RoseCH14_0104043_405-436_2p 12/10/04 1:35 PM Page 405

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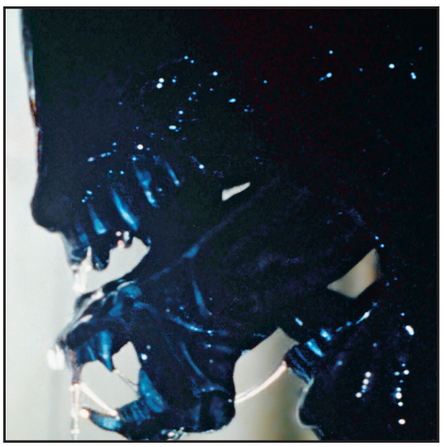
*The parasitoid from the movie* Alien.



# 14

# Parasitism and Mutualism

Biological organisms can both help and harm each other. In this chapter we will explore some of these relationships. On one hand are a vast array of organisms called *parasites*. These organisms complete all or part of their life cycle within or on another organism called a *host,* which suffers some reduction in survival or fertility as a result.

The imaginary parasites in the classic movie *Alien* completed their development within a human host, with results that many of us consider worse than death. One unusual feature about the parasites in *Alien* was that they had no prior history with human hosts, at least not in the first movie. In reality, a fascinating aspect of the biology of parasites is the extreme specialization that is the normal accompaniment of their successful development in particular hosts. As you might expect, hosts often have adaptations that make life difficult for parasites. This type of reciprocal evolutionary change in interacting species is sometimes called *coevolution*. We look at host-parasite interactions in the first part of this chapter, beginning with Module 14.1. Our focus turns to coevolution beginning with Module 14.13.

On the other hand, not all interactions between species are negative. Some species provide benefits to one another. These beneficial interactions are called *mutualisms*. Because mutualisms involve interactions between different species, it is important to understand how such interactions can evolve. If one species provides a behavior or resource that benefits another species, but incurs a cost for doing so, there must be a high likelihood of getting something in return. Otherwise, natural selection would quickly weed out such traits. We find that only under particular ecological conditions do we see mutualistic interactions evolving. Nevertheless, mutualisms present some of the most interesting, complex, and important types of ecological interactions. Beginning with Module 14.6, we consider mutualistic interactions. ❖

RoseCH14_0104043_405-436_2p 12/10/04 1:35 PM Page 406

# HOST-PARASITE INTERACTIONS

## 14.1 The specialized life cycle of parasites makes them useful for controlling certain pest species

A **parasite** is any organism that feeds in or on another individual organism and is dependent on that organism to complete its development. The organism that the parasite feeds on is called a **host**. The fitness effects of the parasite on the host are negative and certainly may result in death. (The difference between a parasite and an *herbivore* is that the herbivore usually feeds on many plants in the course of its lifetime, and it usually does not inflict a severe reduction in fitness on any single individual plant.) Some parasites are very small, such as bacteria and viruses; others, such as worms, flies and fungi, may be quite large.

Small parasites may be transferred from one host to another directly. We are all familiar with many human diseases, from AIDS to the common cold, that are typically transferred directly from one person to another. Small parasites may also be transferred via an intermediate species called a **vector**. Vectors are not usually adversely affected by the parasite, but have a life cycle that ensures transfer to a suitable host. For example, malaria, a severe disease caused by the protozoan *Plasmodium*, requires a mosquito vector to move from one host to another. The mosquito is relatively unaffected by this process.

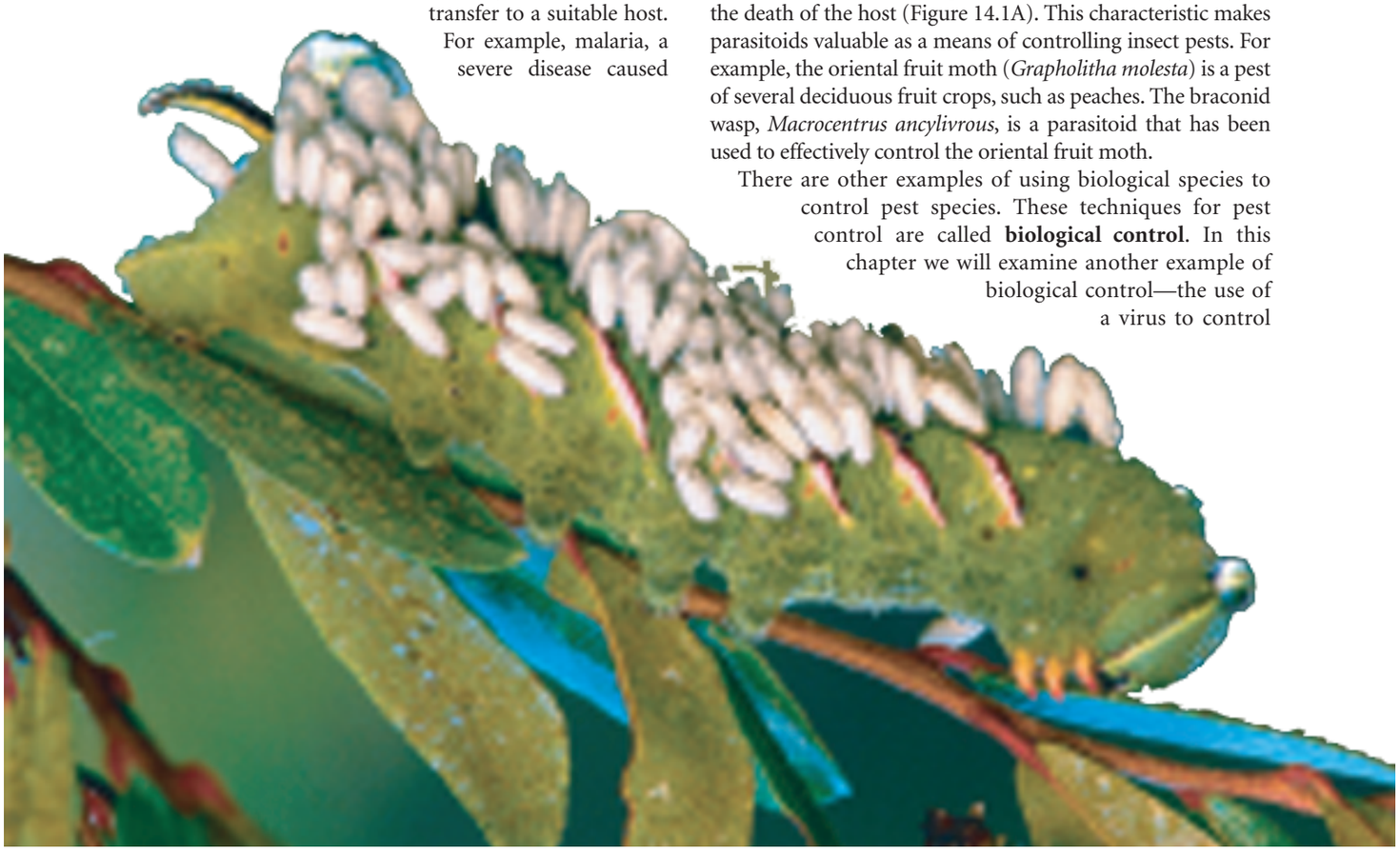


FIGURE 14.1A **A Moth Caterpillar with Emerging Parasitoid Pupae**

### Life Cycle of a Parasite

Many large parasites have specialized and complex life cycles. There may be more than one host species. The host in which the parasite reproduces is called the **definitive host**, while other hosts are called **intermediate hosts**. Often parasites not only have specific species they use as definitive and intermediate hosts, but they also specialize on certain parts of the host organisms for feeding and development. An important question we address in this chapter is: Why have parasites evolved such extreme specialization?

Some insects use other arthropods, usually insects, for the development of their larvae. These insects are called **parasitoids**. Their larvae usually develop within the body of the host. The successful development of the larvae always results in the death of the host (Figure 14.1A). This characteristic makes parasitoids valuable as a means of controlling insect pests. For example, the oriental fruit moth (*Grapholitha molesta*) is a pest of several deciduous fruit crops, such as peaches. The braconid wasp, *Macrocentrus ancylivrous*, is a parasitoid that has been used to effectively control the oriental fruit moth.

There are other examples of using biological species to control pest species. These techniques for pest control are called **biological control**. In this chapter we will examine another example of biological control—the use of a virus to control

rabbits that had become pests in Australia. There has been great interest in biological control, which was used in California as far back as 1889 to control the cottony-cushion scale that threatened to destroy the state's citrus industry. The benefits of biological control relative to pesticides are their reduced cost and lack of toxic environmental effects.

**Effects of Parasites on Population Dynamics** Can parasites affect the population dynamics of their hosts? In theory, they certainly can. In this chapter we will review some of the requirements for host-parasite coexistence.

There is also experimental evidence for the impact of parasites on their host dynamics. For example, red grouse are popular game birds in England. As a result, the numbers of red grouse bagged by hunters have been recorded for some time. These bag numbers are thought to be closely related to the total numbers of birds in the population. The numbers are often highly variable from year to year, as the graph in Figure 14.1B shows. Red grouse are often host to a parasitic nematode that is thought to reduce their fertility. In an experiment, on two different occasions scientists treated grouse in one population with drugs that kill the nematodes. The result of reducing the parasite burden was a marked decline in the magnitude of population fluctuations, as Figure 14.1C shows. This change directly implicates parasites in the population dynamics of these birds.

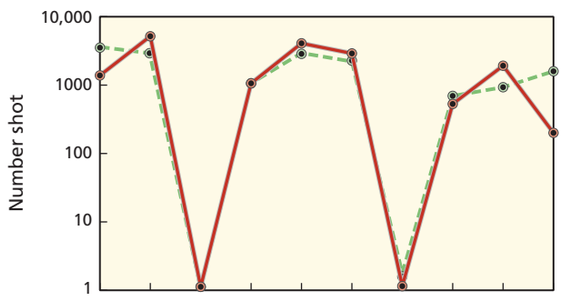



**FIGURE 14.1B The Numbers of Red Grouse in Two Different Control Populations**

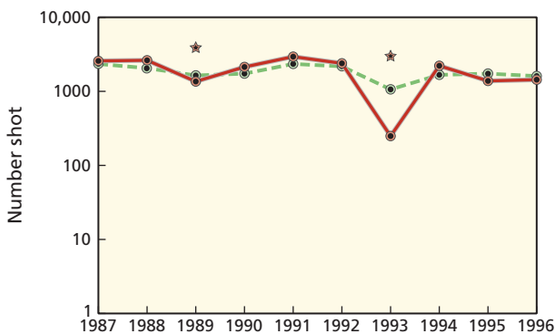



**FIGURE 14.1C The Numbers of Red Grouse in Two Experimental Populations** Antiparasitic drugs were administered to the birds in the two years marked with asterisks.

## 14.2 Parasitoids cannot be too effective at finding hosts if they are to avoid extinction

In many ways the dynamics of hosts and parasitoids are similar to that of predator and prey. However, the relationship between parasitoid reproduction and host death is more direct. One of the first models of host-parasitoid interactions was developed by Nicholson and Bailey in 1935.

This particular model was very simple; it assumed that there was no density dependence in the population growth of either the host or the parasitoid. Each parasitoid was assumed to have an identical chance of attacking and laying eggs in a host. If we let that probability be *a*, and the number of parasitoids be *P*, then the total number of attacks is simply *aP*. In some cases a single host might be attacked multiple times, and some lucky hosts would not be attacked at all. Because the larvae of a parasitoid generally kill the host, the Nicholson-Bailey model assumed that all attacked hosts die and give rise to new parasitoids. It further assumed that only the unattacked hosts are able to reproduce.

We can develop a simple model of the number of new hosts and parasitoids in each generation as follows:

$$\{\text{number of new hosts}\} = \{\text{host birthrate}\} \times \{\text{number of hosts not attacked}\}$$

$$\{\text{number of new parasitoids}\} = \{\text{parasitoid birthrate}\} \times \{\text{number of hosts attacked}\}$$

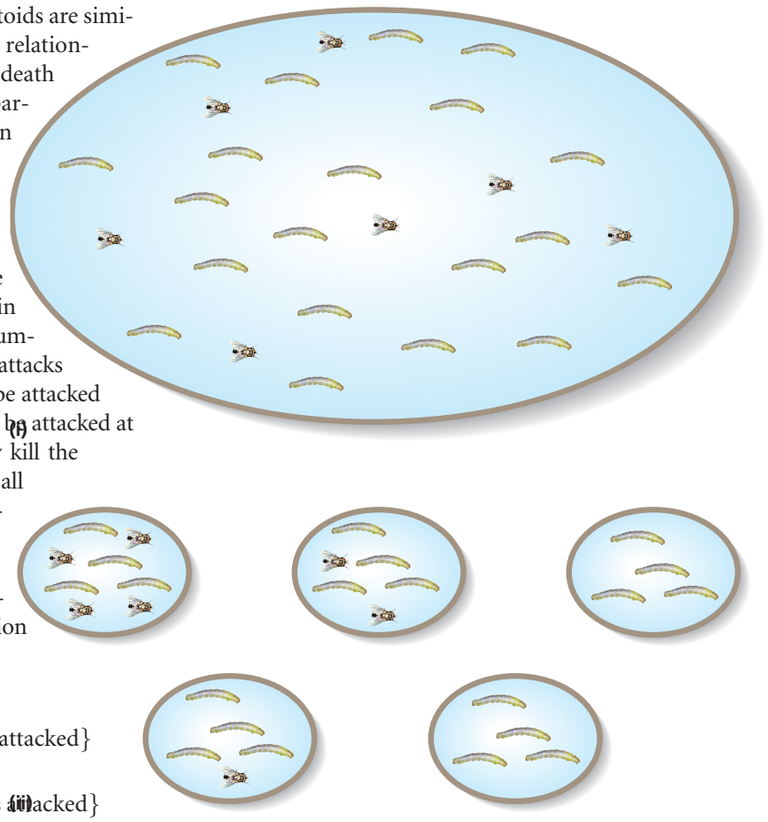



**FIGURE 14.2A** The hosts and parasitoids are evenly distributed throughout the environment (i). The mean number of hosts that are attacked is equal to *aP*. The chance that a single host avoids attack is equal to $e^{-aP}$. If parasitoids show a clumped distribution (ii), then, even though the mean number of hosts attacked is unchanged, the chance of avoiding attack is equal to $[1 + (aP/k)]^{-k}$.

In the original formulation of the Nicholson-Bailey model, the parasitoids and hosts were assumed to be uniformly distributed in the environment, as in part (i) of Figure 14.2A. With these assumptions, the hosts and parasitoids can never coexist, because either the parasite or both the host and parasite eventually go extinct, as in part (i) of Figure 14.2B. These predictions cannot be correct, because many hosts and parasitoids are found to coexist in nature for long periods of time.

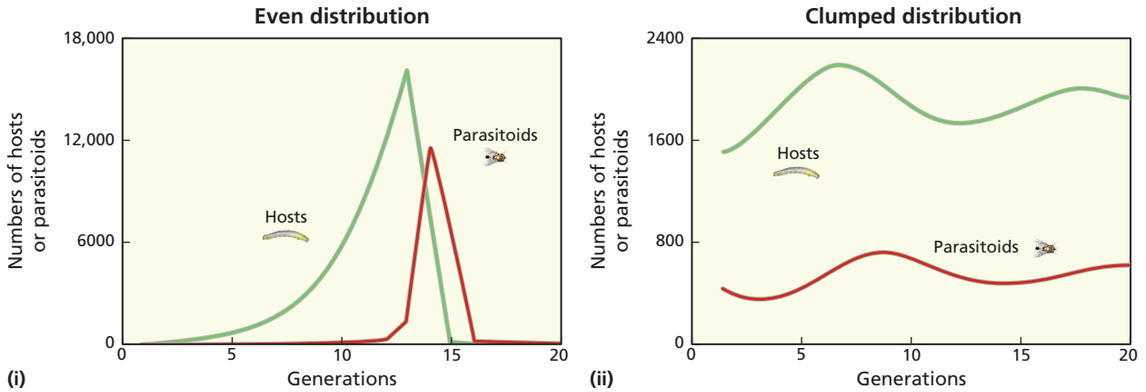



**FIGURE 14.2B** When the parasitoids are evenly distributed, coexistence is not possible (i). However, when the parasitoids showed a clumped distribution enough hosts avoid parasitism that coexistence is now possible (ii).

The Nicholson-Bailey model can predict stable coexistence with small modifications. Suppose that the parasitoids are not evenly distributed in the environment, but instead occur in patches as shown in part (ii) of Figure 14.2A. In some patches there are many parasitoids, and in others very few or none. The degree of patchiness is measured by a parameter we call $k$. If $k$ is less than infinity ($\infty$), then there is some patchiness. If $k = \infty$, then the parasitoids are evenly distributed.

The net effect of patchiness is that there are always more hosts that avoid parasitism than is the case when parasitoids are evenly distributed. For instance, if $aP = 0.5$, then the chance of a host avoiding attack when parasitoids are evenly distributed is 0.6. If parasitoids are clumped ($k = 0.5$), then the chance of avoiding attack is higher: 0.7. It is as if the parasitoids have been unable to find some of the hosts [part (ii) of Figure 14.2A]. Sufficiently high levels of patchiness prevent the host population size from being driven to very low levels and thus going extinct [part (ii) of Figure 14.2B]. In fact, if the patchiness parameter ($k$) is less than one, then both host and parasitoid can stably coexist.

Is the distribution of parasitoids patchy in nature? In some cases it is. For example, consider the distribution of the parasitoid *Cyzenis albicans*, which is found in winter moths. Figure 14.2C shows the actual number of parasitoid larvae per host (dots) compared with the number expected if the parasitoids were distributed evenly (green bars) or in a clumped fashion (red bars). The actual observations are more consistent with a clumped distribution (red bars). In addition, the value of the parameter $k$ for these data is 0.6; this value is consistent with stable coexistence, which can occur with clumped distributions.

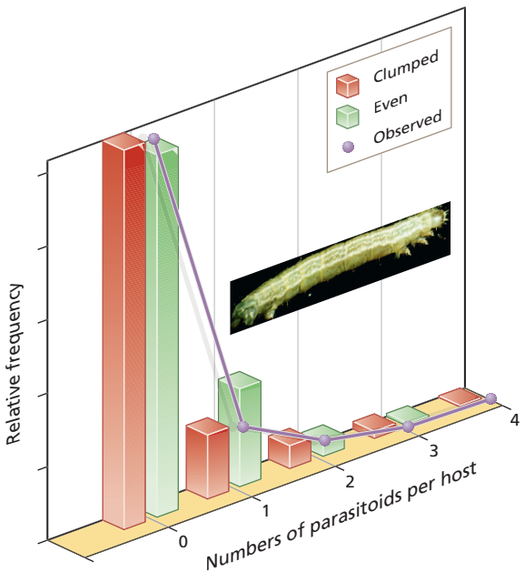



**FIGURE 14.2C** The number of larvae of the parasitoid *Cyzenis albicans* found in winter moth hosts. Most hosts have no parasitoids, and a few have up to four. The observed number of parasitoids per host is closer to the predicted values of the clumped distribution than it is to the even distribution.

## 14.3 Parasites are often very specialized in their feeding habits and life cycles, to match those of their hosts

A characteristic of many parasites is a complicated life cycle that is closely tied to the life cycles of one or more hosts. As an example consider trematodes, a class of parasitic flatworms from the phylum Platyhelminthes. These worms often have elaborate mouth morphologies for attaching to their *definitive* host, the host in which they reproduce. The *intermediate* hosts need to be organisms that are common in the habitat where the definitive host is usually found. Likewise, the intermediate host must permit the trematode to find its way back into the definitive host. This transfer can be accomplished if the intermediate host serves as food for the definitive host, or if the intermediate host is often near food the definitive host will ingest, as Figure 14.3A shows.

The type of parasite life cycle shown in Figure 14.3A is considered highly specialized because the parasite interacts with a very limited number of species. Many nonparasitic organisms

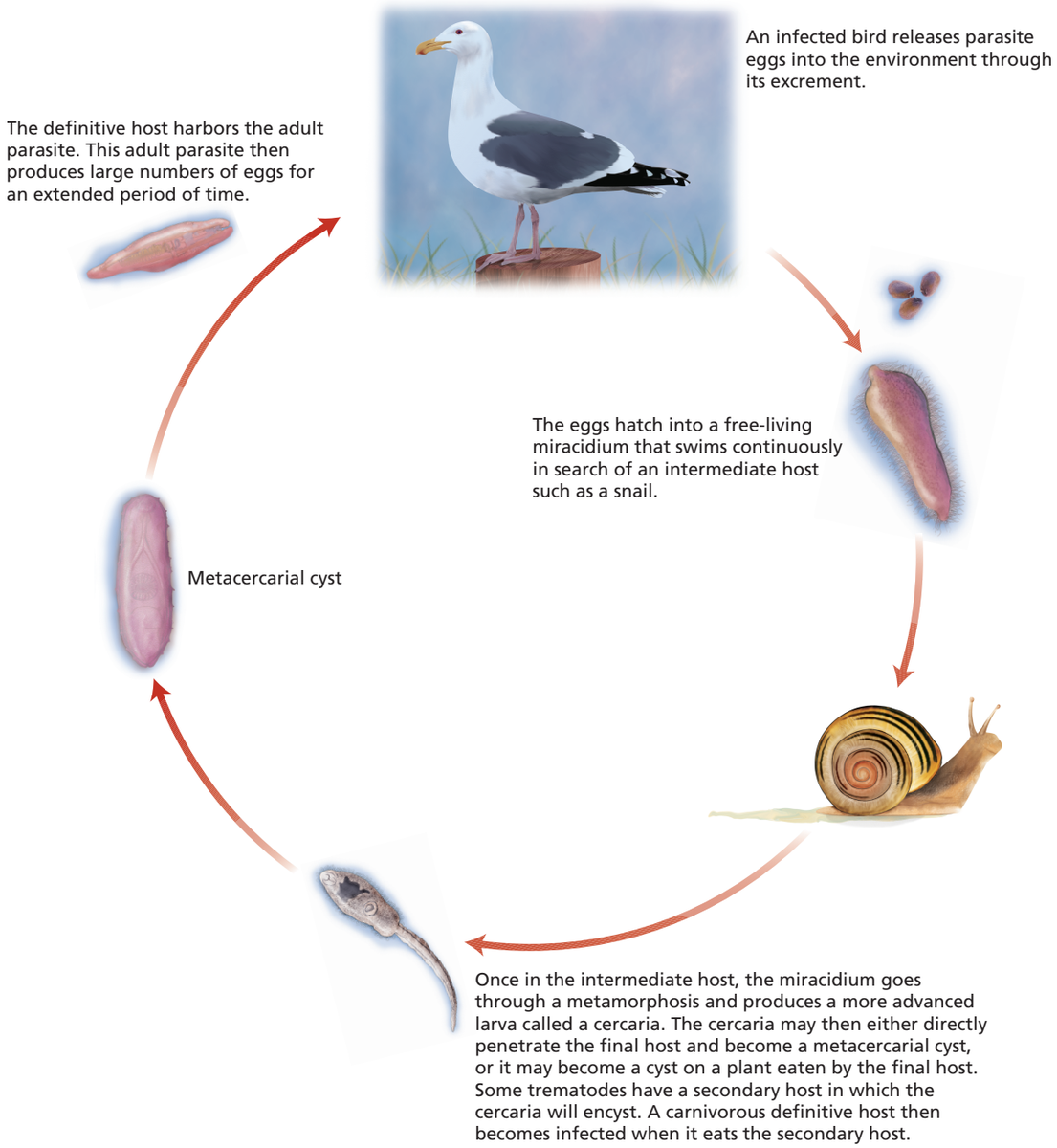



**FIGURE 14.3A The Life Cycle of a Trematode Parasite**

RoseCH14_0104043_405-436_2p 12/10/04 1:35 PM Page 411

have less specialized life cycles. For instance, many seed-eating birds may feed on a variety of seeds from different plants. Carnivorous mammals may eat many different small mammals or birds. Is there something special about parasites that leads to the extreme specialization we often see? The answer lies in the parasitic life cycle. The fact that the parasite completes all or a major part of its development within another organism makes it more likely that parasites will be specialized compared to carnivores or herbivores.

For example, to complete its life cycle, a parasite must clear a number of hurdles. First, many internal and external parasites must have an effective means of attaching to their hosts for long periods of time. Parasites often have elaborate mouth parts or other morphologies for accomplishing this attachment. Some closely related parasites are so specialized that they are unable to attach to the host of their close relatives.

The parasite also needs to be able to withstand the host's defensive responses. Animals have elaborate immune system responses that the parasite needs to withstand. Plants also mount chemical defenses when attacked. Plant parasites eventually have to cope with these chemical defenses. (Herbivores, on the other hand, may simply nibble on a plant and then move on to a different part of the same plant or a new plant altogether. Thus, herbivores do not have to be able to respond directly to a plant's full chemical defense system.)

Finally, parasites may also have to contend with enemies. These enemies may be predators, competitors, or parasitoids. Some hosts may make the parasite more vulnerable to natural enemies than other hosts.

It is probably very difficult for any single parasite to clear all these hurdles by attaching itself to any more than a few host species. Recent research has in fact suggested that many parasite species that had formerly been thought to be generalists actually consist of genetically differentiated populations that are themselves specialists. For example, mallards in England have a trematode parasite, *Echinoparyphium recuvatum.* This parasite was thought to be capable of developing on two different species of snails as intermediate hosts—*Lymnaea peregra* and *Valvata piscinalis.* It now appears that there are two morphologically identical but different species of trematode, one that uses *L. peregra* exclusively as its intermediate host and another that uses *V. piscinalis.* Neither of these sibling trematode species can develop on the other's secondary host. Furthermore, as adults these parasites distribute themselves to different locations in the mallards' intestines, as shown in Figure 14.3B. ❖

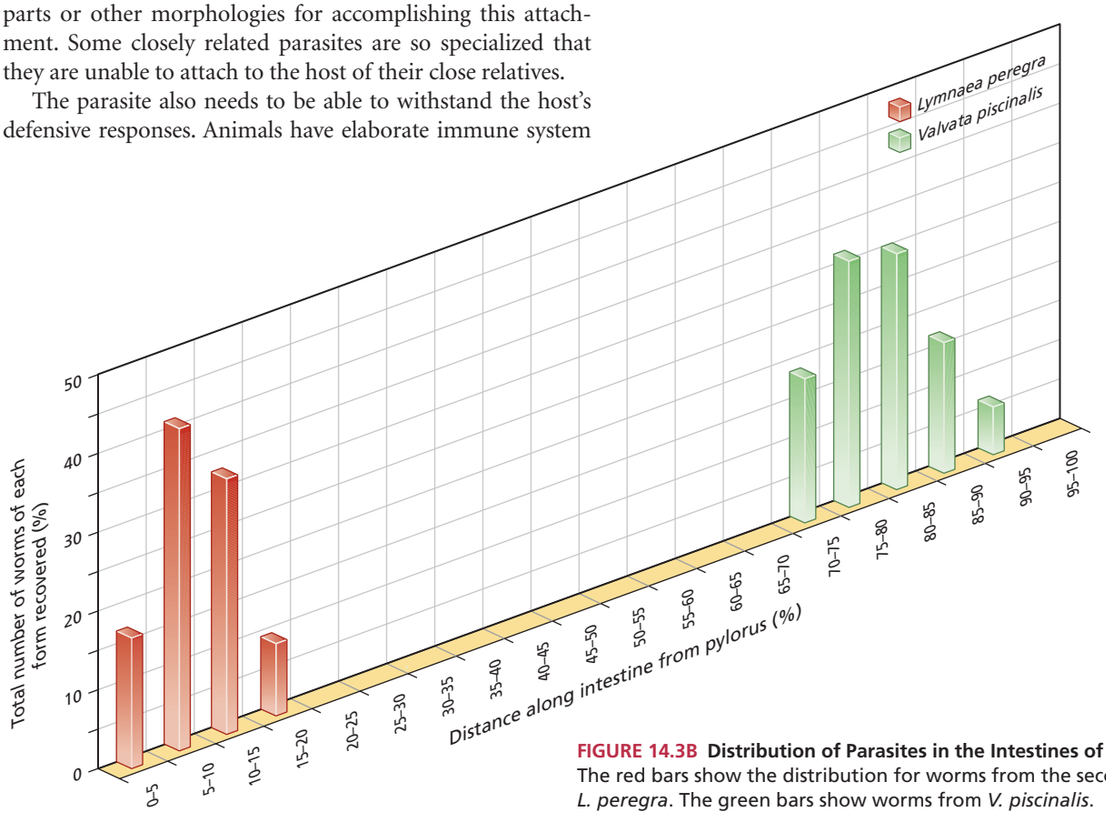



**FIGURE 14.3B Distribution of Parasites in the Intestines of Ducklings** The red bars show the distribution for worms from the secondary host *L. peregra*. The green bars show worms from *V. piscinalis*.

RoseCH14_0104043_405-436_2p 12/10/04 1:35 PM Page 412

## 14.4 As hosts evolve genetic resistance to parasites, the parasites evolve means of overcoming this resistance

The stakes are very high for both parasites and hosts. On one hand, a host may suffer severe reductions in fitness or death when infected by parasites. The parasites, on the other hand, must successfully complete their life cycles in a host if they are to survive. We would expect that evolution would favor any host genotypes that resist attacks by parasites, while parasites would be strongly selected to overcome these host defenses. There is good experimental evidence suggesting that hosts and parasites have evolved elaborate genetic systems that function in these ways.

One such genetic system is the **gene-for-gene system** of host-parasite resistance. Under this system, many genes in the parasite genome might be used by hosts as a means of detecting parasites and destroying them. For instance, each of these genes may code for some chemical compound that is needed for the parasite physiology but is recognizable by the host as foreign. We will call the alleles of these genes ***avirulence alleles***, since they provide the host with a means of controlling the parasite. In Figure 14.4A, step 1, the avirulent allele at locus 1 is designated $V_1$, at locus 2, $V_2$, and so on.

Likewise, suppose that the host has a defense system corresponding to each of the parasite genes. The host is resistant to parasite attack if it has a ***resistance allele*** ($R$) corresponding to any one of the parasite's avirulence alleles ($V$). Thus, a host with the $R_1$ resistance allele would be resistant to a $V_1$ parasite, but an $r_1$ host would be susceptible to a $V_1$ parasite. If the host is resistant, then the parasite may evolve a ***virulence allele*** ($v$) at the appropriate locus. For instance, in Figure 14.4A, step 3, we see a $v_1$ virulence allele appear in the parasite population, effectively overcoming the resistance of the $R_1r_2$ host. At this point, the host must then mount its defense by recognizing the parasite at a different avirulent locus, such as $V_2$ (Figure 14.4A, step 4).

It might seem that the best strategy for a parasite would be to evolve virulence alleles at all relevant loci. Yet this does not appear to happen. Why not? Apparently, maintaining these virulence alleles has a fitness cost that puts a pathogen at a disadvantage if it maintains more alleles than it needs to. Suppose that one pathogen had virulence alleles at three different loci, but the local host could be infected if the pathogen had a virulence allele at only one locus. If a second pathogen genotype appeared with just the single needed virulence allele, then this new genotype could infect the host and also maintain a competitive advantage over the more virulent pathogen.

One example of the gene-for-gene model of host-parasite interactions is the relationship between the wild flax plant and a fungal rust pathogen. One study of natural populations in Australia found 8 different pathogen genotypes and 15 different host genotypes. The most virulent of the rust pathogens had one of the most restricted distributions, as Figure 14.4B shows. This limited distribution shows that virulence is not equivalent to success among pathogens. Likewise, as Figure 14.4B also shows, the host plants often had resistance only to a subset of all possible pathogenic rusts, and one host that was susceptible to all pathogens was quite common in some areas. ❖

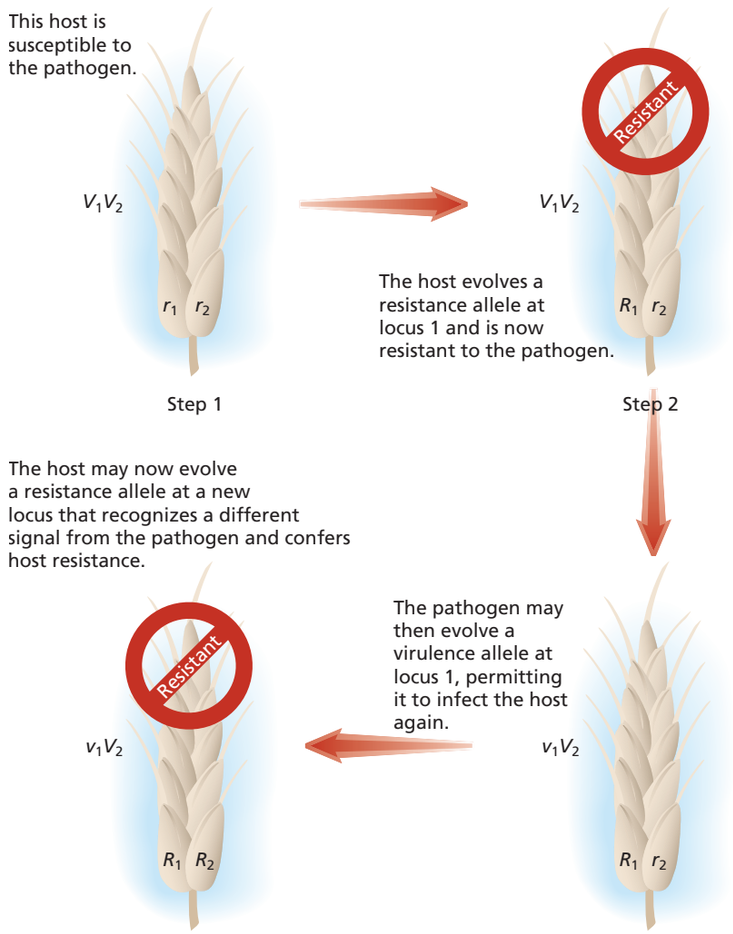



**FIGURE 14.4A Gene-for-Gene System of Host Parasite Resistance**

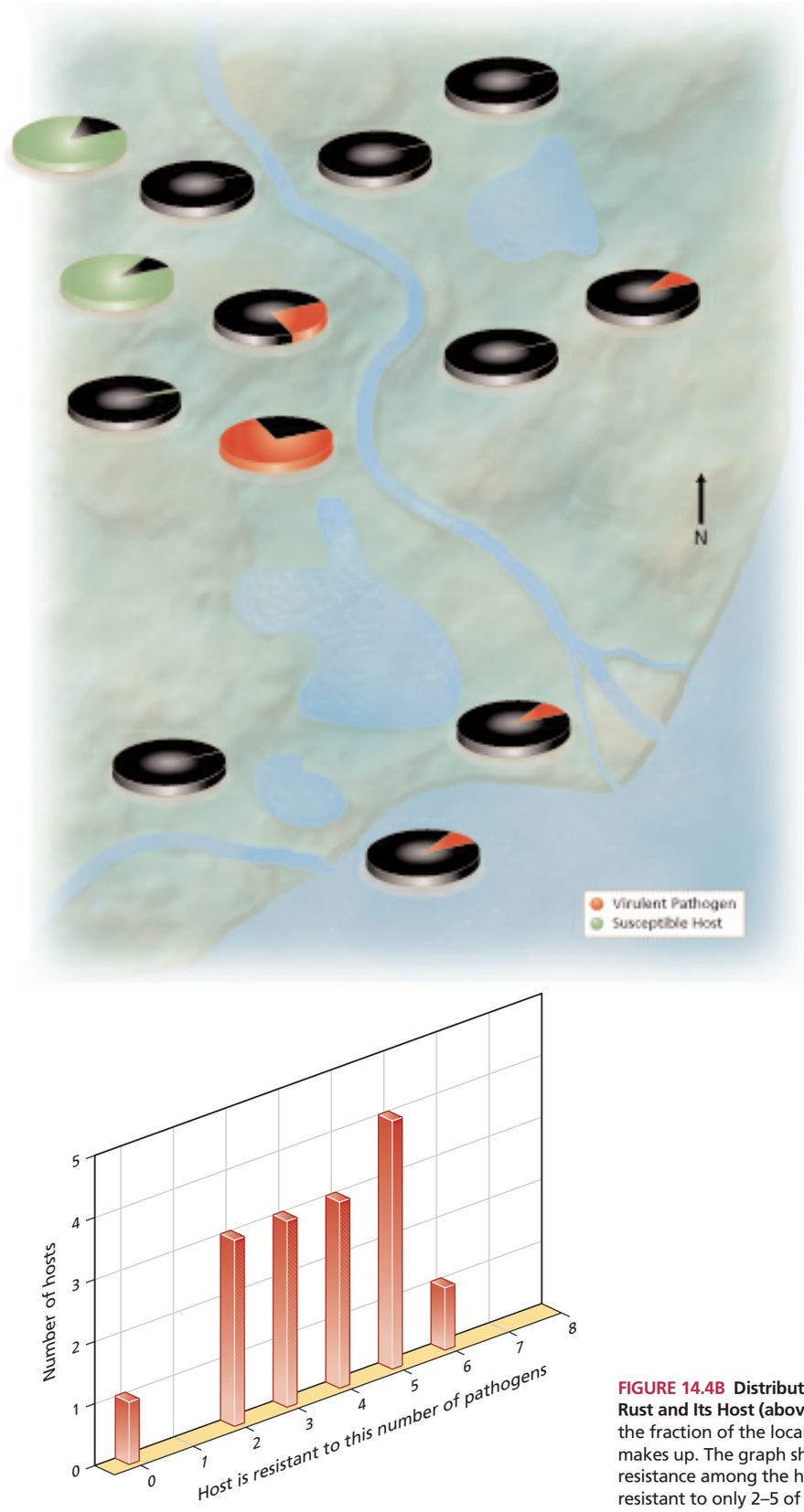



**FIGURE 14.4B Distribution of the Most Virulent Rust and Its Host (above)** Each pie diagram shows the fraction of the local population that each type makes up. The graph shows the frequency of resistance among the hosts. Most hosts are resistant to only 2–5 of the 8 common rusts.

RoseCH14_0104043_405-436_2p 12/10/04 2:31 PM Page 414

## 14.5 The coevolution of hosts and parasites also depends on ecological factors

When the European rabbit was introduced to the Australian continent, it became a major pest. The lack of any serious competitors or predators allowed the rabbit population to become so large that it depleted resources on grazing lands for sheep and cattle. In an attempt to control the rabbit population, in 1950 scientists introduced the myxoma virus, the cause of myxomatosis disease in rabbits. The virus is naturally found in populations of South American rabbits and produces only a mild disease in them. However, in European rabbits myxomatosis is often fatal. In Australia the main vector for disease transmission is the mosquito. If a mosquito bites an infected rabbit, then the mosquito may carry the disease to the next rabbit it bites.

The ease of disease transmission depends not only on the vector but also on how virulent the disease is. For instance, if the disease is very virulent and results in rapid death of the host, then there may be little opportunity for the infected rabbit to transmit the disease, as part (i) of Figure 14.5A shows. Although many rabbits may die, the virus with high virulence may also die out with them. On the other hand, if the virus produces only mild effects and is rapidly controlled by the host immune system, then the levels of virus in the rabbits' blood may be too low to effectively transmit the disease, as Figure 14.5A, part (iii) also shows. Viruses with intermediate levels of virulence may be the most successful. These viruses can multiply to high levels in the host bloodstream, and they persist for a prolonged period because the host does not usually die quickly. This set of conditions increases the chances of successful transmission of the virus to a new host. These factors ultimately favor the evolution of intermediate levels of virus virulence. In fact, samples of virus from the field in Australia show exactly this pattern (Figure 14.5B).

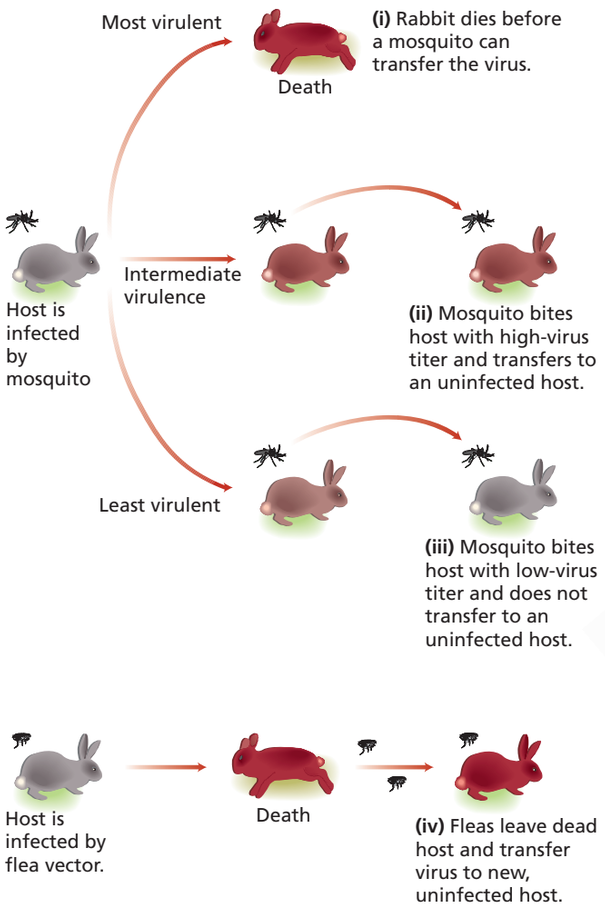



**FIGURE 14.5A Effects of Parasite Virulence on Disease Transmission**

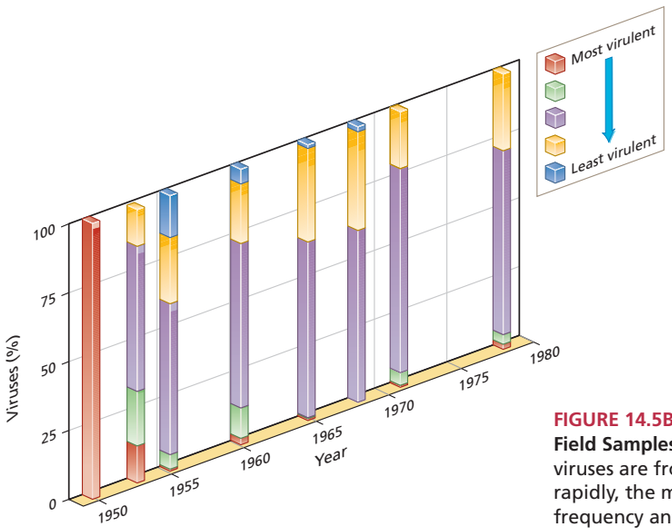



**FIGURE 14.5B Virulence of Myxoma Virus from Field Samples in Mallee, Australia** Initially, all viruses are from the highest virulence class. Very rapidly, the most virulent class diminishes in frequency and the less virulent becomes common.

At about the same time that the myxoma virus was introduced to Australia, it was also introduced to France and England. In England, fleas rather than mosquitoes are the major disease vector. Fleas tend to stay on their host for prolonged periods of time. If a host rabbit dies from myxomatosis, the resident fleas may then move onto a new host, as shown in part (iv) of Figure 14.5A. The life cycle of the flea facilitates the transmission of virus with high virulence. As a result, the level of virulence of the myxoma virus in England is greater than in Australia.

However, the hosts are also evolving. There is, of course, strong selection for increased resistance to the virus as rabbits with low resistance die off. We see in Figure 14.5C a dramatic decline in the virus-related mortality rates among rabbits in England over time.

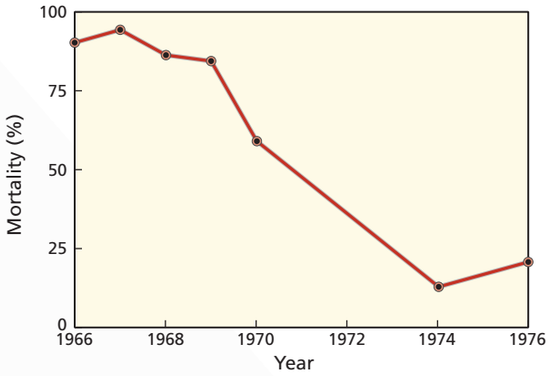



**FIGURE 14.5C Percent Mortality of Rabbits in Norfolk, England, to a Standard Strain of Myxoma Virus**

# MUTUALISTIC INTERACTIONS

## 14.6 Mutualisms may provide several benefits to participating species, including nutrition, protection, and transportation

So far we have considered two types of species interactions, predator-prey and host-parasite, that have negative effects on one of the participating species. **Mutualisms** are interactions between two or more species where each species benefits. Some of these interactions are truly unique and fascinating. Because mutualisms involve genetically isolated species, it is sometimes difficult to understand why one species would evolve behaviors or morphological structures to help another species. To address this question, we will review some of the mechanisms that are thought to be important in the evolution of mutualisms.

In some interactions between species, only one species receives benefits while the second is not affected positively or negatively. These interactions are called **commensalisms**.

Another term that is frequently used is *symbiosis*. This word has been used in many different ways, so we need to define it carefully. We use **symbiosis** to mean a long-term, intimate association between two species. With this definition symbiotic relationships may be mutualistic, parasitic, or commensalistic.

### Types of Mutualisms

Most mutualisms fall into one of three categories. **Transportation mutualisms** are interactions in which one member of the mutualism has gametes or individuals transported by the other mutualist. **Nutrition mutualisms** involve the exchange of nutrients. These nutrients may be carbon sources or some limiting nutrient for growth, like nitrogen. Some species attack or remove competitors or predators that impinge on another species. These relationships are called **protection mutualisms**. Some species interactions may fall into more than one of these categories. For instance, bees transport plant pollen in exchange for nectar. This type of mutualism would be a combination of transportation and nutrition mutualism.

### Do Some Species Exploit Mutualisms?

To understand mutualisms, we also need to understand under what conditions species will exploit mutualisms. If a plant produces nectar, an exploiting insect would gather nectar without transferring pollen. Exploiters are able to gain the benefits of the mutualism without incurring any of the costs. We can find examples of potential exploitation in all the major categories of mutualism. For instance, cleaner fish scour the surface of larger fish for parasites (Figure 14.6A).

**FIGURE 14.6A** **A Small Cleaner Fish Browsing**

This is an example of a protection mutualism from the large fish's perspective. On occasion, the cleaner fish feed on host tissue. The host fish sometimes consumes the cleaner fish.

Transportation mutualisms can be subverted by plants that mimic nectar-producing plants, but actually supply no nectar to their visitors. Many orchids (Figure 14.6B) have nectarless flowers. Nectar robbers (Figure 14.6C) are insects that chew through the corolla of plants and take nectar without pollinating the flower.

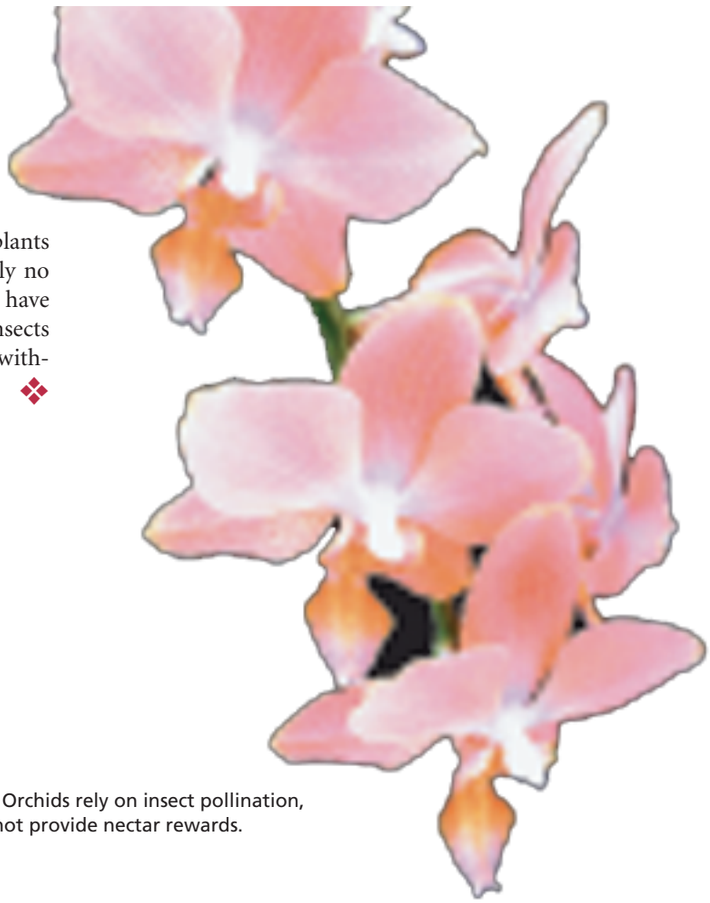


**FIGURE 14.6B** Orchids rely on insect pollination, but often do not provide nectar rewards.

**FIGURE 14.6C** Nectar robbers eat through the flowers of plants and take nectar without pollinating the plant.

RoseCH14_0104043_405-436_2p 12/10/04 2:15 PM Page 418

## 14.7 Mutualisms may involve the reciprocal exchange of essential nutrients

Some of the most important and widespread mutualisms involve the exchange of nutrients. One of the most important is the association between plants in the pea family, the "legumes," and bacteria in the genus *Rhizobium* (Figure 14.7A). The bacteria live in the soil and, through biochemical manipulation, make the legumes produce nodules on their roots, where the bacteria can live. In these nodules, the bacteria receive protection and carbohydrate. In return, the bacteria take nitrogen from the atmosphere and convert it into ammonia, which the plant uses as a source of nitrogen. Because nitrogen is often a limiting resource for plants, the ability to get nitrogen from the atmosphere is a great advantage for legumes.

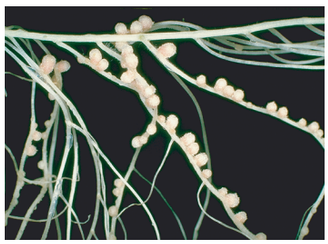
Mycorrhizal fungi also form close associations with the roots of many plants (Figure 14.7A). Ectomycorrhizal fungi send root hairs into the plant root tissue, growing between individual root cells (Figure 14.7A). These fungi break down proteins in dead plant matter and thereby supply their host plant with nitrogen. In return, the plant supplies the fungi with carbon compounds. Arbuscular mycorrhizae are some of the oldest mutualistic associations, originating over 400 million years ago. They are found in over 80 percent of land plants. These mycorrhizae have root hairs that actually penetrate the cells of the plant root. Arbuscular mycorrhizae provide their plant host with phosphorus and receive carbon. Plants with arbuscular mycorrhizae are common in the tropics and grasslands, where phosphrorus is often in short supply.

Lichens result from a close association of fungi with either algae or cyanobacteria. This association is so critical that neither species can live on its own. While the algae and cyanobacteria provide carbon by photosynthesis, the fungi provide protection. Lichen are robust colonists of bare rock and dead wood surfaces.

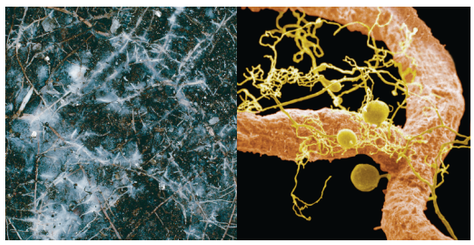
One of the most interesting mutualisms is that between ants from the family *Attini* and fungi from the family *Lepiotaceae*. The ants harvest plant leaves in small disks that they chew to a pulp. They then innoculate the pulp with some of the fungus that they keep growing in underground gardens (Figure 14.7B; see white tufts in the rightmost figure). The fungus is able to digest cellulose in the plant tissue and use it for growth. The ants then harvest fungal tissue for food. This mutualism is thought to have evolved once—over 50 million years ago—and since then, many ant species derived from this common ancestor have continued to cultivate fungus gardens. These gardens are sometimes invaded by a specialized parasitic fungus, *Escovopsis*, which can inhibit the growth of the favored fungi.

Scientists have long noticed a crust coating the cuticle of the *Attini* ants (Figure 14.7B, left figure). This crust is a filamentous bacterium of the genus *Streptomyces*. All species of ant that raise fungal gardens appear to harbor *Streptomyces* on their bodies. Secondary compounds produced by *Streptomyces* have antibacterial properties and are the source of many antibiotics used in medical practice. *Streptomyces* growing on the ants inhibits the growth of *Escovopsis*, but not of many other fungi.

**Nitrogen fixing bacteria.** Bacteria of the genus *Rhizobium* cause legumes to form nodules in their roots, where the bacteria live. The bacteria provide ammonia, a source of nitrogen, to the plants, while the plant provides sugar and protection to the bacteria.



**Mycorrhizal fungi.** These fungi form associations with plant roots. The fungi supply the plants with nitrogen and phosphorus, while the plant supplies the fungus with carbon.



**Lichens.** These are associations between fungi and single-celled algae or cyanobacteria. The algae provide carbohydrate for the fungus, while the fungus provides protection. Neither the fungus or the algae can live on their own. Lichens are abundant in the tundras of the Artic and Antarctic.

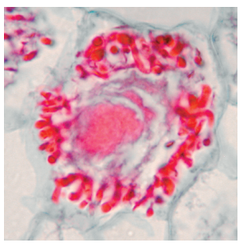


**FIGURE 14.7A Nutrient Mutualisms**

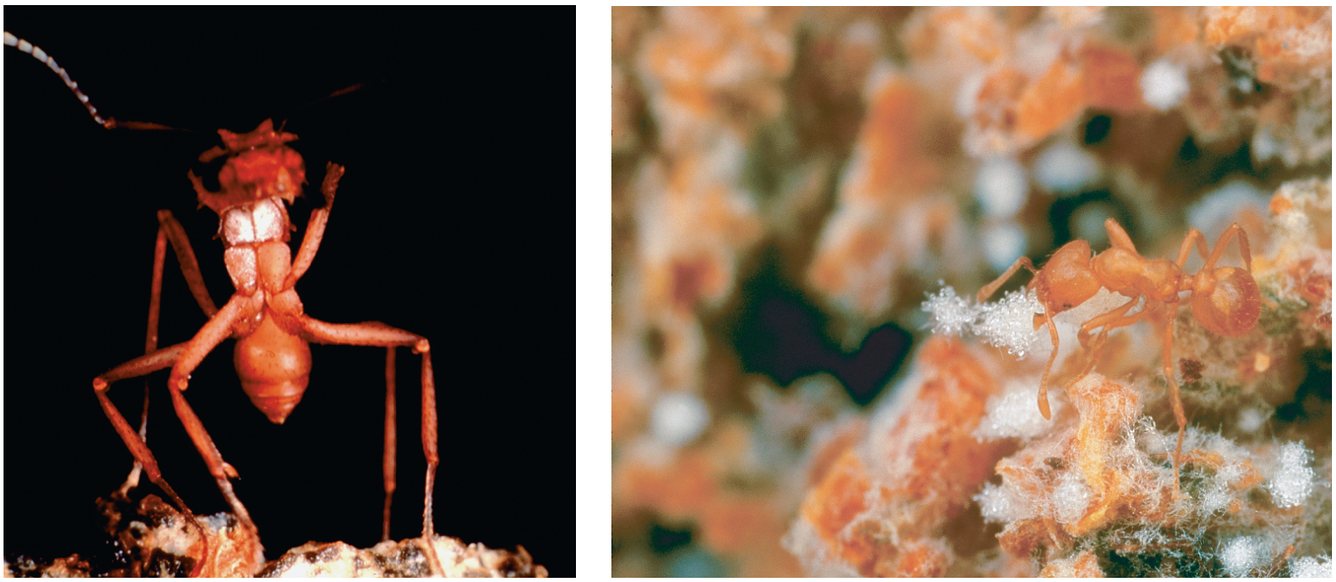


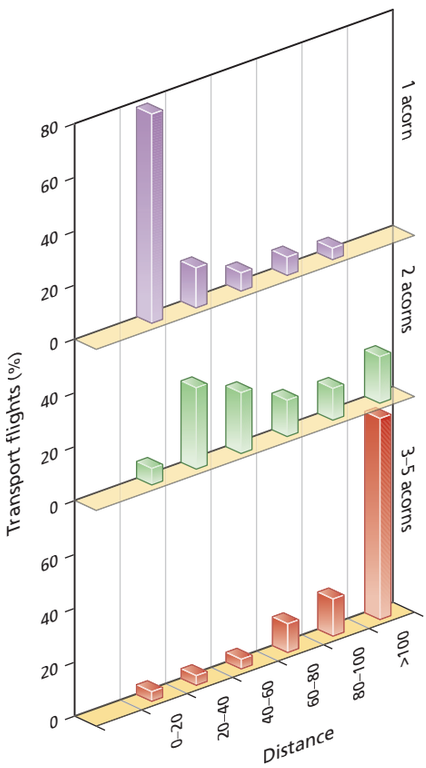
**FIGURE 14.7B** **Fungus Farming Ants**

Thus, it appears as if the ants use *Streptomyces* as a means of controlling the pest species of the fungus *Escovopsis*. *Streptomyces* is faithfully transmitted from parental ants to their offspring by contact, thus maintaining a close and beneficial relationship with these bacteria.

## 14.8 Mutualisms may involve the transportation of individuals or gametes

Pollinators and the plants they visit make up one of the most conspicuous groups of mutualists. Most of us have seen bees visit flowers in the spring and summer months (Figure 14.8A). The goal of the bees is to extract pollen and nectar from flowers. In the course of doing this, they transport flower pollen, sometimes over great distances, and fertilize other flowers. The plant avoids inbreeding and, if it attracts many pollinators, may fertilize large numbers of seeds. Flowers are pollinated by many different animals, including butterflies and hummingbirds (Figure 14.8A). While nutrition is one part of these mutualisms, the transport of gametes is a crucial component.

The transfer of pollen from one plant to another is carried out by a variety of animals including bees (left), hummingbirds (right), butterflies, and other insects. The plant is provided a means of outcrossing and gamete dispersal, while the pollinator receives a nutritional reward from the plant nectar.



The jay Garrulus glandarius collects acorns in its mouth and buries them in the soil. The number of acorns taken on any trips varies. To carry 3–5 acorns, the bird will hold one acorn in its beak and the rest in its throat.

The graphs show that the distance the acorns are moved from the parental tree varies. The jay travels farther, on average, when it carries many acorns.

**FIGURE 14.8A Transportation Mutualisms**

Fertilized seeds may also be dispersed by animal mutualists. The transporting animal often uses the seeds for food. For instance, the jay (*Garrulus glandarius*) can transport up to five acorns at a time (Figure 14.8A). The birds bury these acorns until they are ready to eat them at some time in the future. Individual birds may bury 4600 acorns in a season. Remarkably, the birds appear to recover the seeds from memory, not smell. Acorns that are completely consumed are not dispersed, but many acorns will have sprouted by the time the jay comes back to them. At that point, the jay will eat the soft shoots, but the plant may continue to grow.

Plants that produce large, heavy seeds tend to drop them in the immediate vicinity of the parent tree. This will lead to high levels of competition and low reproductive success for the plant. With the aid of animals that can travel large distances, however, the seeds of a single individual can be distributed to many different locations, some of which are less likely to be as crowded as the immediate vicinity of the parent plant.

Transportation may also involve whole organisms. The carrion beetle, *Necrophorus humator,* carries many small mites on its body (Figure 14.8B). Carrion beetles work cooperatively to bury dead animals that will be used later as food for their young. Although a group of beetles may bury one dead animal, only a single pair of beetles deposits eggs on the buried carcass. The mites hop off the beetles onto the carrion and search out the eggs of the beetle's chief competitor, the fly *Calliphora.* When they find these eggs, the mites pierce their shells and eat the contents.

In experiments where mites were excluded from carrion, beetle larvae were outcompeted by the fly larvae and few beetles survived. Thus, the mites eliminate competitors for the beetles in exchange for transportation to new sites of food.

*Necrophorus humator*

**FIGURE 14.8B Carrion Beetles in Their Underground Brood Chamber**

## 14.9 Mutualism may involve providing protection from predators or competitors

From the examples of mutualism considered so far, we see that the type of benefit gained by each participant in a mutualism may be different. The carrion beetles' mites gain transportation from the mutualism, while the beetles receive protection from a major competitor. For the beetle, this is a substantial benefit. Here we consider some additional examples of mutualisms in which one member receives some sort of protection.

Cowbirds and the oropendula birds of central Panama are part of a mutualism that includes four different species. Cowbirds use oropendulas to raise their young. This type of dependence is called **brood parasitism**. Cowbirds lay their eggs in the oropendula nest, and the oropendula then feed and care for the young cowbirds. Ordinarily oropendulas do not benefit from cowbirds in their nest, because the cowbirds take food that would otherwise go to the young oropendulas. As we might expect, in certain areas of Panama the adult oropendulas are very discriminating, and remove any strange-looking eggs. In these areas, cowbirds often produce eggs that closely mimic the coloration patterns of the oropendula eggs (Figure 14.9A).

In other areas of Panama, cowbirds do not produce mimetic eggs, and the oropendulas are very tolerant of the extra eggs added to their nests by cowbirds. What could explain these two very different behaviors in the same species of bird? It turns out that the discriminating oropendulas almost always occur in areas with large numbers of bees and wasps, while the nondiscriminating oropendulas occur in areas with few bees and wasps. Apparently the presence of bees and wasps keeps away botflies, a parasite of the oropendulas. In areas lacking bees and wasps, there are numerous botflies, and the young oropendulas are infested with these parasites. Fortunately for the oropendulas, the young cowbird chicks actively feed on the botfly larvae they find crawling on their nestmates.

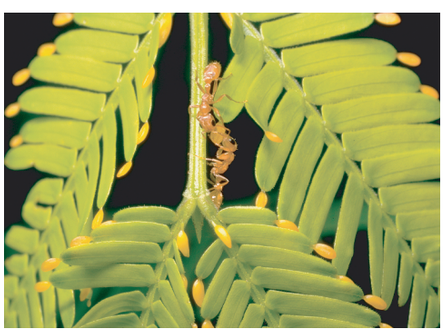
Thus, in botfly-infested areas, the oropendulas improve the chances of their young surviving by raising a few cowbird chicks along with their own. Consequently, these oropendulas do not try to remove cowbird eggs from their nest. But in those areas with large numbers of bees and wasps, cowbirds do not provide benefits to the oropendulas. Instead, they are

**OROPENDULA**
The adult oropendula and its nest are shown on the left.

The oropendula egg on the far left is compared to both types of cowbird eggs.

Cowbird eggs
Mimic
Nonmimetic

Ants and acacias



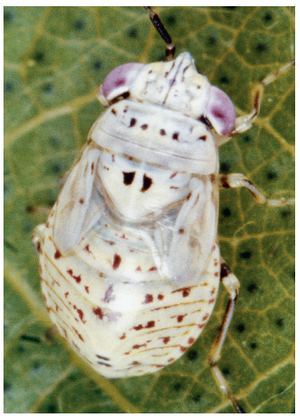
On the left are acacia leaves with the Beltian bodies on the tips. On the right are nectaries at the base of the leaf.

The greatly enlarged thorns of the acacia. The interior is a pithy material that the ants excavate prior to occupying the thorn.

**FIGURE 14.9A Protection Mutualisms**

a drain on parental resources. In these areas, the adult oropendulas attempt to keep their nests free of cowbirds.

Acacia trees in Central America have evolved a number of morphological structures that directly benefit the ants that make their homes in the giant thorns of the acacia. In return, the ants defend the acacias against insect herbivores. The ants also prune neighboring plants that encroach on the acacias' space. At the tips of its leaves, the acacia has specialized structures, called Beltian bodies, that are protein-rich; they are used for food by the ants (Figure 14.9A). The ants also make use of sugar secretions from nectaries at the bases of acacia leaves (Figure 14.9A). But do the ants really benefit the acacia? In one experiment, ants were excluded from some of the branches of acacia trees. Over time, the antless branches were smaller and had fewer leaves than the branches with ants did.



Many plants have small hairs or depressions on the bottoms of their leaves, called domatia (Figure 14.9B). Domatia are found on over 2000 species of plants and seem to be refuges for predatory insects. This suggests that plants may produce these structures to attract insects that will consume herbivorous insects. To test this idea, cotton wool was used to make artificial domatia. Over the course of the growing season, the number of herbivorous spider mites was recorded on plants with added domatia and on those without (see controls, Figure 14.9B). The numbers of predatory bugs on these leaves were also recorded. The results showed a striking decrease in the number of herbivorous insects on the plants with added domatia. Similarly, there was an increase in predatory insects on leaves with added domatia (Figure 14.9B). These results are consistent with the notion that plants have evolved domatia to attract predators and reduce the negative effects of herbivorous insects.

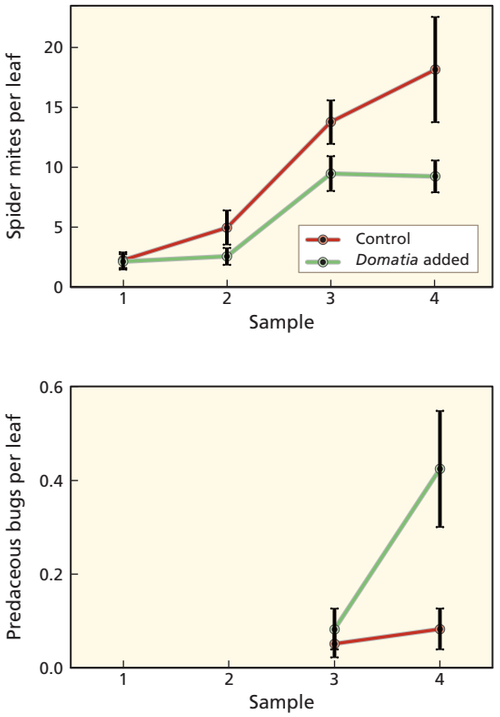



**FIGURE 14.9B** **Adult Big-Eyed Bug on Leaf Domatia**

## 14.10 Mutualisms often evolve as a direct consequence of negative interactions between two or more species

The examples of mutualisms that we have reviewed are remarkable for their diversity of species and mechanisms. These interactions must develop due to the action of natural selection, so it would seem reasonable to suppose that natural selection has left some common thread among these mutualistic associations. In fact, at least two principles serve as common threads among these relationships:

1. Many mutualisms evolve out of initially antagonistic pairwise interactions.
2. Many other mutualisms involve three or more species, including an antagonistic pair.

Now let's consider these ideas in more detail.

We have already reviewed typical negative ecological interactions, including competition, predation, herbivory, and parasitism. Many of these interactions reduce the fitness of at least one species substantially. Thus evolution has often favored traits that help organisms avoid, or reduce the impact of, these negative interactions. The development of alleles that confer resistance to parasites is one example of this type of evolution.

In a similar fashion, as our first principle suggests, many mutualisms are thought to have evolved from an initially negative interaction as a way of reducing the negative effects on fitness. For instance, many insects consume plant spores and seeds. Some plants have reduced the impact of these insects through the evolution of floral nectaries, which provide a food source separate from the plant's pollen. Some insects have also evolved behaviors that help ensure the fertilization of plants (Figure 14.10A). Because a fertilized plant produces more seeds, this translates into more food for seed predators.

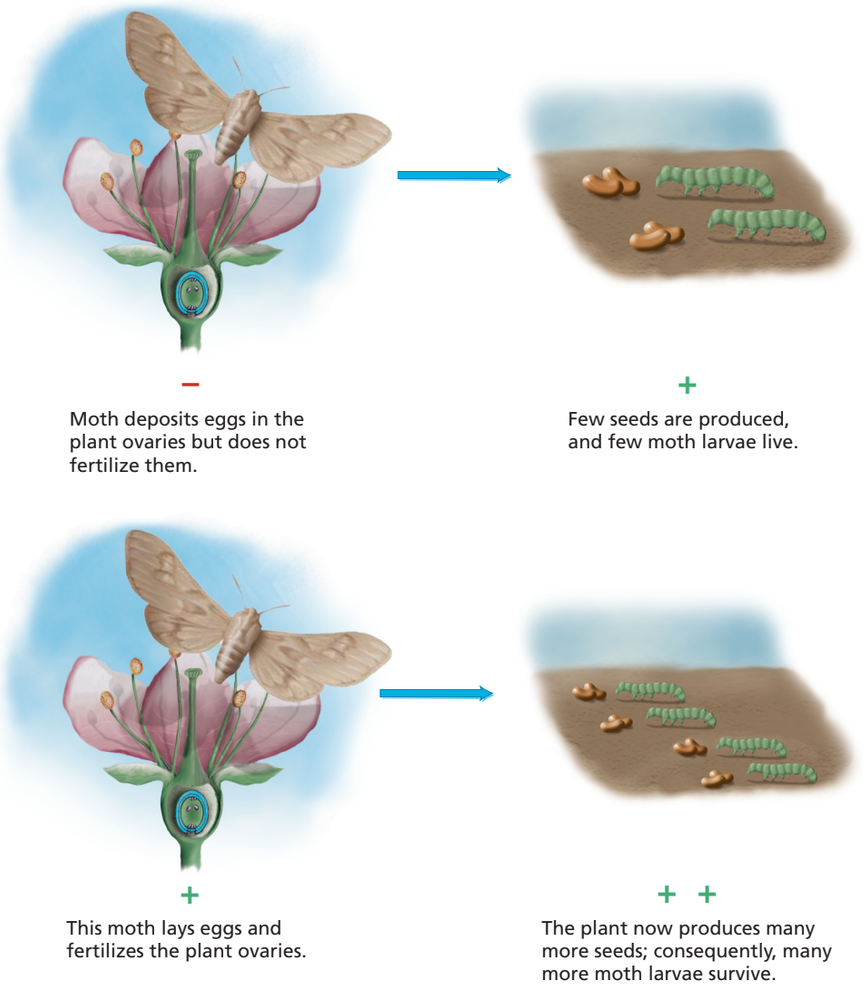



**FIGURE 14.10A Moth-Yucca Mutualism**

Often, the larvae of seed predators consume only a portion of all the seeds produced by a plant. Thus, the net impact of insect fertilization can be positive for both the insect and plant. A good example of this type of relationship is the yucca and yucca moth mutualism (Figure 14.10B).

We have already considered two examples of our second principle in this chapter. Recall that acacias benefit from their interaction with ants because of the beneficial impact of the ants on the negative effects of insect herbivores and plant competitors. The ants effectively reduce the negative impact of other species. We also saw that oropendulas can benefit from raising cowbird chicks that feed on parasitic botflies. However, the relationship between oropendulas and cowbirds can turn from mutualistic to negative as soon as the negative impact of botflies is removed. ❖

(i)

(ii)

**FIGURE 14.10B** (i) A yucca plant in bloom in Eastern Colorado. (ii) The female yucca moth visits the yucca flowers and collects pollen, which it rolls into a ball. The female then visits another yucca flower, where it drills a hole in the ovary wall of the flower and lays its eggs. The female moth then uses the pollen ball to fertilize the flower. The yucca is effectively fertilized, and the moth larvae are guaranteed a good source of seeds.

## 14.11 The evolution of mutualisms should be facilitated when the reproduction of host and symbiont coincides

If mutualisms are beneficial to both participants, shouldn't they always evolve when the opportunity presents itself? The answer is not necessarily. Here we consider a theory about the evolution of cooperation (mutualism) between two organisms that formally have a host-parasite relationship. The interesting aspect of this theory is that, depending on the mode of reproduction, cooperation may or may not evolve.

*How does the symbiont evolve? The answer will depend on the mode of reproduction.*

In Figure 14.11A we show a simple host-parasite system that initially consists of a genetically variable parasite population, indicated by different-colored cells. Two modes of reproduction are considered. With indirect transmission, the parasite infects the host and reproduces or feeds off the host and then leaves. Once free of the initial host, the parasite is free to infect any other suitable host and begin the cycle of growth and reproduction (Figure 14.11A). Direct transmission implies that the reproduction of the parasite is accomplished simultaneously with the reproduction of the host. So all daughters of the host contain replicates or progeny of the original parasite (Figure 14.11A).

We next consider the fitness consequences on host and parasite when the parasite cooperates with the host. By cooperate, we mean that the parasite does not kill or debilitate the host and may do favorable things to its host, like produce a source of nitrogen. For the host, cooperation means not trying to kill the symbiont and providing resources that the symbiont may require for its reproduction. In Figure 14.11B, part (i), we show the evolution (arrows) of the host strategy (cooperate or attack). If the symbiont cooperates, then it will also benefit the host to cooperate and continue to reap these benefits from the symbiont. In this case, the host fitness (green bar) is greater when it cooperates than when it attacks (red bar). Thus, evolution improves fitness when cooperating genotypes of the host become more common. When the symbiont attacks, the host must defend itself. In

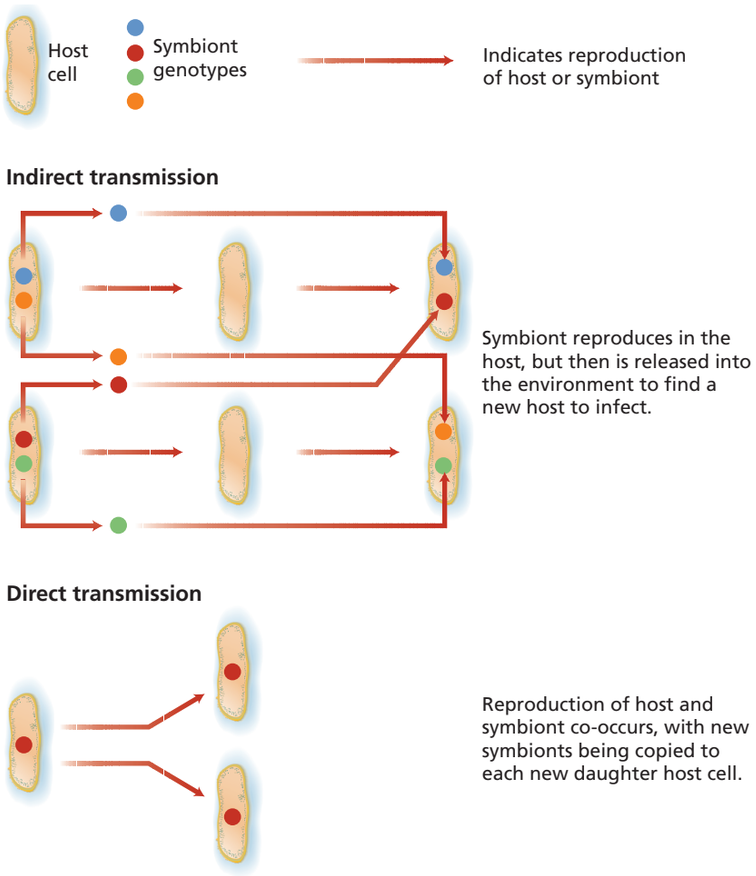
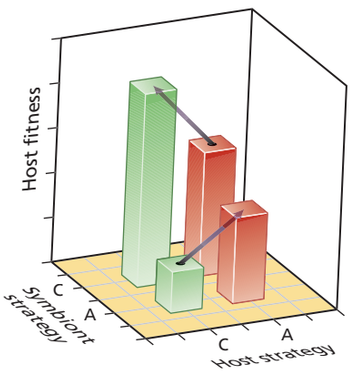



**FIGURE 14.11A Different Modes of Symbiont Transmission**

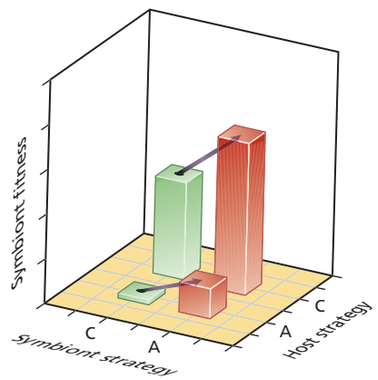
this case evolution will force any host population that cooperates to evolve an attacking phenotype.

How does the symbiont evolve? The answer will depend on the mode of reproduction. Let's first consider indirect transmission, as shown in part (ii) of Figure 14.11B. In this case the symbiont uses a host cell to grow and reproduce temporarily, and then may move on to other hosts. Even if the symbiont cooperated with the host, a second infection from a noncooperating symbiont might kill the host anyway. Thus the symbiont can never be sure of gaining any benefits from cooperation. Because cooperation usually has a cost, the symbiont's fitness will always increase if it adopts an attack stategy, no matter what the host does.

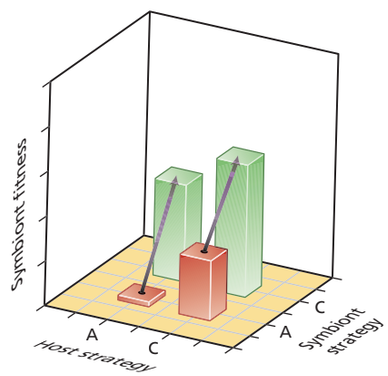
When transmission is direct, cooperation is favored; see part (iii) of Figure 14.11B. In this case, cooperation by the symbiont improves the host's chances of survival, which then directly improve the chances of the symbiont surviving. The symbiont stands to lose only if it attacks its host. Once the symbiont has evolved a cooperative strategy, then based on the previous discussion, we expect the host to evolve cooperation as well. As we will see next, these theories are amenable to experimental tests. ❖




**(i) Host fitness.** The arrows show the direction of evolutionary change. The host and symbiont can assume a strategy to cooperate (C) or to attack (A). If the symbiont cooperates, it will be in the best interests of the host to reap these and additional benefits by cooperating. If the symbiont attacks, then the host must attack to prevent additional damage.




**(ii) Symbiont fitness with indirect transmission.** Because each host may be occupied by multiple symbionts, cooperation by symbiont genotype will be in vain if the host will eventually be killed by a second invading genotype. In this instance, the symbiont will evolve to attach even when the host cooperates.




**(iii) Symbiont fitness with direct transmission.** In this case, the symbiont is transmitted to the daughter host directly. Thus, the fate of the symbiont is more directly related to the fate of the host. Even when the host attacks, the fitness of the symbiont will increase if it cooperates. As we saw in part **(ii)**, once the symbiont adopts a strategy to cooperate, the host will also evolve to cooperate.

**FIGURE 14.11B The Evolution of Mutualism**

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## 14.12 Levels of antagonism between hosts and parasites may depend on the frequency of opportunities for horizontal transfer

We have seen that species interactions may evolve over varied levels of antagonism, at least in theory. But is there evidence for the evolution of different levels of antagonism? In fact, such evidence exists, and it comes from studies of hosts and parasites.

In one type of transmission, called **horizontal transfer**, parasites move from one host to another within the same generation. **Vertical** or **direct transmission** occurs between different generations, with parasites moving from host parents to their offspring. Investigators hypothesized that parasites that depend on vertical transmission would be much more benign than those with many opportunities for horizontal transmission. The reason is that the host needs to survive and reproduce if parasites that rely on vertical transmission are to propagate themselves. Thus, the parasite's fitness is directly related to its host's fitness with vertical transmission.

The hypothesis has been tested with a system of bacteria (*Escherichia coli*) and bacteriophages (R208). (Bacteriophages or simply phages are viruses that infect bacteria.) These phages reproduce continuously in the bacteria, and new phages can pass through the bacterial membrane without killing the bacteria. This particular phage carries a gene for resistance to the antibiotic ampicillin, which makes bacteria infected with phages resistant to ampicillin. Once infected, a bacterium cannot be reinfected by a different phage. On the other hand, these phages typically reduce the fitness of the bacteria by slowing their growth rate.

To test the impact of different types of transmission on parasite virulence, two experimental treatments were set up, and the organisms were permitted to evolve under them. The first treatment, shown in part (i) of Figure 14.12A, was called "high fidelity," because the reproductions of the phage and bacteria were closely linked. These cultures contained antibiotic along with the food medium. As a result, the only bacteria that could survive were those already infected with the phage carrying the resistance gene. Any phage that left bacterial cells could not infect other bacteria, because the other bacteria were already infected. Consequently, the only way for the phage to reproduce was by producing new bacterial cells—in other words, by vertical transmission.

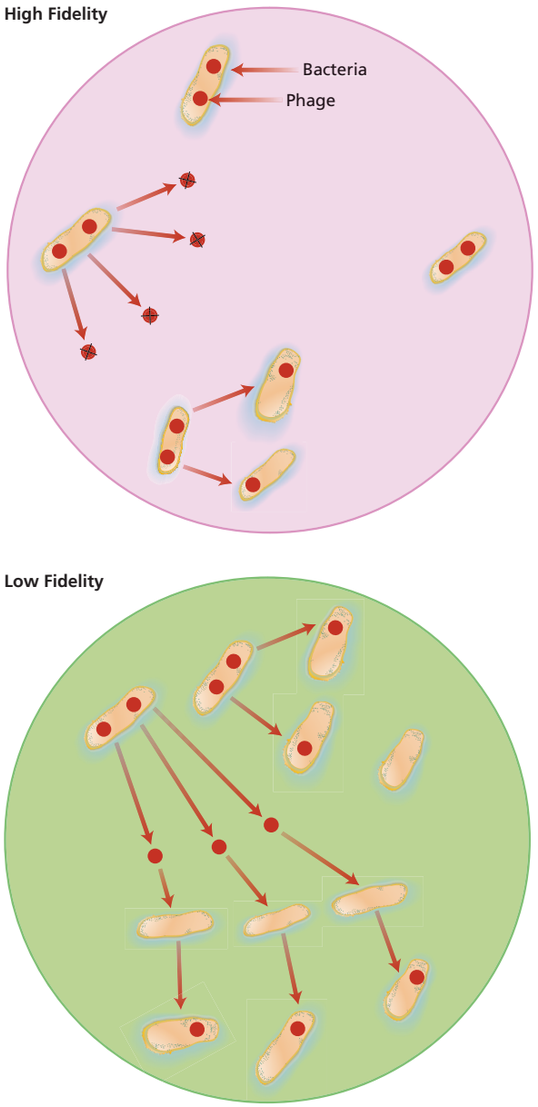
In the second, "low fidelity" treatment, shown in part (ii) of Figure 14.12A, the cultures contained no antibiotic. Uninfected bacteria grew along with the resistant phage-infected bacteria. The phage could reproduce readily by horizontal transmission as well as by vertical transmission.

What were the results of these experiments? The phage-carrying bacteria that evolved under the high-fidelity conditions (which favor vertical transmission) had growth rates 7 to 40 times greater than the growth rates for the phage-carrying bacteria that evolved under low-fidelity conditions (which permit both horizontal transfer and vertical transmission). These results strongly support the notion that the deleterious impact of parasites on the host is greatly reduced when reproduction is vertical.

A second line of evidence for the evolution of different levels of antagonism between host and parasite comes from the study of 11 species of fig wasps (genus *Pegoscapus* or *Tetrapus*) and their nematode parasites (genus *Paradiplogaster*). Let's first review some relevant life history of these wasps and parasites. A fertilized female wasp will enter the part of the flower that will eventually ripen into the fig fruit. This female wasp is called a **foundress**. With pollen she has collected, she pollinates the flower, lays her own eggs, and then dies in the flower. As the fruit and seeds ripen, the wasp offspring mature, mate inside the fig, and then disperse to start the next generation. Some species of wasps have only a single foundress per fig. Other species often have two or more females laying eggs in the same fig. In a single-foundress fig, all offspring are siblings. With multiple foundresses, both full siblings and unrelated wasps develop in the same fig.

Each species of fig wasp has a distinct species of nematode parasite. Within the fig, these nematodes crawl onto newly emerged fig wasps and enter their bodies. They begin to consume each wasp's body and develop into adults. Obviously, the nematodes can have a negative impact on the reproductive capacity of their host wasp. After a female wasp has reached another fig and died, the adult nematodes emerge from her body, mate, and lay eggs that develop alongside the wasp eggs.

In single-foundress figs, transmission of parasites is entirely vertical, from parents to offspring. However, in multiple-foundress figs, nematodes have opportunities for horizontal transfer by infecting wasps that are unrelated to their host. An examination of the number of wasp offspring produced by different species of nematode-infected wasps showed that the greatest numbers of offspring occurred among wasps that usually reproduced as single foundresses, as Figure 14.12B shows. This result is consistent with the idea that parasite virulence will be reduced if parasites are largely dependent on vertical transmission. ❖




**(i)** In these cultures bacteria are grown with antibiotic, so only those carrying a phage can survive. Phages that emerge from the bacteria have no hosts to infect. Thus, the only way for the phage to reproduce is via reproduction of the bacterial host.

**(ii)** In these cultures there is no antibiotic. Phages can emerge from their host and find many other uninfected hosts. The phages can also reproduce via reproduction of their host, but they are not dependent on this mode of reproduction.

**FIGURE 14.12A Experimental Control of Phage Transmission**

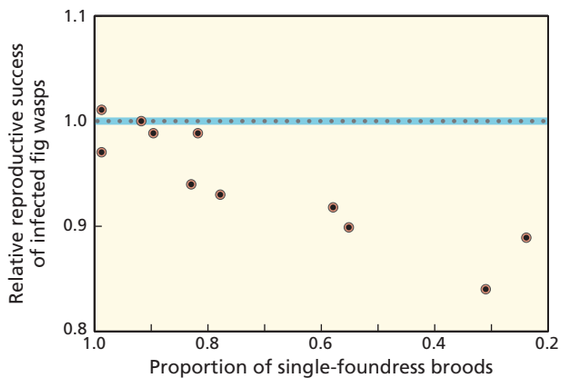



**FIGURE 14.12B Reproductive Success as a Function of the Frequency of Single-Foundress Broods**

# THE COEVOLUTIONARY PROCESS

## 14.13 Coevolution is a complex process that may depend on selection, migration, and genetic drift

We can define **coevolution** as the reciprocal evolutionary change of interacting species. Paul Ehrlich and Peter Raven first used the term *coevolution* in 1964. In their paper, they discussed the evolution of interactions between plants and insect herbivores.

**Coevolution and Speciation:** Ehrlich and Raven noted that many plants produce chemical compounds that are toxic to many but not all insects. They suggested that when a new mutation permits a plant population to produce a toxic compound that no insect can tolerate, the plant can then expand its range into new territories and habitats. The plant population may then form a new species. Sometime later, mutations in an insect population may allow the insects to tolerate the newly evolved plant toxins, permitting the insects to follow the plants into these new adaptive zones. New insect species would eventually appear in those areas where the new plant species appeared.

This is only one way that coevolution may accompany speciation. Bacteria have often become associated with plant and animal cells and are transferred to their host's offspring through the mother's egg. Occasionally these bacteria can cause a reduction in the viability of zygotes, if both egg and sperm are not from individuals that possess these bacterial associates. This type of incompatibility can lead to the reproductive isolation and potential speciation of populations with the bacterial symbionts. For instance, some populations of the fruit fly *Drosophila simulans* are infected with a rickettsia bacterium called *Wolbachia*. These parasites are passed on from the mother to her offspring, no matter what type of male she mates with (infected or uninfected). However, uninfected females that mate with infected males show a severe decline in the viability of their zygotes. Although the sperm of the infected males does not carry the parasite, the parasite alters the sperm in some fashion that makes it incompatible with the uninfected female's egg.

The presence of the *Wolbachia* parasite was first detected in fruit-fly populations of southern California, and through the mid 1980s it spread rapidly to central and northern California (Figure 14.13A). Uninfected females would be nearly reproductively isolated if they moved to an area with a high infection rate.

In the modules that follow, we will see that many bacterial parasites and mutualists have a long coevolutionary history with their hosts. Molecular genetic markers and modern methods of phylogenetic reconstruction reveal the close associations of these bacteria and their hosts.

**Coevolution of Interactions Depends on Selection, Gene Flow, Drift, and Local Extinctions** To understand the coevolution of interactions between different species, we need to consider the distribution of interacting populations. It is easy to think that interactions between coevolving species should evolve at the species level. However, species usually exist as many partially isolated populations. Even though these populations may exchange migrants with neighboring populations, genetic differences are likely to exist between these populations. We saw examples of this type of genetic differentiation in the different populations of flax and rust (see Figure 14.4B). The course of evolution may change as a result of these genetic differences. Local populations may also go extinct and later be recolonized.

The process of recolonization may be important for the long-term evolution of interactions between competing species. Initially, interactions between two close competitors may lead to the local extinction of one of two competing species. However, the opportunity for recolonization of the

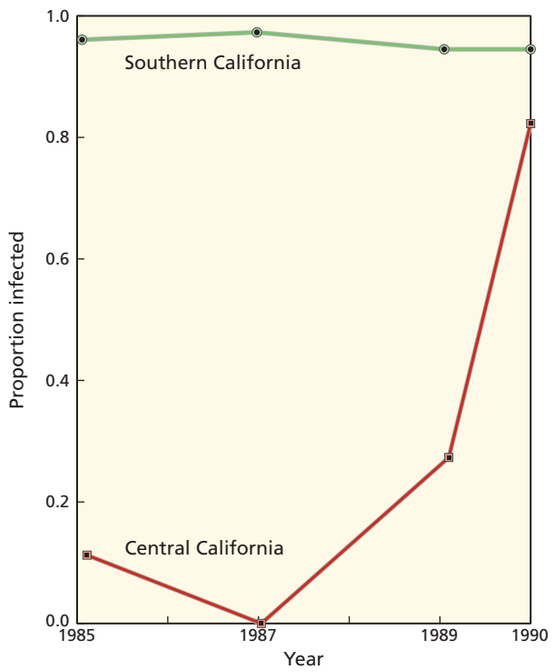



**FIGURE 14.13A Frequency of Infected Individuals in Two California Populations** The infection was first detected in Southern California and rapidly spread north.

habitat from neighboring populations permits continued interaction and perhaps coevolution of these competing species.

The distributions of interacting species may differ. Thus, in part of the range of each species, there may be no coevolution due to the absence of the other species. A good example that we have already discussed is the behavior of oropendulas, which is quite different in regions with bees than in regions without bees (see Module 14.9). Consequently, the coevolution of traits within a species can vary from population to population.

In addition, the physical environment may vary over a species' distribution and lead to different evolutionary outcomes. For instance, in 1954 Thomas Park showed that in hot-moist environments the flour beetle, *Tribolium castaneum*, was competitively superior to its close relative *T. confusum*, but in cold-dry environments *T. confusum* was always competitively superior. It is reasonable to expect that the types of interactions that evolve may be greatly influenced by such variation in the physical environment.

If this geographic view of coevolution is valid, we ought to see examples of local populations within a species that have specific adaptations that permit interactions with a local second species. One example is bees of the genus *Rediviva* and plants of the genus *Diascia* that the bees pollinate in southern Africa. One bee species, *Rediviva neliana*, is widespread and appears to be the primary pollinator of 12 different species of *Diascia*. However, local populations of *R. neliana* usually occur with only one species of *Diascia*. The bees are attracted to the flowers of *Diascia* by an oil that they use for food. To retrieve the oil, the bee must insert its forelegs down the length of the flower's spur, as Figure 14.13B shows. Different species of *Diascia* have different spur lengths, and there is corresponding variation in the length of the foreleg of the local population of *R. neliana*. In fact, the correlation between foreleg length and spur length is greater than 90 percent. Thus, it appears that as a species *R. neliana* does not specialize on any single species of *Diascia*, but at a local population level there has been close coevolution between plant and pollinator.

**FIGURE 14.13B** ***Rediviva neliana*** **Removing Oils from** ***Diascia capsularis*** The flower is cut away to show the foreleg of the bee as it is inserted into the spur of the flower.

## 14.14 Host-parasite phylogenies reveal common histories of speciation

The tight association between the life cycles of hosts and their parasites suggests that their evolution has been closely linked. If a host moves to a new habitat, the parasite will either have to adapt to these new conditions or go extinct. If these types of movements and the subsequent isolation and adaptation are sufficient to create a new host species, it is not unreasonable to suppose that the parasites might undergo similar evolutionary transitions.

These conjectures can be studied by modern techniques of phylogenetic reconstruction. Suppose that molecular genetic information is available for a group of parasites, and that information is used to construct a phylogenetic tree as described in Chapter 2. In Figure 14.14A we show five parasite species labeled by letters *a, b, c, d*, and *e*. Their four hypothetical ancestors are identified with uppercase letters F, G, H, and I.

Each of these parasites can survive on one or more hosts. The parasite tree can be used to develop numerical estimates of similarity among the hosts. As an example, parasites *d* and *e* share ancestors F, G, H, and I, so their hosts should be more similar than the hosts of parasites *e* and *a*. Using only the parasite phylogeny, a host phylogeny can be constructed and then compared to an independently derived host phylogeny. If these two host phylogenies are congruent, as in the example in part (i) of Figure 14.14A, then there would appear to be coevolution of hosts and parasites. That is, as the host speciated, the associated parasites speciated in tandem.

Of course, some parasites may recently have switched to a particular host. In such cases of recent host switching, we would not expect the phylogenies to be congruent, because the parasite is not a recent descendant of parasites from this host lineage. In

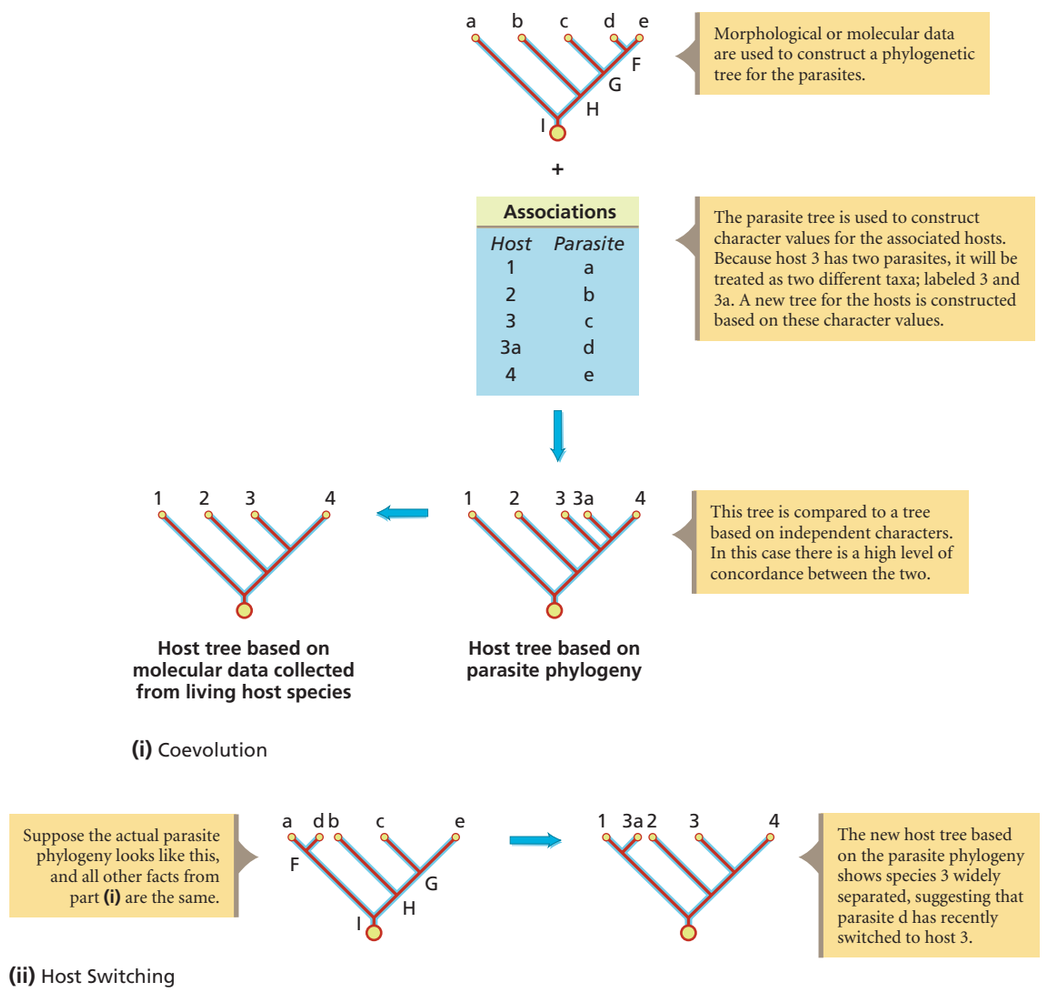



**FIGURE 14.14A** Phylogenies may be used to reveal patterns of host-parasite evolution.

part (ii) of Figure 14.14A, we show a different parasite phylogeny (with the position of species *d* changed) that produces a different host phylogeny. The host phylogeny has host 3 in two very different locations. Because the host labeled 3a is out of its expected position, we would infer that parasite *d* has recently switched to host 3, whereas parasite *c* has coevolved with host 3.

These methods have been used to study six primate species, as shown in Figure 14.14B: humans (H), Old World monkeys (OW), gorillas (Go), orangutans (O), chimpanzees (C), and gibbons (G) and their associated pinworm and tapeworm parasites. The accepted phylogeny of these primates is shown on the right side of Figure 14.14B. The phylogeny based on the parasite phylogeny is shown on the left. Because most primates have several parasites, subscripts are used to show information from different parasites. The black lines in the parasite-derived phylogeny show connections that are congruent with the established phylogeny. The parasites that gave rise to these branches would be candidates for coevolved species. The orange lines show links that indicate possible host-switching events. ❖

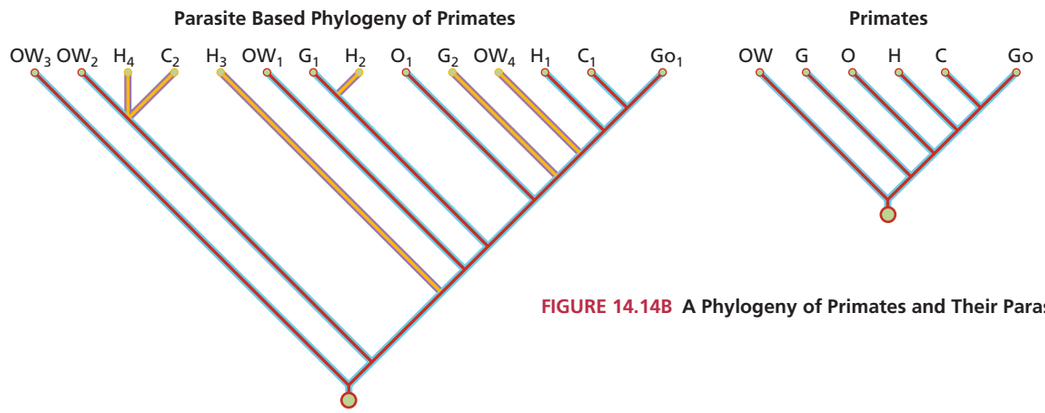



**FIGURE 14.14B** **A Phylogeny of Primates and Their Parasites**

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## 14.15 Coevolution of bacteria and eukaryotic hosts shows little switching between pathogenic and mutualistic lifestyles

Many bacteria have developed close associations with eukaryotic hosts. These bacterial **symbionts** live within the host's body, often within the host's cells. They may have negative or positive effects on the hosts. We have noted previously that many mutualistic interactions develop from previously antagonistic interactions. Is the same true for bacterial symbionts? An analysis of the phylogeny of many pathogenic and mutualistic bacteria (Figure 14.15A) shows that pathogens and mutualists tend to cluster. This clustering suggests that mutualists are more likely to evolve from bacteria that have already established a mutualistic interaction or at least not a pathogenic one. There would appear to be little switching between pathogenic and mutualistic lifestyles.

Why should this lack of switching be the case? We outline a possible explanation in Figure 14.15B. In the course of adapting to life within a host, many genes needed by free-living bacteria are lost. For pathogenic bacteria, this adaptation may often involve the loss of genes for biosynthetic pathways that are unnecessary for bacteria that derive their nutrition from a host. The close adaptation to the host cells may in turn create very small populations of bacteria that rarely come into contact with other bacteria. Many mutualistic bacteria are highly compartmentalized in their host cells and are transmitted maternally by their host from parent to the host offspring. These life cycles reduce the effective population size of the bacteria as well as the opportunities for recombination, making the loss of bacterial genes even more likely. After such severe specialization, the chance that a pathogenic bacteria could become mutualistic is very unlikely, since it now lacks many important genes that might be needed to benefit a host.

As an example, consider aphids, the insect pests of many plant species. Within the body cavity of many aphids is a special structure that holds bacterial symbionts from the genus *Buchnera*. These bacteria are found only in aphids and cannot grow outside of the cells of aphids. The bacteria have the ability to make the essential amino acid tryptophan, which is found in short supply in the aphids' diet. In fact, the *Buchnera* overproduce tryptophan for use by their aphid hosts.

There are many species of aphids with bacterial symbionts that can be compared in a phylogenetic analysis. These analyses show the *Buchnera* symbionts to be closely related to each other, having a common ancestor 150–250 million years ago. ❖

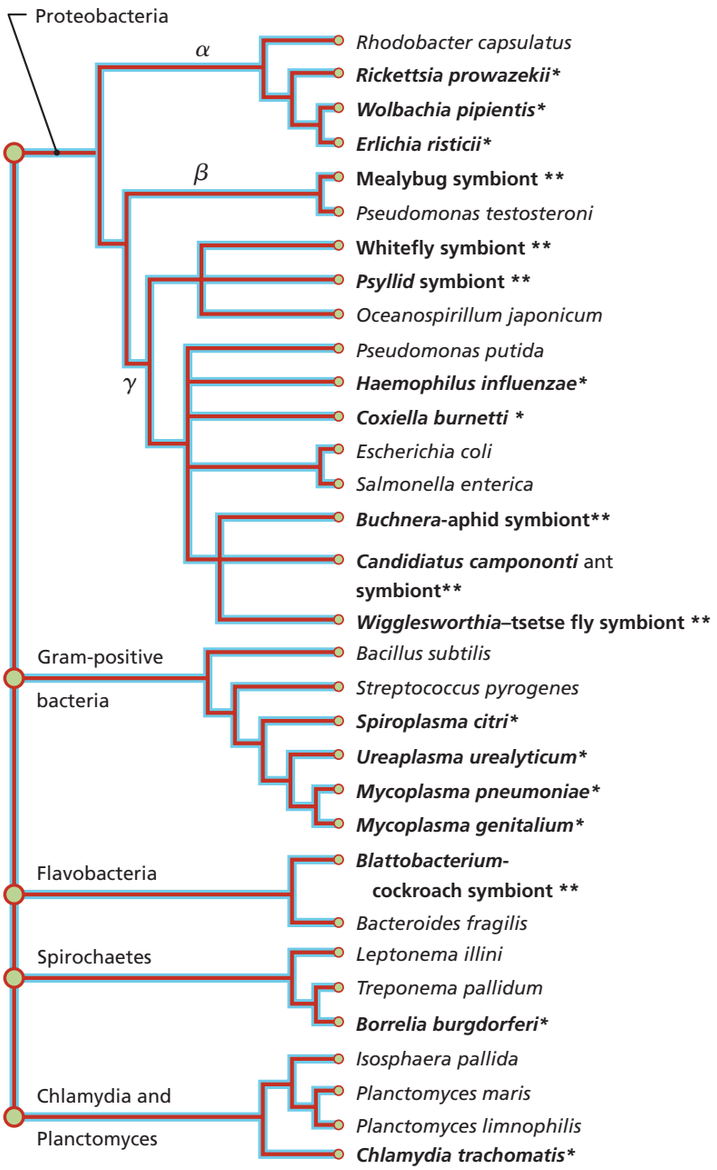


**FIGURE 14.15A Pathogenic and Mutualistic Clades within the Eubacteria** The single asterisk (*) identifies pathogens; the double asterisk (**) identifies mutualists. Symbiotic bacteria are in bold.

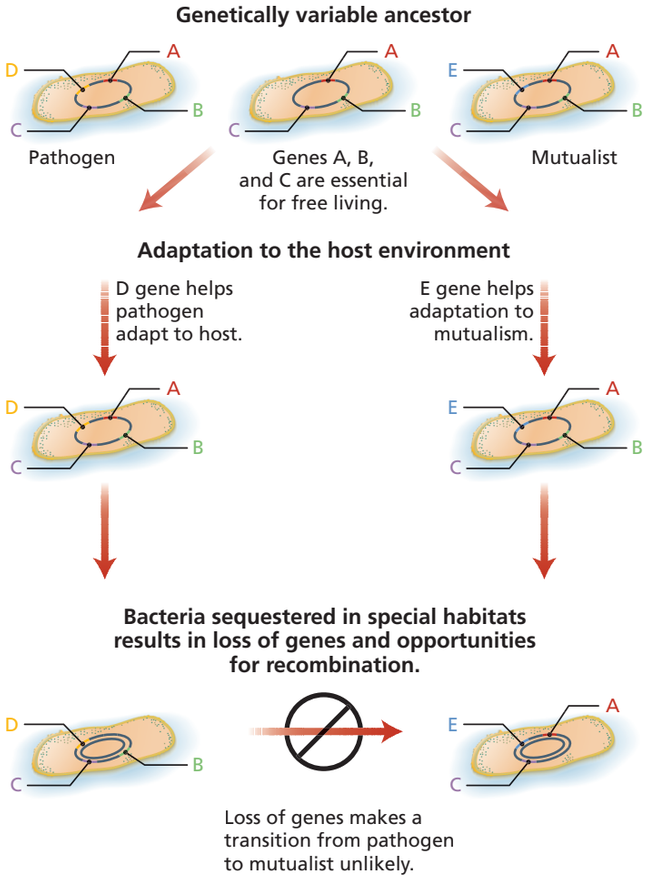


**FIGURE 14.15B** Bacterial adaptation to a host environment makes the transition from pathogen to mutualist unlikely.

## SUMMARY

1. Parasites reduce the survival and fertility of their host organisms. In some instances, parasites kill their hosts.
   - **a.** Virulent parasites can drive their hosts to extinction if they are very effective at finding hosts.
   - **b.** Simple models of host-parasite dynamics show that when the distribution of hosts is clumped, the host-parasite populations are more likely to reach a stable population equilibrium.
2. Many parasites have complicated life cycles wherein they alternately live in a definitive host, where they reproduce, and an intermediate host.
   - **a.** The parasite can find its way to new definitive hosts via the intermediate host.
   - **b.** Given the reduction in fitness caused by a parasite, there is strong selection for host genotypes that can effectively attack parasites. Likewise, the parasite will experience strong natural selection for genotypes that are able to overcome the host's defenses.
   - **c.** Evidence of this evolutionary arms race can be found in natural populations of hosts and parasites today.
3. Not all interspecies interactions involve negative effects on one species. Mutualisms are multiple species interactions wherein all participants experience positive effects from the interactions.
4. There are three basic types of mutualism.
   - **a.** In nutrition mutualisms, one or more species receive some nutritional benefit from the interaction.
   - **b.** Protection mutualisms involve one species protecting a second species from competitors or predators in exchange for some reward.
   - **c.** One species in a transportation mutualism will distribute the gametes or individuals of a second species in exchange for some reward.

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5. Models of the evolution of mutualisms suggest that they are more likely to evolve when the reproduction of a symbiont occurs together with the reproduction of the host. Experiments with bacteria and phages have lent support to this view.
6. Species that have close symbiotic relationships are expected to show some concordance in patterns of speciation. Modern molecular techniques can be used to study this type of close relationship, which is observed in primates and their parasites.

## REVIEW QUESTIONS

1. Why are hosts and parasitoids more likely to stably coexist when the hosts have a patchy distribution?
2. Suggest some reasons to explain why not all flax plants are resistant to all possible genotypes of rust.
3. What aspects of the life histories of mosquitoes and fleas have an important impact on their ability to be disease vectors?
4. Give an example of each of the following: (i) transportation mutualism, (ii) protection mutualism, (iii) nutrition mutualism.
5. What is the difference between direct and indirect symbiont transmission? How do these different modes of transmission affect the evolution of cooperation?
6. Explain and give examples of how coevolution may vary over the range of a species.

## KEY TERMS

avirulence allele
biological control
brood parasitism
coevolution
commensalism
definitive host
direct transmission
foundress
gene-for-gene system
horizontal transfer
host
indirect transmission
intermediate host
mutualism
nutrition mutualism
parasite
parasitoid
protection mutualism
resistance allele
symbiont
symbiosis
transportation mutualism
vector
vertical transmission
virulence allele

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