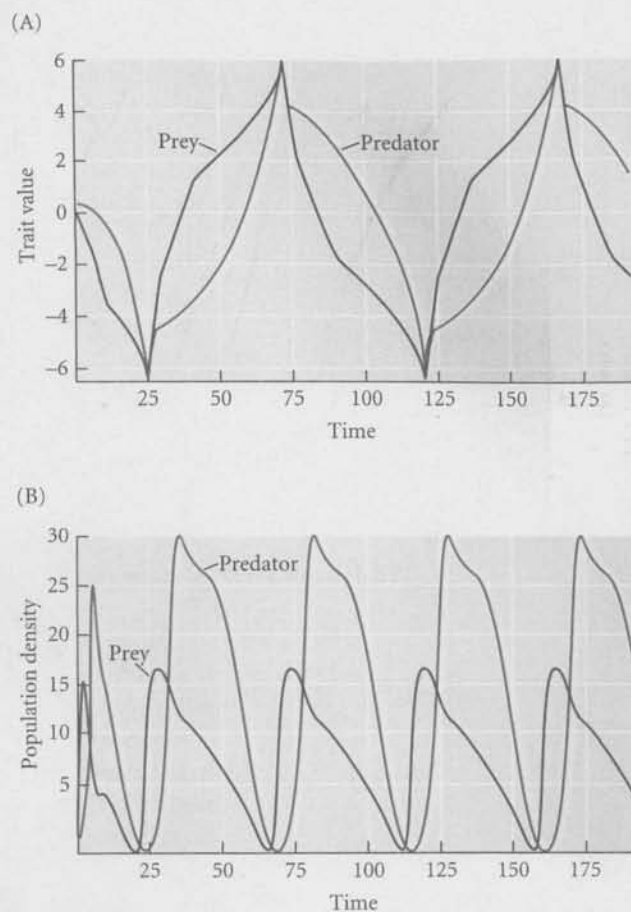
**Figure 18.8** Computer simulation of coevolution between prey and predator in which the optimal predator phenotype (e.g., mouth size) matches a prey phenotype (e.g., size). (A) Evolution of character state means. As a character state diverges from a reference value, its fitness cost prevents it from 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.)

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 greatly 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. Continuing cycles of change in the characteristics of both species might result, and these genetic changes may contribute to cycles in population density (Figure 18.8).

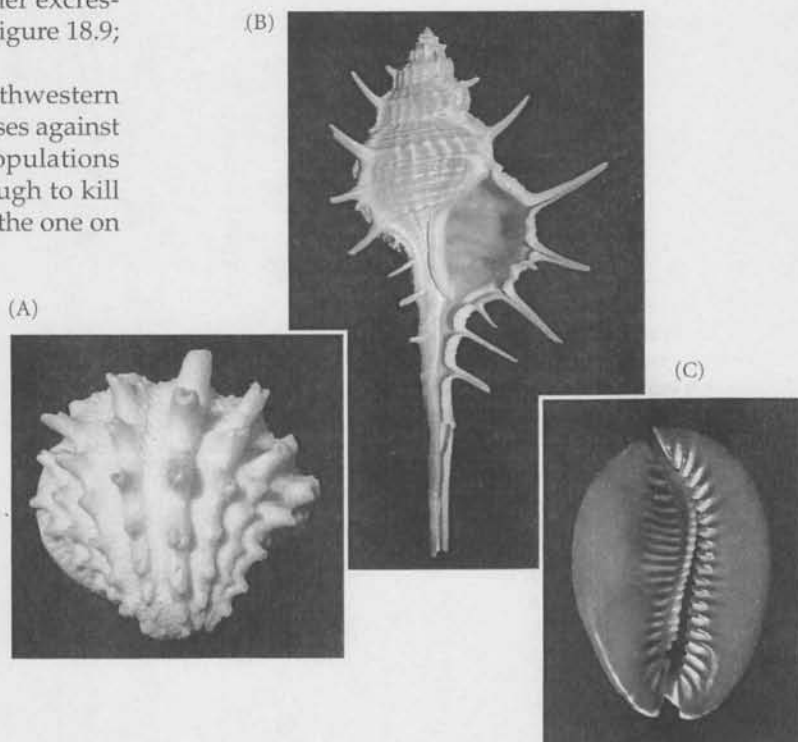
#### Examples of predator-prey coevolution

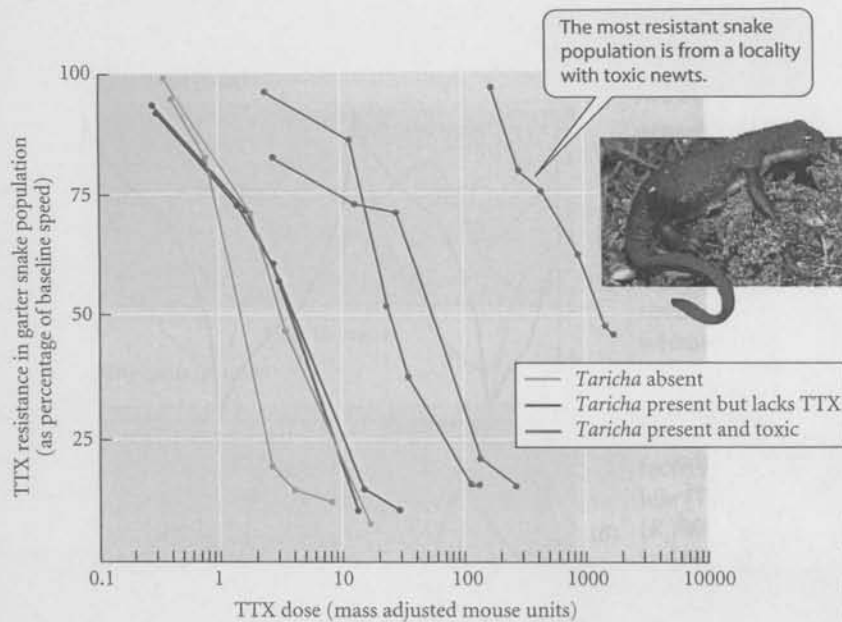
It has not yet been possible to obtain data on long-term coevolution in natural populations, but there is plentiful indirect evidence that enemies and victims affect each others' evolution. For example, during the Mesozoic, new, highly effective predators of molluscs, such as shell-crushing fishes and crustaceans that could crush or rip shells, evolved. The diversity of shell form in bivalves and gastropods then increased as various lineages evolved thicker shells, thicker margins of the shell aperture, or spines and other excrescences that could foil at least some of these predators (Figure 18.9; Vermeij 1987).

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, 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



**Figure 18.9** Some features of living molluscs that, like those that evolved in the Mesozoic, provide protection against predators. Spines on the shells of bivalves of the genus *Arcinella* (A) and gastropods of the genus *Murex* (B) prevent some fishes from swallowing the animal and may reduce the effectiveness of crushing predators. (C) The narrow aperture of *Cypraea mauritiana* prevents predators from reaching the gastropod's body. (Photos by D. McIntyre.)





**Figure 18.10** Variation in TTX resistance, measured by crawling speed after injection in relation to dose, in garter snakes 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 © Henk Wallays.)

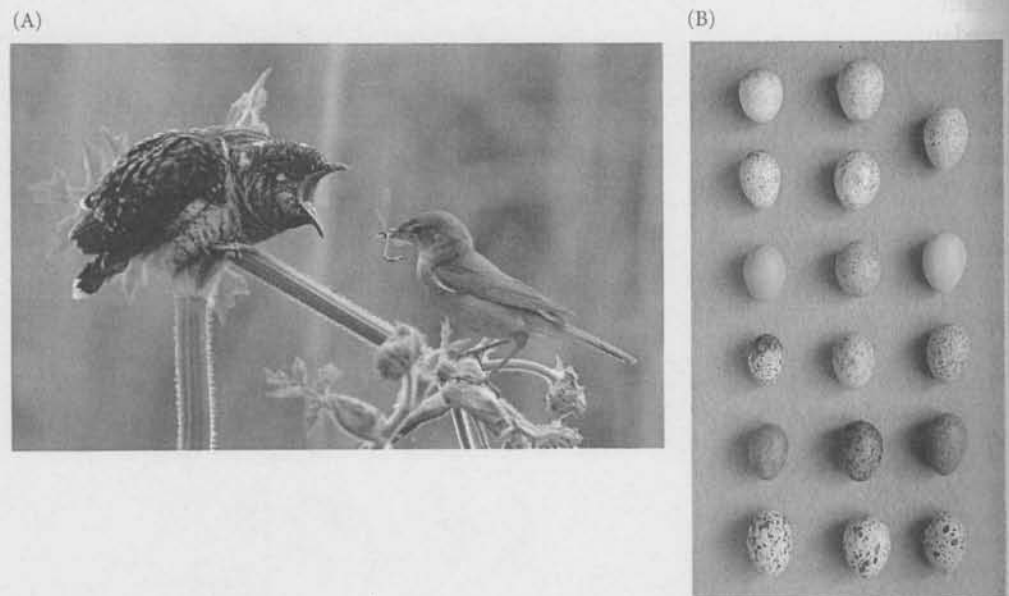
times more resistant to TTX than allopatric populations (Figure 18.10). Similarly, many species of insects feed on plants that bear diverse chemical toxins and have evolved a variety of mechanisms of resistance to those toxins. Plants in the carrot family, for example, contain toxic furanocoumarins, but the

high activity of a detoxifying enzyme enables larvae of the black swallowtail butterfly (*Papilio polyxenes*) to feed on such plants with impunity (Berenbaum 1983).

Brood-parasitic birds, such as cowbirds and some species of cuckoos, lay eggs only in the nests of certain other bird species. Cuckoo nestlings eject the host's eggs from the nest, and the host ends up rearing only the parasite (Figure 18.11A). 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 their 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 European cuckoo (*Cuculus canorus*) contains several different genotypes that prefer different hosts and lay eggs closely resembling those of their preferred hosts (Figure 18.11B). Some other individuals lay nonmimetic 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

**Figure 18.11** (A) A fledgling European cuckoo (*Cuculus canorus*) being fed by its foster parent, a reed warbler (*Acrocephalus scirpaceus*). (B) Mimetic egg polymorphism in the 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 second column shows a cuckoo egg laid in the corresponding host's nest. The match is quite close except for cuckoo eggs laid in dunnock nests. 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.)



bird species, Nicholas Davies and Michael Brooke (1998) found that species that are not parasitized by cuckoos (due to 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 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, but that their ability to reject cuckoo eggs has selected against the cuckoo genotypes that parasitized these species.

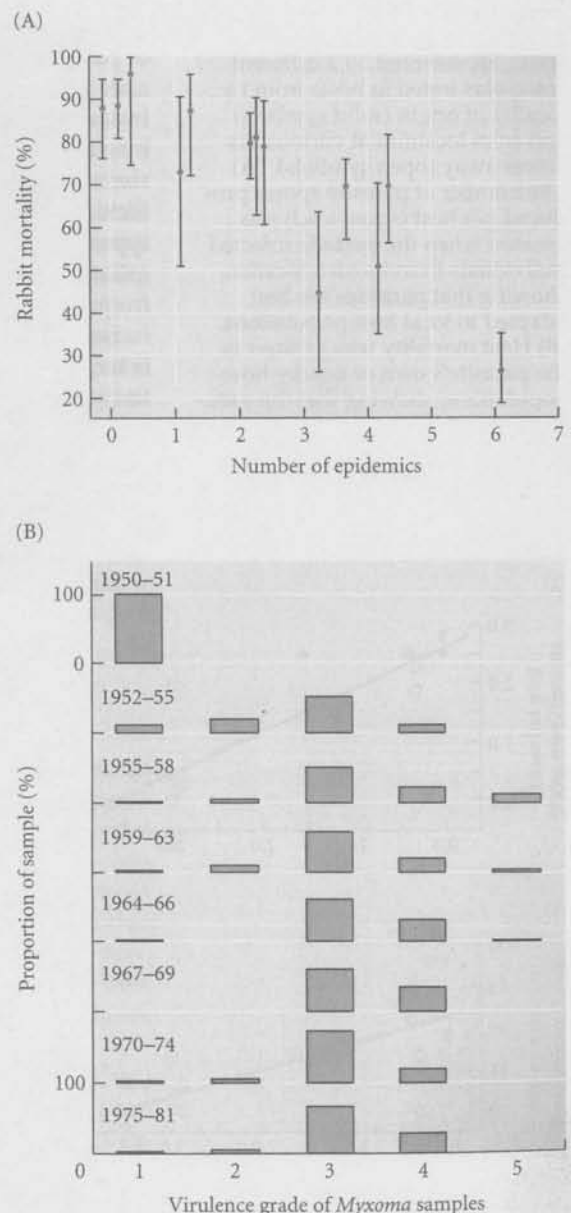
### Infectious disease and the evolution of parasite virulence

The two greatest challenges that 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 (see Chapter 15). Other parasites are transmitted **horizontally** among hosts in a population via the external environment (e.g., human rhinoviruses, the cause of the common cold, are discharged by sneezing), via contact between hosts (e.g., the causes of venereal diseases, such as the gonorrhea bacterium), or via carriers (VECTORS, such as the mosquitoes that transmit the malaria-causing protist and the yellow fever virus).

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 (Ewald 1994; Bull 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 (Figure 18.12A), and virus samples from wild rabbits were tested for virulence in a standard laboratory strain of rabbits (Figure 18.12B). 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 as a whole did not become 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).

**Figure 18.12** Coevolution in rabbits and myxoma virus after the virus was introduced into the rabbit population in Australia. (A) Mortality in field-collected rabbits exposed to a standard virus strain declined as the wild population experienced more epidemics. (B) Virus samples from the wild, tested on a standard rabbit stock, were graded from low (1) to high (5) virulence. Average virulence decreased over time, but stabilized at an intermediate level. (A after Fenner and Ratcliffe 1965; B after May and Anderson 1983.)





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 due to parasitism (and is a function of the parasite's virulence),  $d$  is the mortality rate of hosts 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 parasite's reproductive rate within the host—but this variable is often proportional to  $v$ , since the parasite uses the host's resources (energy, protein, etc.) to reproduce. Thus  $b$  and  $v$  may be correlated, in which case the parasite evolves greater virulence. If, however,  $v$  becomes too great, the host may die before parasites can be transmitted to new hosts, so there is counterselection against extreme virulence.

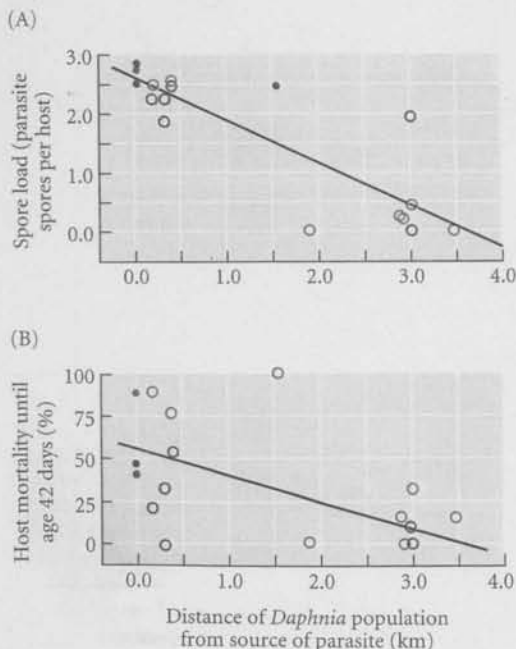
Among many factors that may affect the level of virulence that evolves, three bear special mention. First, each host may be viewed as containing a temporary population (deme) of parasites. Demes that kill their host before transmission contribute less to the total parasite population than more benign 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, however, each host is infected by multiple, unrelated genotypes of parasites, 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).

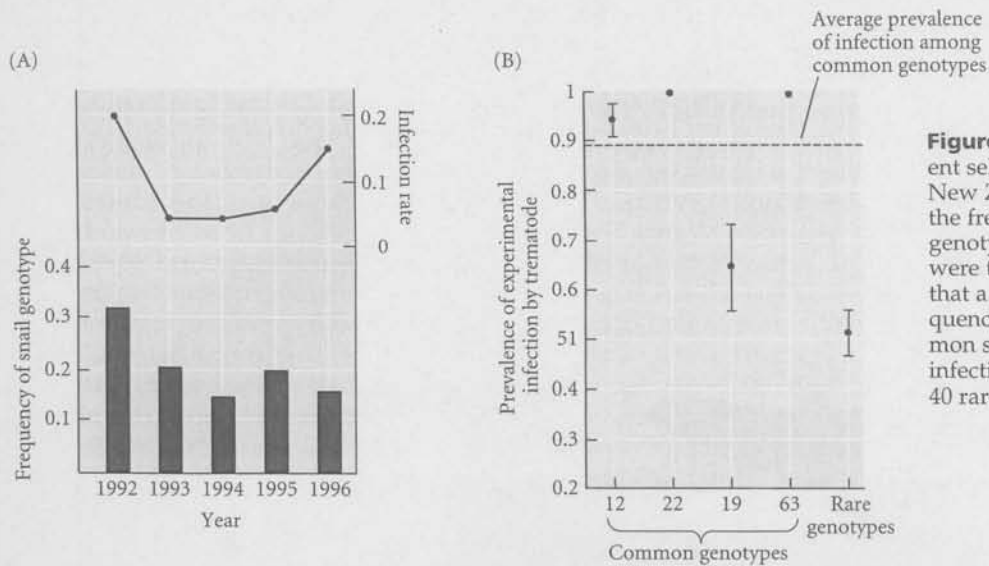
Second, if hosts rapidly become immune to the parasite (i.e., if  $r$  in the above equation is large), selection favors rapid reproduction—that is, outrunning the host's immune system—by the parasite. Because this may entail greater virulence, an effective immune system (or a drug that rapidly kills 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 the 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 18.13). 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.

**Figure 18.13** 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 co-evolved. (After Ebert 1994.)





**Figure 18.14** Evidence of frequency-dependent selection for resistance to a trematode in a New Zealand freshwater snail. (A) Changes in the frequency of each of several asexual snail genotypes, here represented by genotype 12, were tracked by the infection rate, suggesting that a genotype has lower fitness when its frequency is high. (B) Three of four recently common snail clones were more susceptible to infection by the trematode than were a group of 40 rare clones. (After Dybdahl and Lively 1998.)

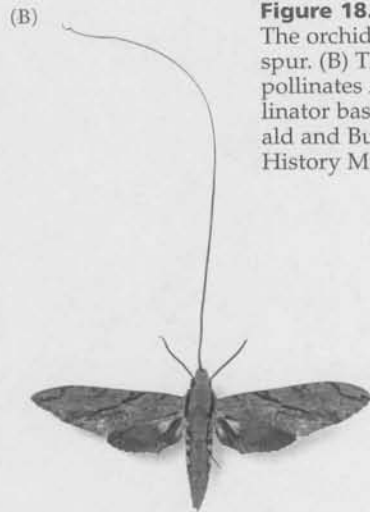
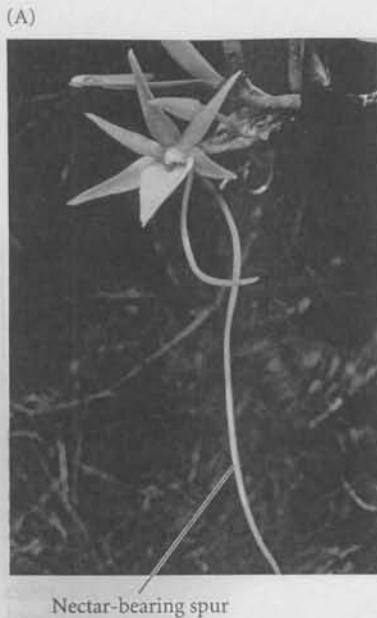
A study by Mark Dybdahl and Curtis Lively (1998) on a freshwater snail (*Potamopyrgus antipodarum*) and its trematode parasite (*Microphallus* sp.) in New Zealand is particularly interesting because of the evidence it provides both on coevolution and on the advantage of sexual reproduction (see Figure 17.21). The snail population includes both sexual and parthenogenetic individuals. When the trematode infects a snail, it reproduces prolifically within the snail and completely sterilizes it. Like the microsporidian parasites that infect *Daphnia*, the trematodes are more capable of infecting snails from their own population than those from other populations. 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 (Figure 18.14A). This observation suggests that rare snail genotypes have a selective advantage because they are resistant to the most prevalent parasite genotypes (and lose their advantage as they become more common; see Figure 18.6). 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 (Figure 18.14B). (As noted in Chapter 17, this observation supports the hypothesis that sexual reproduction could be advantageous because it generates new, rare, resistant genotypes.)

## 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 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 18.15; 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 re-



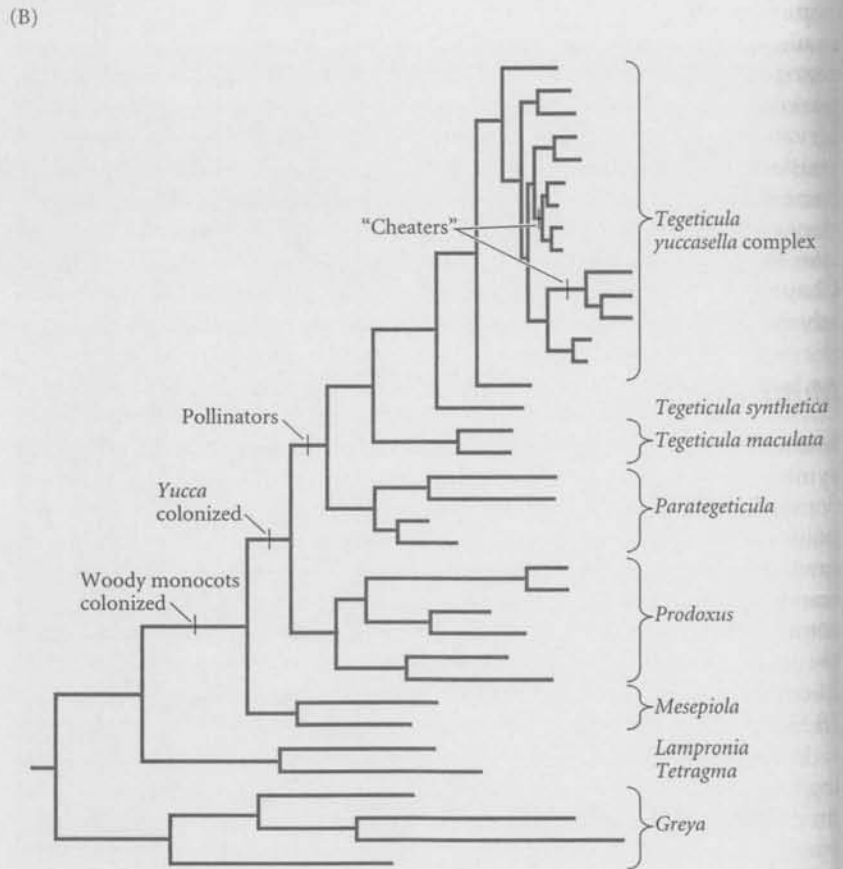


**Figure 18.15** Mutualisms may result in extreme adaptations. (A) The orchid *Angraecum sesquipedale* bears nectar in an exceedingly long spur. (B) The long-tongued sphinx moth *Xanthopan morgani praedicta* pollinates *A. sesquipedale*. Darwin predicted the existence of such a pollinator based on seeing the orchid in a London greenhouse. (A © Gerald and Buff Corsi/California Academy of Sciences; B © The Natural History Museum, London.)

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 18.16A). 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 18.16B).

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 in one or both species 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 en-

**Figure 18.16** *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 within *Tegeticula*. (A courtesy of O. Pellmyr; B after Pellmyr and Leebens-Mack 1999.)



dosymbionts 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 altogether. Some mutualisms indeed appear to conform to these principles. For example, the *Buchnera* bacteria that live within the cells of aphids and are vertically transmitted (see Figure 18.3A) 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 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 many developing seeds in the flower are consumed by the larvae. The moth could lay more eggs per flower—indeed, she distributes eggs among many flowers—so 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.

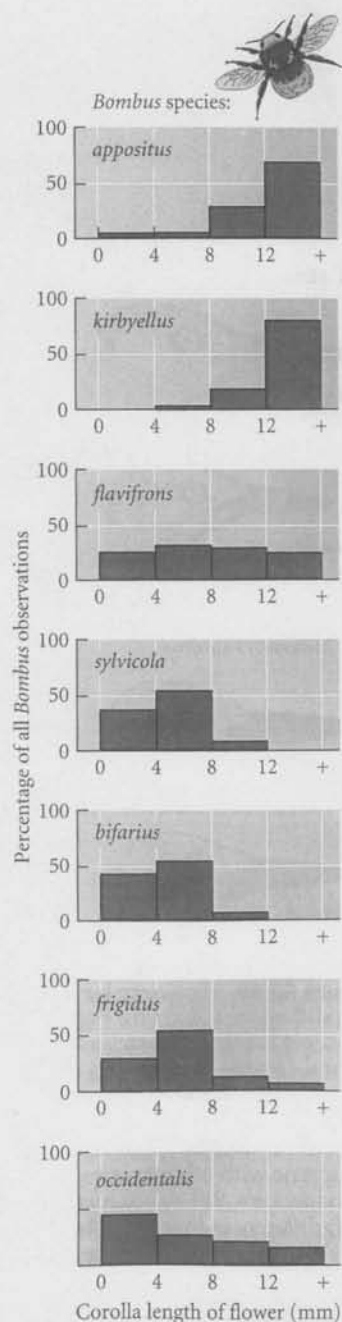
Mutualisms are not always stable over evolutionary time: many species cheat. For instance, many orchids secrete no nectar for their pollinators, and some practice downright deceit: they release a scent that mimics a female insect's sex pheromone, attracting male insects that accomplish pollination while "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 18.16B). 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).

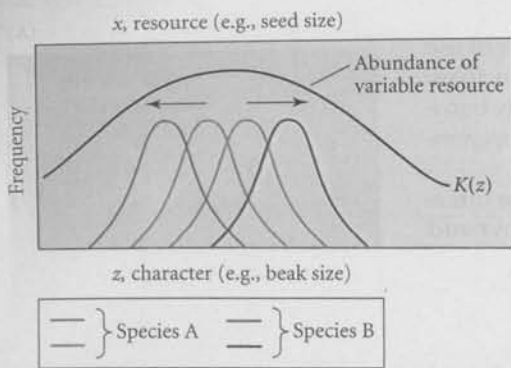
### The Evolution of Competitive Interactions

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 a good deal of 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 (Figure 18.17). 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 suffer competition from members of both their own species and the other species (Figure 18.18). 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

**Figure 18.17** Differences in resource use among closely related species are illustrated by bumblebees (*Bombus*) in Colorado. Some species obtain nectar and pollen from flowers of different corolla lengths (which are generally different species). These differences are correlated with the length of the bee's proboscis. Those species that use flowers with similar corolla lengths have different altitudinal distributions. For example, *B. appositus* and *B. kirbyellus* live at low and high altitudes, respectively, and *B. frigidus*, *B. bifarius*, and *B. sylvicola* have successively higher altitudinal distributions. (After Pyke 1982.)





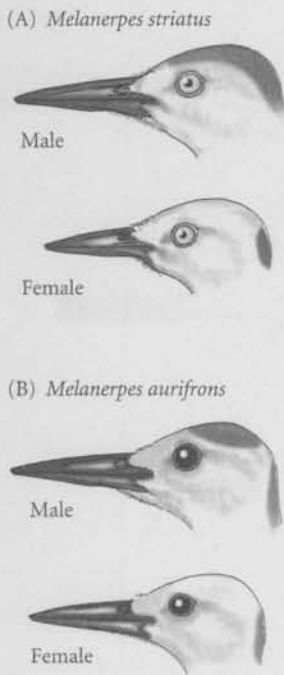
**Figure 18.18** A model of evolutionary divergence in response to competition. The  $x$ -axis represents a quantitative phenotypic character ( $z$ ), such as bill size, that is closely correlated with some quality of a resource, such as the average size of the food items eaten by that phenotype. The curve  $K(z)$  represents the frequency distribution of food items that vary in size. 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.

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 (see below).

Because recombination among loci restricts the variance in a polygenic character that determines resource use (see Chapter 13), a broad spectrum of resources may not be fully utilized by just one or two species. In that case, one or more additional species, differing from the first two, may be able to invade the community. Both the invaders and the previous residents may then evolve further shifts in resource utilization that minimize competition. The species may also diverge in other respects that reduce competition, such as habitat use. For example, although some of the bumblebee species described in Figure 18.17 differ in proboscis length and thus in the flowers they use, others are similar in this respect, but those species occupy different habitats (i.e., altitudinal zones).

Brown and Wilson (1956) coined the term **character displacement** to describe a pattern of geographic variation wherein sympatric populations of two species differ more greatly in a characteristic than allopatric populations. One possible reason for such a pattern is that the characteristic is associated with the use of food or another resource, and that the species have evolved differences in resource use where they would otherwise compete with each other. (Hence, "character displacement" is often used to mean the process of divergence 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). For example, the Galápagos ground finches *Geospiza fortis* and *G. fuliginosa* differ more in bill size where they coexist than where they occur singly (see Figure 9.27). 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). A rather similar example is the case of sticklebacks in the *Gasterosteus aculeatus* complex. In northwestern North America, several lakes each have two reproductively isolated forms, one benthic and one limnetic (see Figure 16.8), which differ in body shape, mouth morphology, and the number and length of the gill rakers. Other lakes have only a single form of stickleback, with intermediate morphology (Schluter and McPhail 1992).

**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 18.19; Selander 1966).



**Figure 18.19** 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 species of woodpeckers. Bill size is correlated with differences in feeding behavior, so greater sexual dimorphism results in broader resource use in *M. striatus*. (After Selander 1966.)



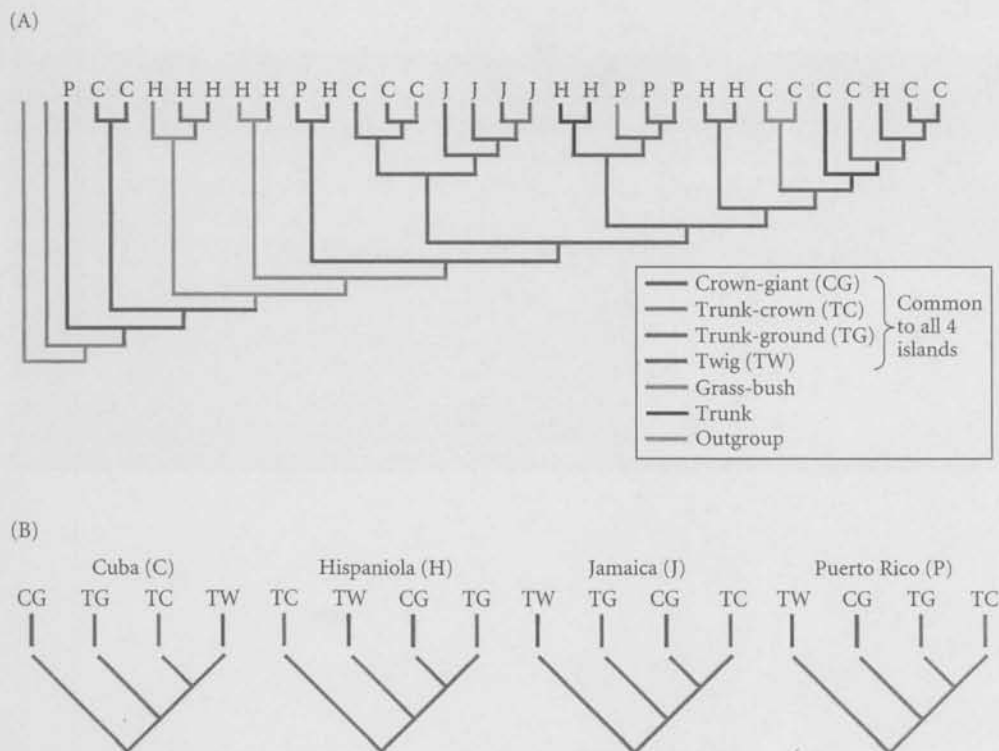
### Community patterns

Of all interspecies interactions, competition has been most emphasized in ecologists' attempts to detect and explain repeatable patterns in ecological communities. Competition is often supposed to limit species diversity within contemporary assemblages, and it may have affected species diversity over long periods of evolutionary time (see Chapter 7).

To some extent, ecological interactions may guide the evolution of interacting species along predictable paths, resulting in convergent patterns. This doesn't always happen, however; for example, blood-drinking bats are restricted to tropical America, even though the abundant hoofed mammals in Africa would provide plenty of food for such species. Similarly, the species diversity of lizards that live in deserts in North and South America is lower on both of those continents than in Australia, where lizards are more diverse in deserts and also occupy wetlands, a habitat that very few American lizards use (Schluter and Ricklefs 1993).

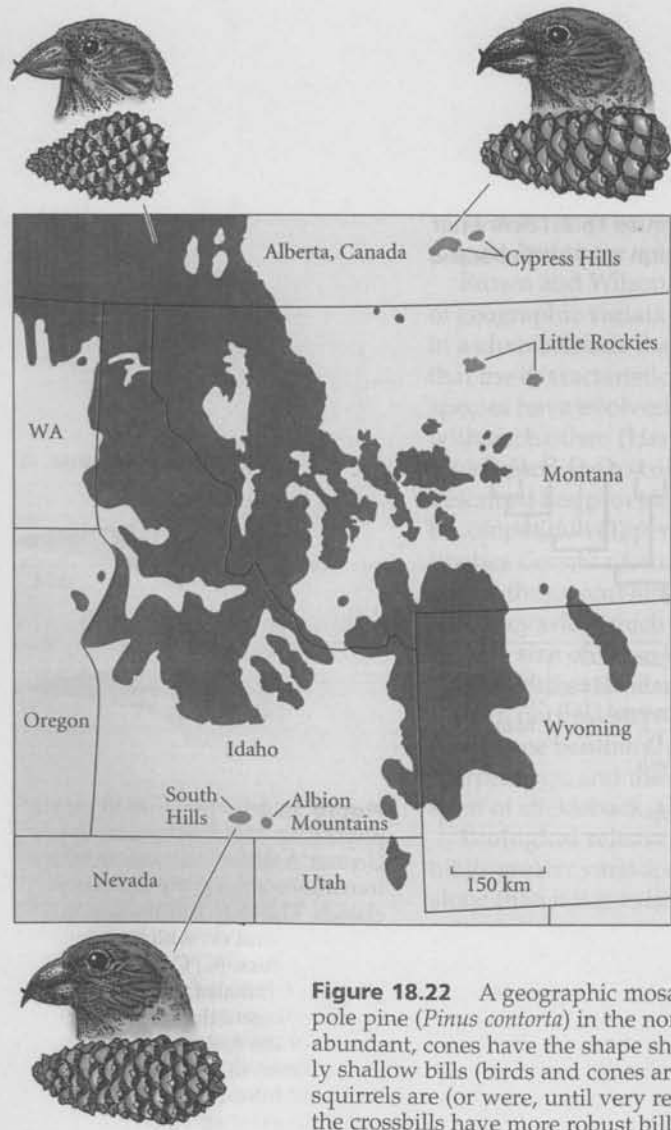
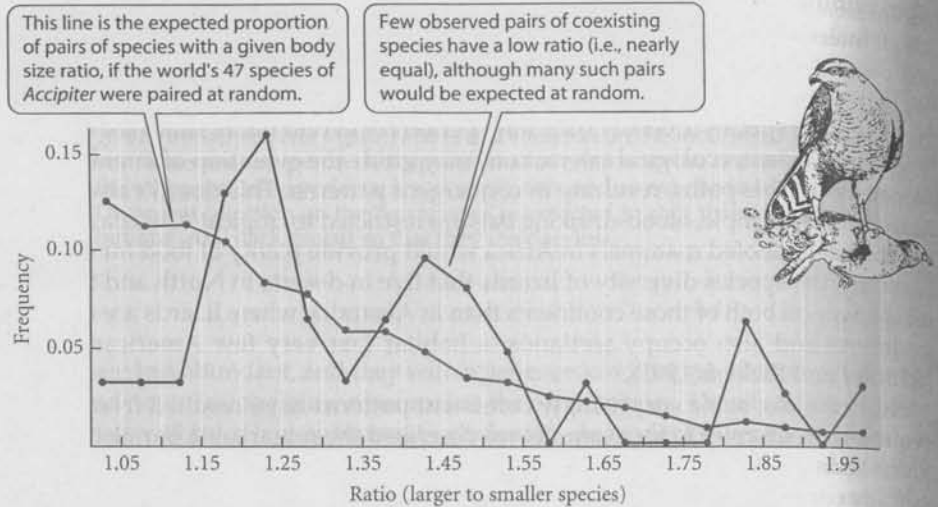
Nevertheless, some surprisingly consistent patterns have resulted from convergent evolution. In Chapter 6, for example, we described the remarkable parallel evolution of *Anolis* lizards on different Caribbean islands, each of which has morphologically and ecologically corresponding species that typically seek food in different microhabitats (see Figure 6.21). Cuba, Hispaniola, Jamaica, and Puerto Rico all have clades with four ecomorphs that are adapted for foraging in four different forest microhabitats: on the crowns of trees, in the trunk-crown region, on twigs, and in the trunk-ground area (Figure 18.20). The most reasonable interpretation of this pattern is that as new species have arisen on each island, they have evolved in similar ways to avoid competition by adapting to the same kinds of previously unused microhabitats.

In a similar vein, species of forest-dwelling bird-eating hawks (*Accipiter*) that differ in body size differ correspondingly in the size of the prey species they usually take. Pairs of sympatric species of *Accipiter* consistently differ more in body size than if pairs of species were taken at random from the 47 species in the world (Figure 18.21; Schoener 1984). Such examples suggest that principles of ecological organization may confer some predictability on the course of evolutionary diversification.



**Figure 18.20** (A) A molecular phylogeny of *Anolis* species in the Greater Antilles indicates frequent transitions among the ecomorph classes. The letters at the top indicate the island on which each species occurs. (C, Cuba; H, Hispaniola; J, Jamaica; P, Puerto Rico). (B) A phylogenetic tree, for each island, of the four ecomorphs that are common to all the islands, extracted from the full phylogeny. (After Losos et al. 1998.)

**Figure 18.21** Throughout the world, coexisting species of bird-eating hawks (*Accipiter*) differ more in body size than would be expected if species were selected at random. Hawks of different sizes feed on correspondingly different species of prey. These data imply either that coexisting species evolve differences in prey use to reduce competition or that only species that differ in prey use can coexist. (After Schoener 1984.)



**Figure 18.22** A geographic mosaic of coevolution. The colored area represents the distribution of lodgepole pine (*Pinus contorta*) in the northern Rocky Mountains. In most of this area (red), red squirrels are abundant, cones have the shape shown at the upper left, and red crossbills (*Loxia curvirostra*) have relatively shallow bills (birds and cones are drawn to relative scale). In peripheral mountain ranges (blue), red squirrels are (or were, until very recently) absent. Here the cones differ in shape and scale thickness, and the crossbills have more robust bills. (After Benkman et al. 2003.)

**Multispecies interactions**

Each species in an ecological community interacts with several or many other species. Consequently, its evolutionary response to interaction with one species may be influenced by the effect of another, in any of many possible ways. Two examples will illustrate this point.

**A THREE-SPECIES SELECTION MOSAIC.** John Thompson (1999) has observed that the selection imposed on a species by its interactions with other species may vary from one geographic population to another, resulting in a **geographic mosaic** of coevolution. Selection may be stronger in some places than in others, or even favor different characteristics, and gene flow among such populations may result in locally inadequate adaptation. Craig Benkman and his collaborators (Benkman 1999; Benkman et al. 2003) have studied such a geographic mosaic of interactions among lodgepole pine (*Pinus contorta*) and two seed predators, the red squirrel (*Tamiasciurus hudsonicus*) and the red crossbill (*Loxia curvirostra*) (Figure 18.22).

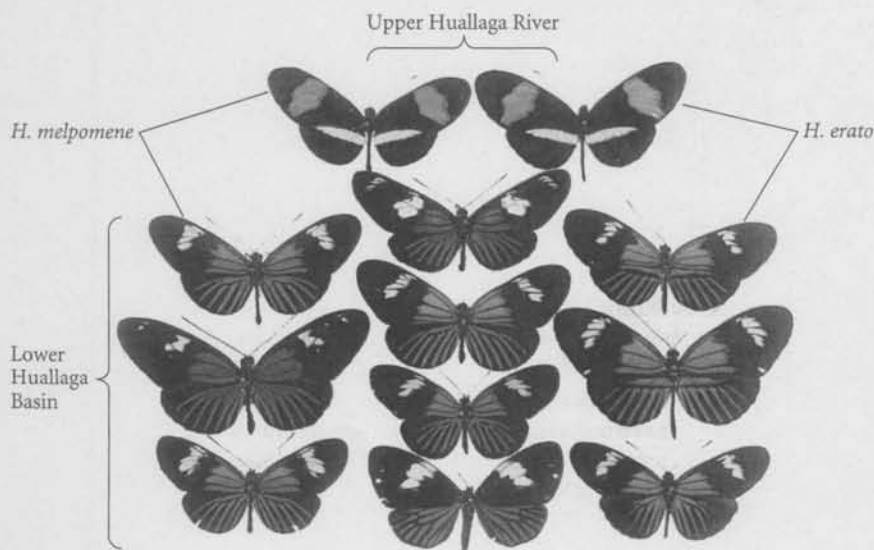
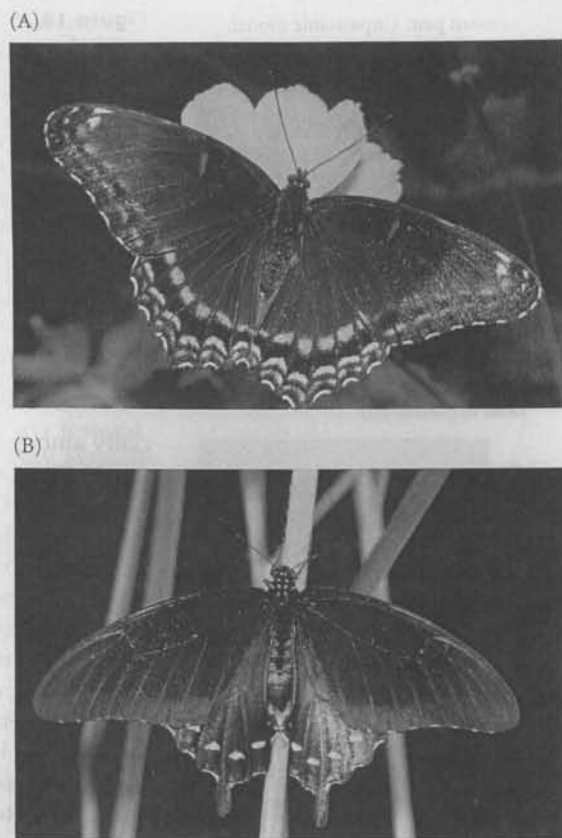
Throughout much of the distribution of the pine in the northern Rocky Mountains, squirrels harvest and store great numbers of cones and are the primary consumers of pine seeds. Benkman et al. have found that squirrels prefer narrow cones that have a high ratio of seed kernel to cone mass, and so impose selection for wider cones with fewer seeds. Red crossbills, which feed almost exclusively on pine seeds that they extract from cones with their peculiarly specialized bill, are much more abundant in a few small mountain ranges where squirrels are absent than where squirrels occur. Crossbills feed less effectively on larger, wider cones that have thicker scales—and these are

**Figure 18.23** Batesian mimicry. The palatable red-spotted purple butterfly (*Limentis arthemis*; top) resembles the pipevine swallowtail (*Battus philenor*; below) which stores distasteful, poisonous chemicals that it obtains from the plant it eats when it is a larva. Predators that learn, from unpleasant experience, to avoid the model also will tend to avoid attacking the mimic. (*Limentis* © Michael Gadomski/Photo Researchers, Inc.; *Battus* © S. McKeever/Photo Researchers, Inc.)

precisely the characteristics that have evolved in pine populations that suffer seed predation only from crossbills. Correspondingly, crossbill populations in these locations have evolved longer, deeper bills than in regions where red squirrels occur. These bill characteristics have been found, in tests of caged crossbills, to enhance feeding efficiency on large, thick-scaled cones. Thus coevolution between pines and crossbills is apparent where these species interact strongly, but where squirrels are the dominant seed predator, they drive the evolution of cone characteristics, and crossbills adapt accordingly.

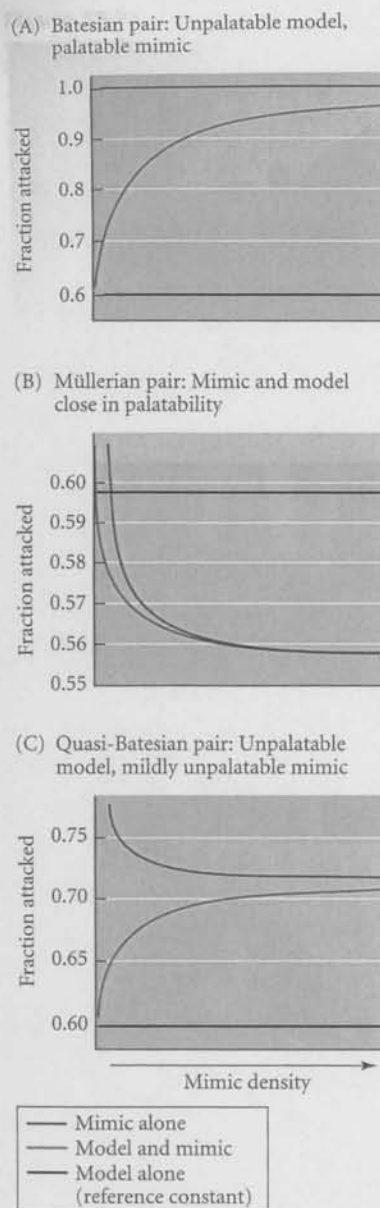
**MIMICRY RINGS.** Defensive mimicry, in which one or more species gain protection against predators from their resemblance to one another, provides model systems for studying many evolutionary phenomena (Mallet and Joron 1999; Joron and Mallet 1998; Turner 1977). Traditionally, two forms of defensive mimicry have been recognized (see Chapter 3). In Batesian mimicry, a palatable species (a mimic) resembles an unpalatable species (a model; Figure 18.23). In Müllerian mimicry, two or more unpalatable species are co-mimics (or co-models). In both cases, predators learn, from unpleasant experience, to avoid potential prey that look like the unpalatable species. (Such learning has been experimentally documented, especially with birds preying on butterflies and other insects.) Often, although not always, the models and mimics display conspicuous aposematic (warning) patterns.

Groups of species that benefit from defensive mimicry are known as MIMICRY RINGS. In many cases, mimicry rings include both strongly unpalatable and mildly unpalatable species; the latter may be “quasi-Batesian” mimics of the more unpalatable species. In many cases, several mimicry rings are found in the same region, each consisting of multiple species of similar Müllerian mimics and often including some palatable Batesian mimics (and/or mildly unpalatable quasi-Batesian mimics) as well (Figure 18.24). Espe-



**Figure 18.24** 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 drainage, 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.)





**Figure 18.25** Computer simulations of the probability of predator attack on model-mimic pairs of prey species. In each graph, a constant probability of attack on the unpalatable model, when it is alone, is assumed, and the probability of attack is scaled relative to that level. (A) A palatable mimic experiences high predation when its model is absent (“mimic alone”), much lower predation when it is rare, and increasingly higher predation as its density increases relative to that of the model. (B) A Müllerian species pair in which one species (“mimic”) is only slightly less unpalatable than the other (“model”). As the mimic’s density increases, predators’ aversion is reinforced at a higher rate, so predation on both species declines. (C) A mildly unpalatable “quasi-Batesian” mimic, if alone, suffers somewhat less predation as its density increases because predators learn to avoid it—but then soon forget and attack again, because they have had only a mild aversive experience. High densities of the mimic will result in higher predation on the model because predators are only seldom strongly deterred. Hence the aposematic color pattern tends to lose its advantage. (After Mallet and Joron 1999.)

cially among swallowtail butterflies, Batesian mimics are sometimes polymorphic within populations, with each morph resembling a different unpalatable model (e.g., the African swallowtail *Papilio dardanus*; see Figure 9.2A). 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 18.24).

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, however, it has recently swallowed a tasty butterfly with that phenotype, it will be more, not less, inclined to eat the next butterfly with that 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 (Figure 18.25A). (The degree of unpalatability of the model also affects the outcome because the more unpleasant the predator’s experience has been, the longer its aversion to that color pattern is likely to last.) Mimetic polymorphism in Batesian mimics such as *Papilio dardanus* can therefore evolve by frequency-dependent selection: a rare new phenotype that mimics a different model species will have higher fitness than a common mimetic phenotype, simply because it is less common and predators will not have had an opportunity to learn that butterflies with that phenotype are palatable rather than unpalatable.

Since Müllerian mimics jointly reinforce aversion learning by predators, there is likely to be strong stabilizing selection for a common color pattern in all sympatric unpalatable species (Figure 18.25B). However, many apparent Müllerian mimics, such as *Heliconius melpomene*, may actually be mildly unpalatable quasi-Batesian mimics, lowering the effectiveness of the aposematic color pattern (Figure 18.25C). Mutant phenotypes in a quasi-Batesian species might have a selective advantage if they resembled a different mimicry ring with much more abundant or much more unpalatable model species (Mallet and Joron 1999). This hypothesis is likely to account for geographic variation in mimetic patterns.

## Summary

1. Coevolution is reciprocal evolutionary change in two or more species resulting from the interaction between 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 between 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.