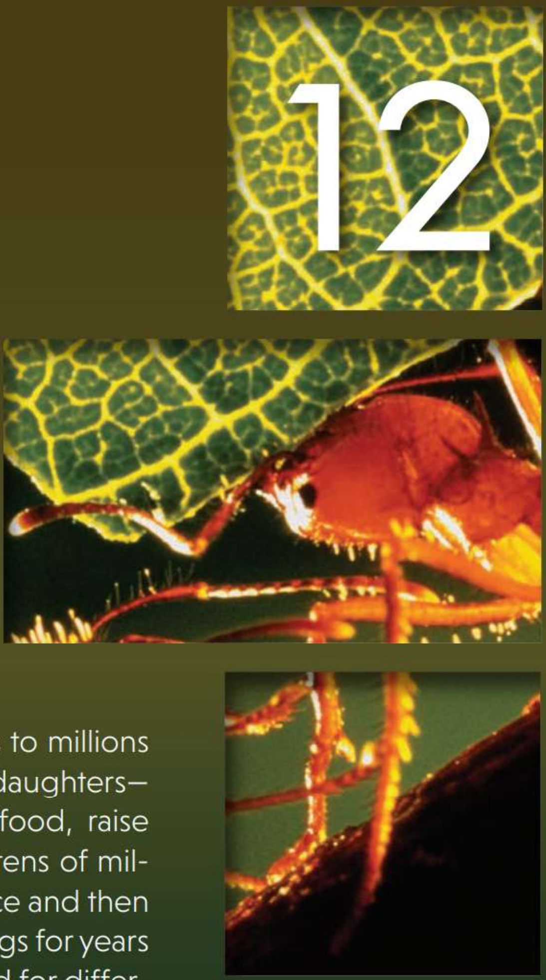
# 12

# Cooperation and Conflict



Look at an ant nest. It is familiar, yet utterly remarkable. Hundreds to millions of individuals—a mother and her many, many nonreproducing daughters—perform a complex ballet of cooperative behaviors to gather food, raise offspring, and defend the nest. Leafcutter ant nests can include tens of millions of individuals, all daughters of a single queen that mated once and then stored sperm in her reproductive tract so that she could fertilize eggs for years afterward. These workers differ in size and form and are specialized for different tasks. Some are soldiers that defend the nest, some cut and bring home pieces of leaves, and some are farmers that chop up the leaves and use them to grow a fungus that provides the colony's food. All these individuals sacrifice their own reproduction to increase the fitness of their queen.

But not all ants are so unselfish. In some species, female workers kill their brothers and nephews, and sometimes even kill their mother [64]. What could possibly lead to the evolution of such extreme forms of altruism and aggression in ants?

As you likely know from personal experience, complex relations within families are not limited to ants. Cooperation and conflict are found at all levels of biological organization [66]. Genes compete against genes, and offspring fight with their parents. Cooperation is also ubiquitous: the functioning of your body depends on harmonious interactions among its cells. The goal of this chapter is to understand when evolution results in cooperation and when it results in conflict.

Leafcutter ants (*Atta*) carry leaf fragments to their subterranean nest, where they are used to grow a fungus that is the ants' only food. Leafcutters are among the thousands of species of social insects with sterile workers that cooperate in highly complex yet cohesive families.

## The Costs and Benefits of Interacting

A useful way to think about the interactions among individuals within a species starts with a table that involves just one actor and one recipient [36]. Interactions are classified by how they affect the fitnesses of the two individuals:

| | | Effect on actor | |
|---|---|---|---|
| | | + | − |
| Effect on recipient | + | Mutualistic | Altruistic |
| | − | Selfish | Spiteful |

If the fitness of both individuals is increased, the action is **mutualistic**. If the actor's fitness increases but the recipient's is harmed, then the action is **selfish**. In the opposite situation, the actor suffers but the recipient benefits, and the action is **altruistic**. Last, if both individuals are harmed, the action is **spiteful**. When the fitness interests of two individuals are different, they are in **conflict**. When one individual's behavior benefits another (as in mutualism and altruism), the behavior is **cooperative**. The evolution of cooperation and conflict depends on when these kinds of behaviors are favored by natural selection. Understanding how they evolve is a major goal in the field of *behavioral ecology*.

Before diving into the details, it is important to understand the vocabulary used in this field. Although conflict and cooperation are studied in organisms ranging from bacteria to plants to vertebrates, most of the research is done on animals. As in much of biology, the language in this field is drawn from everyday speech. When we say that an organism "cooperates" or "cheats," we are describing the fitness effects of its behavior. We do not mean that animals—much less microbes or genes—consciously plan their actions. After all, a "selfish gene" is nothing more than a sequence of DNA base pairs.

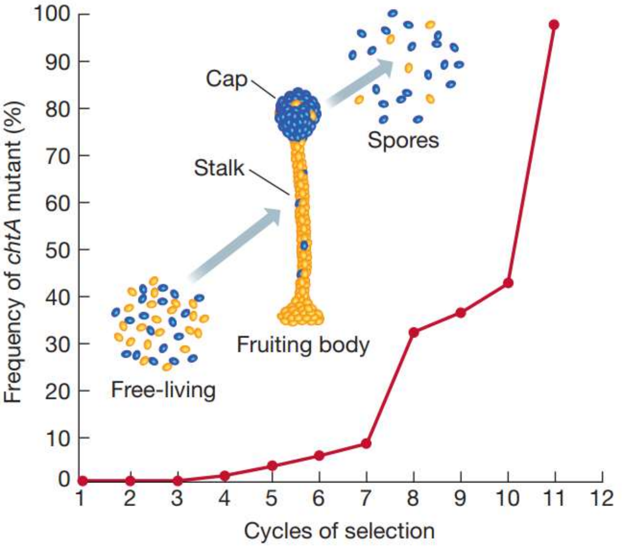


**FIGURE 12.1** In the slime mold *Dictyostelium discoideum*, cells with a mutation at the *chtA* locus are cheaters that behave selfishly. In a mixture of wild-type cells (in yellow) and cells with the *chtA* mutation (blue), the mutant cells become concentrated in the cap and so are more likely to form the reproductive spores. Over the course of 11 growth and development cycles, the frequency of the selfish mutant increased in laboratory culture. (After [19].)

## Social Interactions and Cooperation

It is far from obvious how natural selection could favor cooperation. An individual can "cheat," meaning that it can benefit from the actions of others without providing benefits to them in return. If a cheater has high fitness in a population of cooperators, say because it conserves resources or reduces the risk of harm, then a mutation that causes individuals to cheat will spread, and cooperation can collapse.

The evolutionary puzzle of cooperation is illustrated by the unicellular slime mold *Dictyostelium discoideum* (**FIGURE 12.1**). This species has an odd life history [71]. When food is scarce, individual cells aggregate to form a "slug." The slug wanders a bit, then transforms into something like a very small mushroom with a spherical cap on top of a stalk. Cells in the cap form spores that disperse. The cells in the stalk die without reproducing, sacrificing themselves for the good of the cells that make the spores. Some cells carry a cheater mutation that makes spores but that avoids contributing to the stalk. In laboratory culture, the frequency of this mutation increases over the course of several life cycles [19].

Why, then, hasn't this mutation spread to fixation in natural populations, ending the cooperative behavior of the stalk-forming cells?

By analogy, why don't all ants in a colony reproduce, and why don't all humans cheat on their taxes? Until the 1960s, many biologists supposed that evolution might favor traits that benefit the population or species as a whole, even if they were detrimental to the individual (for example, by forming a stalk or committing suicide to relieve pressure on a scarce food supply). Because selfish cheater genotypes are expected to increase within populations, a trait that benefits the group would have to evolve by selection among groups, rather than by selection among individual organisms within the groups (see Chapter 3). Such **group selection** was thought to involve the increased survival of populations of altruistic individuals, and a high extinction rate of populations of selfish individuals. But simple group selection of this kind is likely to be uncommon, because it requires a high rate of population formation and extinction to counteract the strong fitness advantage of selfish individuals. Evolutionary biologists have discovered a variety of other ways that evolution causes cooperation to evolve at the expense of pure selfishness [47, 68, 81]. A key distinction among them is whether or not interacting individuals are relatives.

**FIGURE 12.2** European starlings (*Sturnus vulgaris*), threatened by a marsh harrier (*Circus aeruginosus*), form a tight flock. Each individual finds safety in numbers, and the density of starlings is greatest in the center of the flock because the safest place for every individual is in the center, behind as many other birds as possible. The harrier is the larger, isolated bird at right. Courtesy of Dr. Giangiorgio Crisponi.

## Cooperation among Unrelated Individuals

Natural selection favors the evolution of cooperation among unrelated individuals when the fitness costs of cooperation are equaled or surpassed by the direct fitness benefits, that is, an increase in fitness of the individual performing the behavior. An individual that joins a group can lower its risk of predation simply by finding safety in numbers [37]. This explains why birds fly in flocks, fishes swim in schools, and ungulates roam in herds (**FIGURE 12.2**). Predators such as wolves hunt cooperatively, and share prey that a single individual could not capture by itself [16]. These behaviors are beneficial to both the actor and the recipient.

The benefits of cooperation are sometimes delayed. In the lance-tailed manakin (*Chiroxiphia lanceolata*), a subordinate male forms a long-lasting association with an unrelated dominant male. The two males in this team court females by an elaborate display that they perform at the same site year after year (**FIGURE 12.3**). The males leapfrog over each other frenetically, making synchronized vocalizations as they do. Females strongly prefer teams with highly coordinated displays, and they almost always mate with the dominant male [21, 53]. When the dominant male dies, the subordinate inherits the display site, is joined by another male, and becomes the dominant male—although he may have had to wait as long as 13 years to do so. The benefit of joining a dominant male is delayed and uncertain, but a subordinate male has no choice if he is to have any chance of reproductive success.

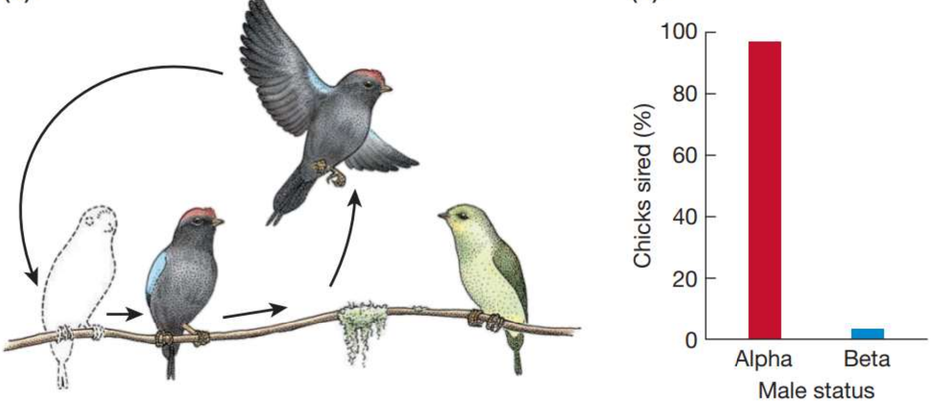


**FIGURE 12.3** (A) Two male lance-tailed manakins (*Chiroxiphia lanceolata*) perform a cooperative leapfrogging courtship display to a female. The dominant male obtains all, or almost all, copulations. (B) The reproductive success of dominant (alpha) males, as determined genetically, is much higher than that of subordinate (beta) males. (A after [2]; B after [21].)

## *Reciprocity*

Robert Trivers suggested that cooperation can evolve when one individual provides a fitness benefit to another, as long as the second individual is likely to return the favor later [74]. This kind of cooperation is called **reciprocity**. It can evolve if there are repeated interactions between individuals, if individuals recognize and remember each other, and if the benefit received is great enough to outweigh the cost of providing the benefit to others [47]. Reciprocal cooperation is known in many species of fishes, birds, and mammals [73].

Mathematical models predict the conditions under which reciprocity is favored by natural selection. While cooperative behaviors in most organisms are innate and involve no active thought, those behaviors have close parallels to some kinds of human interactions that have been well studied by economists. The famous evolutionary biologist John Maynard Smith introduced **game theory** from economics to the study of the evolution of social behaviors. Some situations that occur in humans and other animals are described by the "prisoner's dilemma" [4]. Here each of two individuals will do best by acting selfishly, but if both individuals act selfishly, they will do worse than if they both cooperate (**BOX 12A**). Game theory models show that selfish behavior is favored if individuals interact only once, but that repeated interactions can favor cooperative behavior. Thus, reciprocity can be favored when the association between individuals is so long-lasting that the benefits that each partner provides to the other feed back to the individual's own benefit [68].

Vampire bats (*Desmodus rotundus*) risk starvation if they do not get a blood meal every night (**FIGURE 12.4A**). Unrelated individuals form long-term social bonds and regurgitate blood to members of their group [83]. As a result, individuals with friends are less likely to starve. Social bonding also pays off in primates (**FIGURE 12.4B**). Offspring of female yellow baboons (*Papio cynocephalus*) that have strong bonds with other females survive better than offspring of females with weaker bonds [69]. Cooperation was able to evolve in vampire bats and baboons because individuals have long histories of repeated interactions.

Mathematical models also show that, under some conditions, cooperation is enhanced if one of the partners in an interaction punishes selfish individuals:

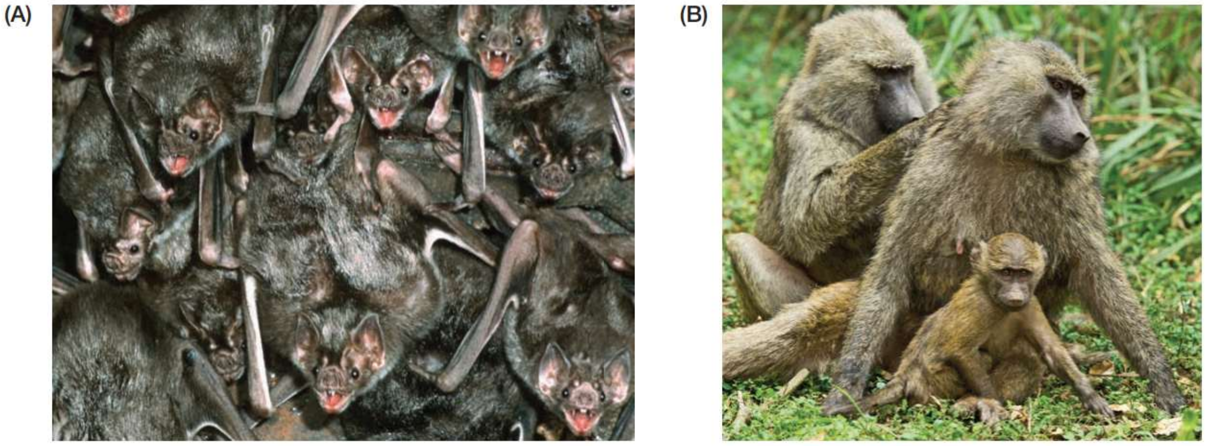


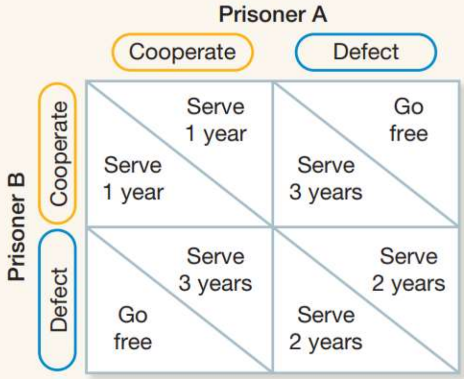
**FIGURE 12.4** Mammal species that display reciprocity between individuals. (A) The vampire bat *Desmodus rotundus* forms roosting groups in which members that have fed successfully sometimes feed regurgitated blood to other members of the group. (B) Among primates, such as these yellow baboons (*Papio cynocephalus*), social alliances between individuals are reinforced by activities such as grooming.

BOX 12A

## Evolutionarily Stable Strategies

An important tool used to understand the evolution of cooperation is the concept of an **evolutionarily stable strategy**, or **ESS**. This is a behavior (or "strategy") with fitness greater than, or at least equal to, that of any other possible behavior if all individuals in the population behave that way. If a mutation causing a different behavior appears in a population that is at an ESS, it will not have a fitness advantage and thus will not spread. The population's behavior is therefore evolutionarily stable.

Theoretical biologists have studied how and when cooperation will evolve by determining the ESS for simplified scenarios that capture the essence of common types of social interactions. A famous example of one of these scenarios is the "prisoner's dilemma." Two gang members are caught and isolated so that they can't communicate with one another during interrogation. The jailers explain to the prisoners their options. If they both defect from their partnership and admit the terrible things they did together, they will each serve 2 years in prison. If they both cooperate with each other by refusing to talk to the authorities, they will each serve only 1 year. The last possibility is that the prisoners do different things. The prisoner who defects will be rewarded by immediate release, while the prisoner who tries to cooperate with his partner by remaining silent will be punished with 3 years in prison. These outcomes are summarized in this table:



| | | Prisoner A | |
|---|---|---|---|
| | | Cooperate | Defect |
| Prisoner B | Cooperate | Serve 1 year<br>Serve 1 year | Go free<br>Serve 3 years |
| | Defect | Serve 3 years<br>Go free | Serve 2 years<br>Serve 2 years |

What should they do? Looking at the table, we see that Prisoner A does better if he defects than if he cooperates, no matter what Prisoner B does. The best strategy is therefore to defect, and if both do that they will spend 2 years in prison. The situation is a dilemma, however, because the prisoners could do better if they both cooperated, since then they would each serve only 1 year.

What does the prisoner's dilemma tell us about the evolution of cooperation in animals? In some species, individuals work together to hunt, attract mates, and raise families. We can use a table like this one to show the fitness effects of the different possible behaviors. Given that table, a mathematical analysis can be used to find the ESS, which predicts the behavior we expect to see in that population. If a single interaction between two individuals has the potential outcomes shown in the table, the ESS is for both to defect. We therefore predict that natural selection will not favor cooperation in single encounters between unrelated individuals.

The situation becomes more interesting, however, if the same individuals interact repeatedly. Imagine that a mated male and female are caring for their eggs in a nest. Each day, a predator attempts to take some of the eggs. Should the male and female cooperate by defending the nest, which risks injury, or should they defect and run from the predator? After a few days, the male and female learn whether their partner tends to cooperate or to defect, and each can adjust his or her behavior accordingly. Mathematical analysis shows that this situation is much more favorable to the evolution of cooperation. One behavioral strategy that has high fitness is called "tit for tat" [4]. Here each individual starts by cooperating, and then does whatever the other did in the previous round. Another strategy with high fitness is for each individual to repeat its previous action whenever it has done well in the last few interactions, but to change if not [57]. These theoretical results help explain why humans and other animals are much more likely to cooperate when they interact repeatedly with the same individuals.

punishment alters the ratio of benefit to cost [22, 28]. The punishing partner may impose "sanctions," terminating the relationship by withholding benefits from the other partner. Some of the best evidence is found in eusocial insects, as we will see shortly. One role of the immune system is to kill cancer cells, which are selfish members of the otherwise cooperative society of cells that make up an animal's body.

## Shared Genes and the Evolution of Altruism

Many species provide care for their offspring, often at great effort and risk to their own survival. Mammals and birds feed their young and in some species (including our own) teach them how to survive. Grasshoppers invest energy in their eggs and invest time by burying them for safety. Plants endow their embryos with endosperm and surround them with husks, fleshy fruits, and structures that aid dispersal. In short, parents are altruistic. They enhance the fitness of other individuals—their offspring—at a cost to themselves.

Doesn't this altruism violate the selfish principle of natural selection? "The answer is obvious," you reply. "Fitness is measured by successful reproduction, and what would the mother's fitness be if all her offspring died?" That is precisely the solution. A gene can leave more copies of itself to the next generation if it increases the odds that the individual's children will survive.

This logic can be extended to more distant relatives. J. B. S. Haldane, one of the founders of evolutionary genetics, was once asked if he would give his life to save a drowning brother. He replied, "No, but I would to save two brothers or eight cousins." Haldane (who was a genius) had rapidly calculated the conditions under which natural selection will favor saving drowning relatives.

In a groundbreaking paper, William D. Hamilton reasoned that from a gene's point of view, fitness has two components [36]. Consider an allele that causes individuals to act altruistically, for example by saving drowning brothers. An individual carrying the allele can pass copies of it to his or her own children. This is the allele's **direct fitness**. The allele can also pass extra copies of itself to the next generation as the result of the increased fitness of relatives that benefit from the altruistic individual's actions. This is the allele's **indirect fitness**. The allele's **inclusive fitness** is the sum of its direct and indirect fitness. These concepts have been important in understanding not only cooperation, but also parent-offspring conflict, spite, sex ratios, dispersal, cannibalism, genomic imprinting, and other phenomena [47, 81, 1, 7].

The most common way that altruism between related individuals evolves results from **kin selection**, a type of selection based on indirect fitness. An allele that causes an individual to act altruistically decreases the fitness of the actor, but that act increases the fitness of others. If they are related to the actor, then more copies of the allele can be passed to the next generation, and the altruistic behavior can spread through the population.

This logic is formalized in **Hamilton's rule**. It states that an allele that causes an altruistic behavior will spread if the following condition is met:

$$r\,B > C \tag{12.1}$$

The left-hand side of this inequality represents the effect of the behavior on the indirect fitness of the allele. The quantity $r$ is the **relatedness**, also known as the coefficient of relationship. (Be aware that $r$ is used elsewhere in this book to represent recombination rates and correlation coefficients.) Relatedness is easiest to calculate when the allele is rare. In that case, $r$ is the probability that if the allele is carried by the actor, then it is also carried by the recipient of the altruistic behavior. $B$ is the *fitness benefit to the recipient*, that is, the average increase in the number of offspring that the recipient will have as a result of the altruistic behavior. From the allele's point of view, the altruistic behavior increases its fitness through the recipient just as if it caused the actor to have $r\,B$ more children of its own. The right-hand side of Inequality 12.1 represents the effect of the behavior on the direct fitness of the allele. $C$ is the *fitness cost to the actor*, that is, the decrease in the number of offspring that individual will have as the result of acting altruistically.

## BOX 12B

## Calculating Relatedness

The relatedness between the copies of a gene in two individuals, symbolized by *r*, depends on how those individuals are related and how the gene is inherited. Relatedness is simplest to calculate when an allele for altruism is rare. In that case, *r* is the probability that if an actor carries the allele, then the recipient also carries it. For the autosomes of a diploid species (Figure 12.B1), the alleles in a mother are related to those in her offspring, with *r* = 0.5. The alleles in a given daughter are also related to those in her brothers and sisters, with *r* = 0.5. Patterns of relatedness are different in hymenopterans, which are haplodiploid (Figure 12.B2). Alleles in a mother (queen) are related to those in her sons and daughters by *r* = 0.5. Males are haploid, have no father, and inherit all of their genes from their mother. If a worker (female) carries a rare allele, the only way her brother can also carry it is if she inherited the allele from their mother (probability = 1/2) and if the mother passed the allele to her son (probability = 1/2). The alleles in the brother are therefore related to those in the worker by *r* = 1/2 × 1/2 = 0.25. However, there are two ways that a new queen (the worker's sister) might also carry the worker's allele. The worker might have inherited the allele from their mother (with probability = 1/2), and if so the mother might have passed it to the sister (with probability = 1/2). Alternatively, the worker might have inherited the allele from their father (with probability 1/2). If so, then her sister is certain to carry it also, because males are haploid and always transmit all of their genes to all of their offspring. The alleles in the new queen are therefore related to those in the worker by *r* = (1/2 × 1/2) + 1/2 = 0.75.

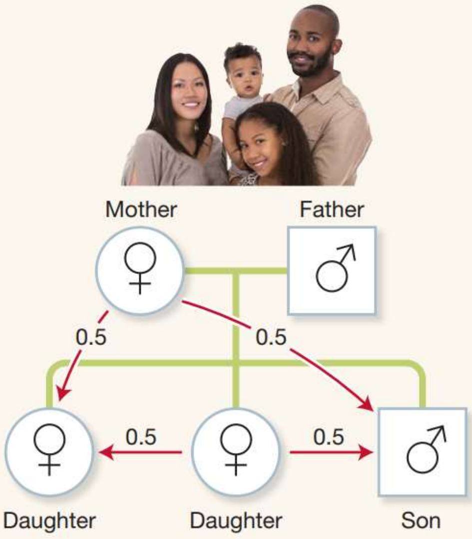


**FIGURE 12.B1** Relatedness in diploid species.

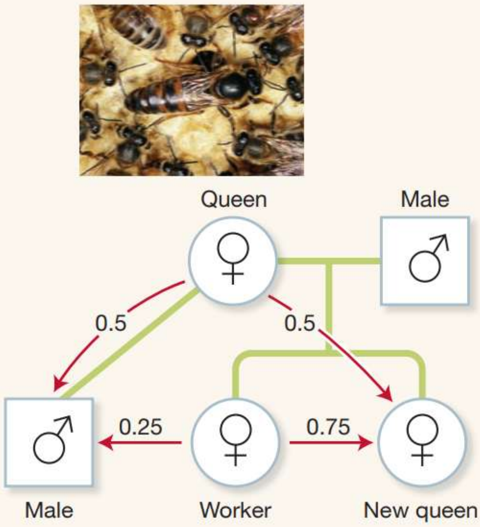


**FIGURE 12.B2** Relatedness in haplodiploid species.

The overall effect of an allele on its inclusive fitness is the sum of the allele's indirect and direct effects, which is: $r B - C$.

In short, Hamilton's rule says that an allele will spread if the increase in indirect fitness outweighs the loss of direct fitness caused by the altruistic behavior. In fact, the rule applies to all behaviors, not just altruistic ones. It even works when *B* or *C* is negative, as when the actor benefits directly (in which case $C < 0$).

To make these ideas concrete, consider an autosomal locus in a female of a diploid species (**BOX 12B**). If she carries a rare allele for an altruistic behavior, there is a probability of 1/2 that it came from her mother and an equal chance that it came from her father, so a female's relatedness to each of her parents is $r = 1/2$. What about her relatedness to her siblings? No matter which parent the female inherited the allele from, there is a chance of 1/2 that a brother or a sister also inherited the allele, and so she is again related to them by $r = 1/2$. More distant relatives have lower relatedness. For example, the probability that a full cousin also carries the allele is $r = 1/8$. (Do you now understand Haldane's comment about saving drowning brothers and cousins?)

Inequality 12.1 implies that the more distantly related the beneficiaries are to the altruist, the greater the fitness benefit to them must be for the altruistic trait to spread. If an allele causes females to give care to random offspring in the population, it will not increase in frequency. That is because the fitness of all genotypes would be enhanced equally by the altruism, while the allele would still suffer a direct fitness cost. In terms of Inequality 12.1, the relatedness of random offspring to an altruistic female is $r = 0$. If there is any cost to providing care, then $C > 0$ and so the condition for the spread of the allele is not met.

Thus kin selection can favor altruism only if individuals are more likely to help kin than nonkin. Altruism can be directed toward relatives when individuals are able to distinguish related from unrelated individuals. Remarkably, female Mexican free-tailed bats (*Tadarida brasiliensis*) can find their own pups in caves that harbor millions of young bats roosting at a density of 4000 per square meter [52]. The cues used by some species to recognize kin are genetically based, while in others the cues are caused by a shared environmental imprint. Individual colonies of many ants have a distinctive odor. Nestmates cooperate with each other and battle with ants from other nests, and they discriminate between friend and foe using the odors [85].

Even if individuals cannot identify kin, they can preferentially express altruism toward kin if relatives tend to be near each other, and this can enable altruism to evolve. For example, local colonies and troops of many primates, prairie dogs, and other mammals are composed largely of relatives, and these species perform altruistic behaviors, such as giving warning calls if they see a predator [50].

In the wild turkey (*Meleagris gallopavo*), males cooperate in their mating displays (**BOX 12C**). Some males court females solo, but others form teams of brothers that are much more successful [46]. In teams of two males, only the dominant male fathers offspring, and his subordinate brother does not mate. Then why should a male choose to be a subordinate? Consider his options. If he chooses to be a subordinate, he will forgo the matings he could have if he were solo. This is $C$, the cost of his altruistic behavior. But by displaying with his brother, the subordinate increases his brother's mating success, which represents the fitness benefit to his brother, $B$. That results in a gain of indirect fitness for the subordinate, $r\,B$, that more than offsets the cost. Hamilton's rule is satisfied, and so an allele that causes a male to display as a subordinate will spread. On average, each copy of the allele will leave 0.8 extra copies of itself to the next generation as the result of altruism. Box 12C explains the calculation in detail.

The deer mouse *Peromyscus maniculatus* is sexually promiscuous, and sperm of several males compete for fertilizations in a female's reproductive tract. Sperm gain inclusive fitness by teaming up to form aggregates with other sperm from the same male, making it more likely that one of them will fertilize an egg. Kin selection theory predicts there should be no advantage to aggregation in species without sperm competition. That prediction is confirmed: the sperm from the same male do not preferentially aggregate in a closely related monogamous species (*P. polionotus*) [25].

Even bacteria can cooperate. *Pseudomonas aeruginosa* requires iron, which it takes up from its environment by binding iron atoms with proteins called siderophores that the bacteria excrete into their environment. Bacterial cheaters, however, take up iron bound with the siderophores produced by others, and they avoid paying the cost of producing siderophores themselves [34]. The outcome of competition between genotypes that excrete siderophores (cooperators) and genotypes that do

## BOX 12C

## Altruistic Mating Displays In Turkeys

Wild turkeys (*Meleagris gallopavo*) display in teams of dominant and subordinate brothers. Dominant males have higher fitness (measured by the average number of offspring) than subordinates and males that display solo. Subordinate males increase the reproductive success of their dominant brothers from 0.9 to 7, which gives a benefit to the dominants of $B = 7 - 0.9 = 6.1$ offspring. The cost to a subordinate of teaming up with his brother is the subordinate's loss of direct fitness from not displaying solo: $C = 0.9$ offspring. A subordinate does not mate, so his direct fitness is 0. Genetic analysis shows that, on average, a subordinate and dominant male are related by $r = 0.42$. (It seems not all pairs are full brothers.) The indirect fitness gained by a subordinate through cooperating with his dominant brother is $rB = 0.42 \times 6.1 = 2.6$ offspring. That value is greater than the cost, $C$, and so Hamilton's rule is satisfied: an allele that causes a male to join his brother as a subordinate will spread. The altruistic behavior increases the allele's inclusive fitness by $rB - C = 1.7$ offspring. Each of those offspring has a probability of 1/2 of inheriting the allele, so each copy of the allele leaves $1/2 \times 1.7 = 0.8$ extra copies of itself to the next generation as the result of its altruistic behavior.

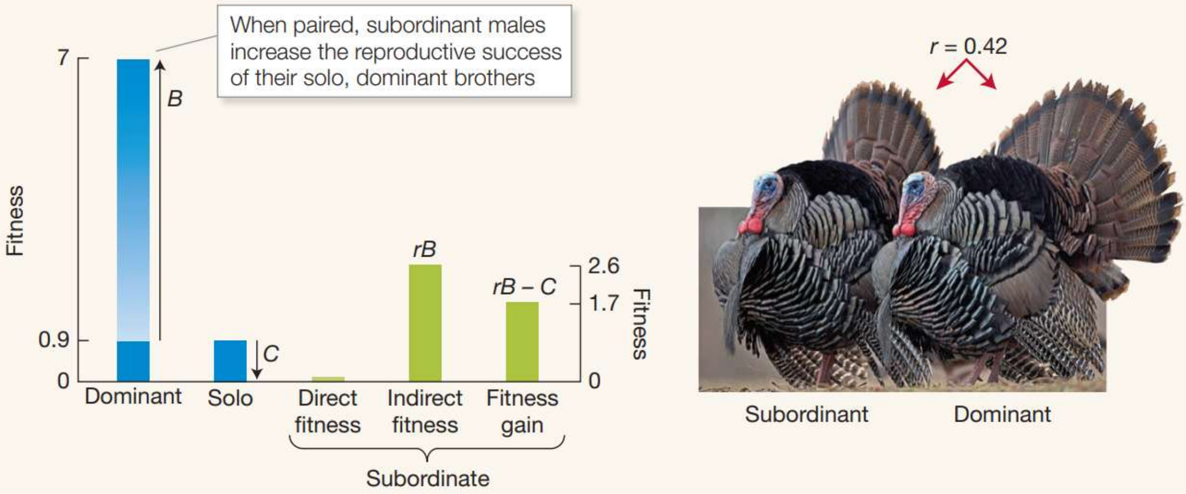


**FIGURE 12.C1** (After [46].)

not (cheaters) depends on the environment they grow in (**FIGURE 12.5**). The bacteria can be maintained in the lab under conditions to produce either high or low relatedness between them, and either strong or weak competition between relatives. When the bacteria have low relatedness and are in a strongly competitive environment, the cheaters win. But when the bacteria are closely related and are in a weakly competitive environment, the cooperators can drive the cheaters to extinction.

Another pathway to the evolution of altruism is by the "green beard" effect, which occurs when a single gene codes for a phenotypic trait that enables its carrier to recognize and help other individuals with the same trait (for example, a green beard) [20]. This situation is uncommon in nature, but a few cases have been described [31]. One comes from the slime mold that we discussed earlier (see Figure 12.1). The *csA* gene encodes a cell adhesion protein that binds to the same protein in the membrane of other cells. This acts as a green-beard recognition system: cells with *csA* adhere to each other and pull themselves into aggregations. Cells that have the *csA* gene knocked out act as cheaters. If they manage to get into an aggregation with cells that have *csA*, their lower adhesion makes it more likely that

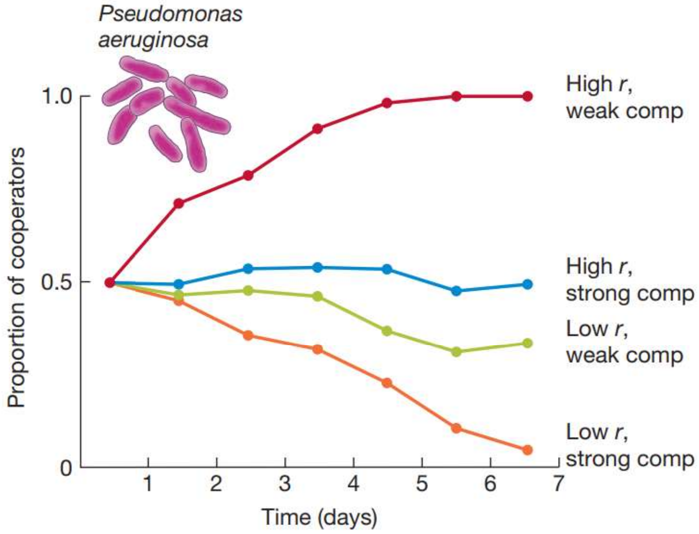


**FIGURE 12.5** Evolution of cooperation in an experiment with the bacterium *Pseudomonas aeruginosa*. The cooperator genotype excretes siderophores, which are used by neighboring bacteria to take up iron from the medium. The cheater genotype does not excrete siderophores, but benefits from the siderophores made by others. Bacteria evolved in cultures that were maintained with either low relatedness (low *r*) or high relatedness (high *r*), and with either weak competition (weak comp) or strong competition (strong comp) between relatives. The cooperator genotype increased in frequency when there was high relatedness and weak competition. (After [34].)

they will end up as spores. Cells with the *csA* gene are more altruistic, and they are able to prevent the cheaters from spreading in the population because they are more effective at recognizing each other and forming aggregations [62].

### *Spite*

A behavior is spiteful if it harms both the actor and the recipient. Spite is the antithesis of altruism, but inclusive fitness theory predicts that spiteful traits can evolve. The conditions needed are that the actor be *less* closely related to the recipient than to an average member of the population, and that *harming* the recipient enhance the fitness of other individuals in the population that are more closely related to the actor [82].

An example of spite comes from bacteriocins, toxins that are secreted by many bacteria and that kill susceptible bacteria [67]. Bacteriocin-producing genotypes are resistant to the toxin because of a resistance gene that is tightly linked to the gene for the toxin. Producing bacteriocin reduces growth. However, genotypes that make bacteriocins increase in laboratory cultures [41]. By killing susceptible cells, they free up resources and enhance the growth of relatives that also carry the producer gene.

## Conflict and Cooperation in Close Quarters: The Family

Some interactions within families are the epitome of cooperation, while others are the most extreme forms of conflict imaginable [23, 55]. Evolutionary biology provides unique perspectives on how and why families function as they do.

### *Conflict between mates*

Although males and females must cooperate to produce offspring, conflict between mates is also pervasive [3]. A male can often benefit from mating with a female that is already inseminated since he may father some of her offspring. In contrast, the female often cannot increase her fecundity by mating more than once, but she can become infected, be injured, or lose time if she does. This results in **sexually antagonistic selection**, in which a trait that is favored to increase in one sex is favored to decrease in the other. In many species, males inflict harm on their mates. Groups of male mallard ducks sometimes drown females during forced copulations. Female bedbugs suffer reduced survival from traumatic insemination in which the male mates with his partner by piercing her abdominal wall [72].

Internal fertilization offers an opportunity for mates to manipulate their partners chemically. When *Drosophila melanogaster* mates, the male's ejaculate includes a cocktail of "accessory gland proteins" as well as sperm. These proteins alter the

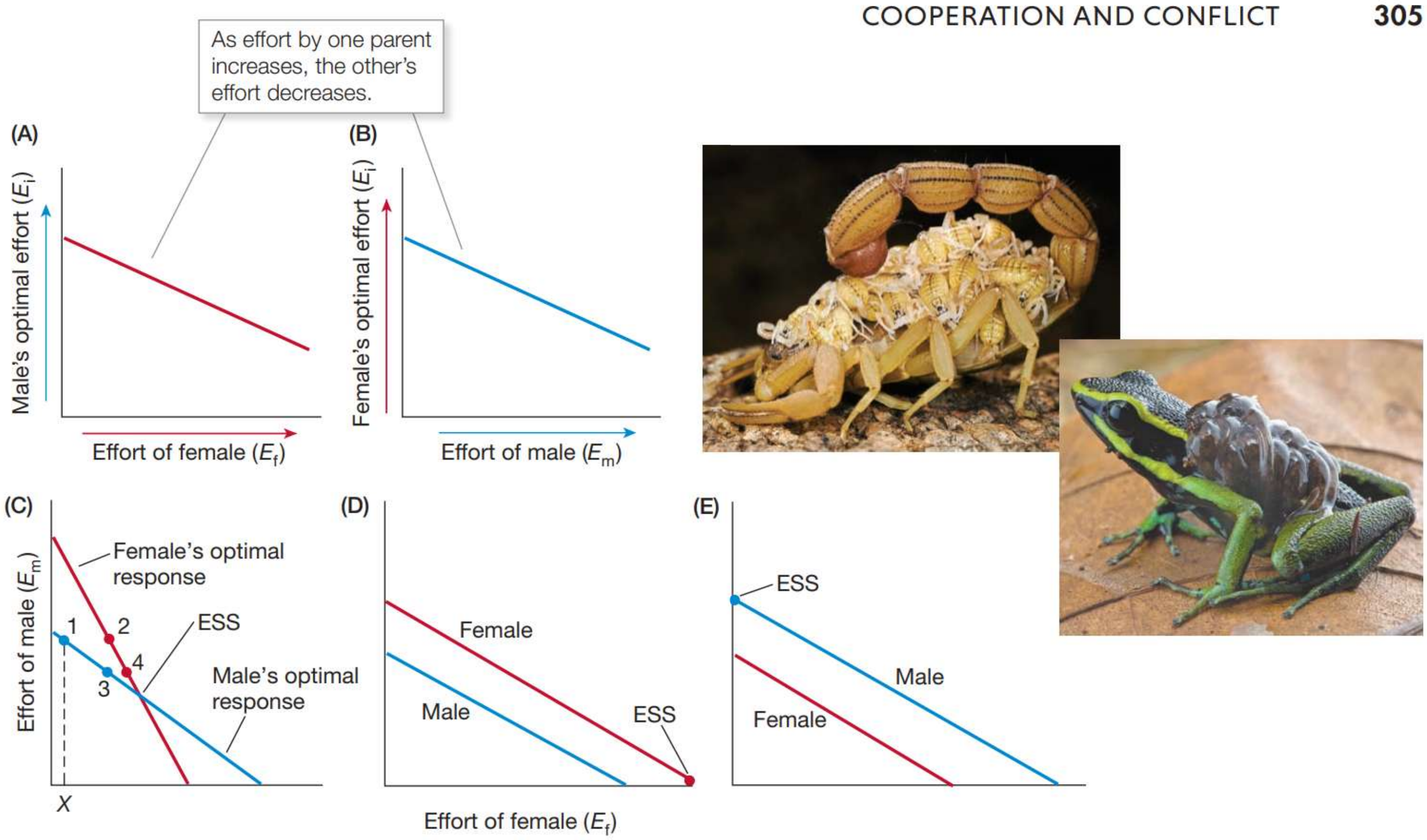


**FIGURE 12.6** Analysis of the evolution of parental care using an evolutionarily stable strategy (ESS) model. (A, B) The optimal parental effort expended by each member of a mated pair declines as the effort expended by its partner increases. (C) Curves for males (blue) and females (red) plotted together. Their intersection marks the ESS. If, for example, the population starts with female effort ($E_f$) equal to X, male effort ($E_m$) evolves to point 1. This favors $E_f$ to evolve to point 2 on the female's optimality line, which then favors $E_m$ to evolve to point 3; but then $E_f$ evolves to point 4. Eventually, $E_m$ and $E_f$ evolve to the intersection (the ESS), no matter what the initial conditions are. (D, E) Conditions can occur in which the optimal curves for the sexes do not intersect and the ESS is care by only the female (D), as in this scorpion, or the male (E), as in this poison dart frog (*Epipedobates trivittatus*). (After [17].)

female's reproductive physiology, causing her to lay eggs more rapidly. The fitness advantage to the male is that if the female later remates, his sperm will have already fertilized a larger number of her eggs. But the accessory gland proteins also decrease the female's fitness by shortening her life span [13]. William Rice designed a clever experiment in which male *D. melanogaster* could evolve but females could not [65]. After 30 generations of experimental evolution, the fitness of males had increased compared with controls, but females that mated with these males suffered greater mortality, probably because of enhanced semen toxicity. This result suggests that males and females are continually evolving, but in balance, so that we cannot see the change unless evolution in one sex is prevented.

The evolutionary interests of males and females often conflict. In many bird species that are socially monogamous, a female can copulate with another male, and her partner ends up rearing some offspring that are not his own. Even parental care involves potential conflict. Whether both parents, one parent, or neither care for their young varies greatly among species [15]. Providing care increases offspring survival, which enhances the fitness of both parents and their offspring. But parental care also carries the costs of risk, time, and energy. In species with biparental care, each parent benefits by leaving as much care as possible to the other partner. Decreasing parental care is favored by selection as long as any loss in the fitness of the current offspring is more than offset by the gain in the potential for future offspring. If offspring survival is almost as great with care from just one parent as from two, selection favors individuals that abandon the brood to the care of their partner (**FIGURE 12.6**). Selection favors defection more strongly in the

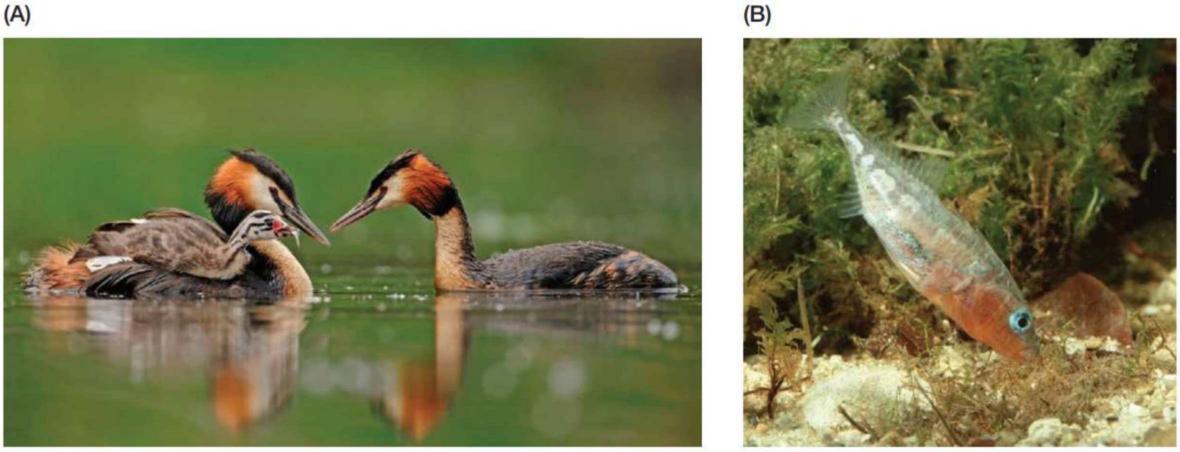


**FIGURE 12.7** Parental care. (A) Great crested grebes (*Podiceps cristatus*) exemplify the many bird species in which both parents care for the young. (B) A male three-spined stickleback (*Gasterosteus aculeatus*) builds and cares for a nest containing egg clutches fathered by him. This activity can attract additional females to mate with him.

parent that pays the greater cost in caring for the offspring (in terms of lost opportunities for further reproduction).

This theory may explain major patterns in parental care [15]. In birds and mammals that must feed their young, parental care is more costly for males than for females, because males could potentially obtain other matings in the time they spend rearing a brood. That may explain why parental care in those animals is generally provided by females or by both mates (**FIGURE 12.7A**). In contrast, many fishes and frogs guard their eggs and young, but most do not feed their offspring. Males can often mate with additional females while they guard the eggs already in their nest (**FIGURE 12.7B**). In contrast, females can increase their reproductive success only by replenishing the massive resources they have spent on producing eggs. To do that, they must abandon the nest to forage. That may explain why in fishes and frogs, males provide parental care more often than females.

### *Murder in the family*

Sometimes an individual's fitness is enhanced by killing the young of its own species [15, 38]. In lions (see Figure 10.12), baboons, and many other social mammals, males kill the offspring of other males, then father their own offspring with their victim's mothers (**FIGURE 12.8**). Selection can favor this behavior for two reasons: it eliminates the genes of competing males, and females become fertile and sexually receptive sooner if they are not nursing young. This behavior occurs mostly in species in which social groups contain more females than males and in which sexual selection is likely to be strong [48]. In this situation, there are few possible fathers of the new offspring from females whose offspring are killed, so the fitness benefit is more likely to go to a murderous male than if there were an even sex ratio.

While the murder of unrelated young might make evolutionary sense, how can we explain the fact that in some species parents kill their own children? Infanticide can be a way of adaptively regulating brood size [55]. A bird's fitness is proportional to the number of its surviving offspring, which equals the number of eggs laid, multiplied by the probability that each egg survives. Survival may decrease as number of eggs increases because of competition among the offspring for food, and because parental care of a large brood can reduce the parent's subsequent reproduction (see Chapter 11). Female mice kill some of the young in their litter

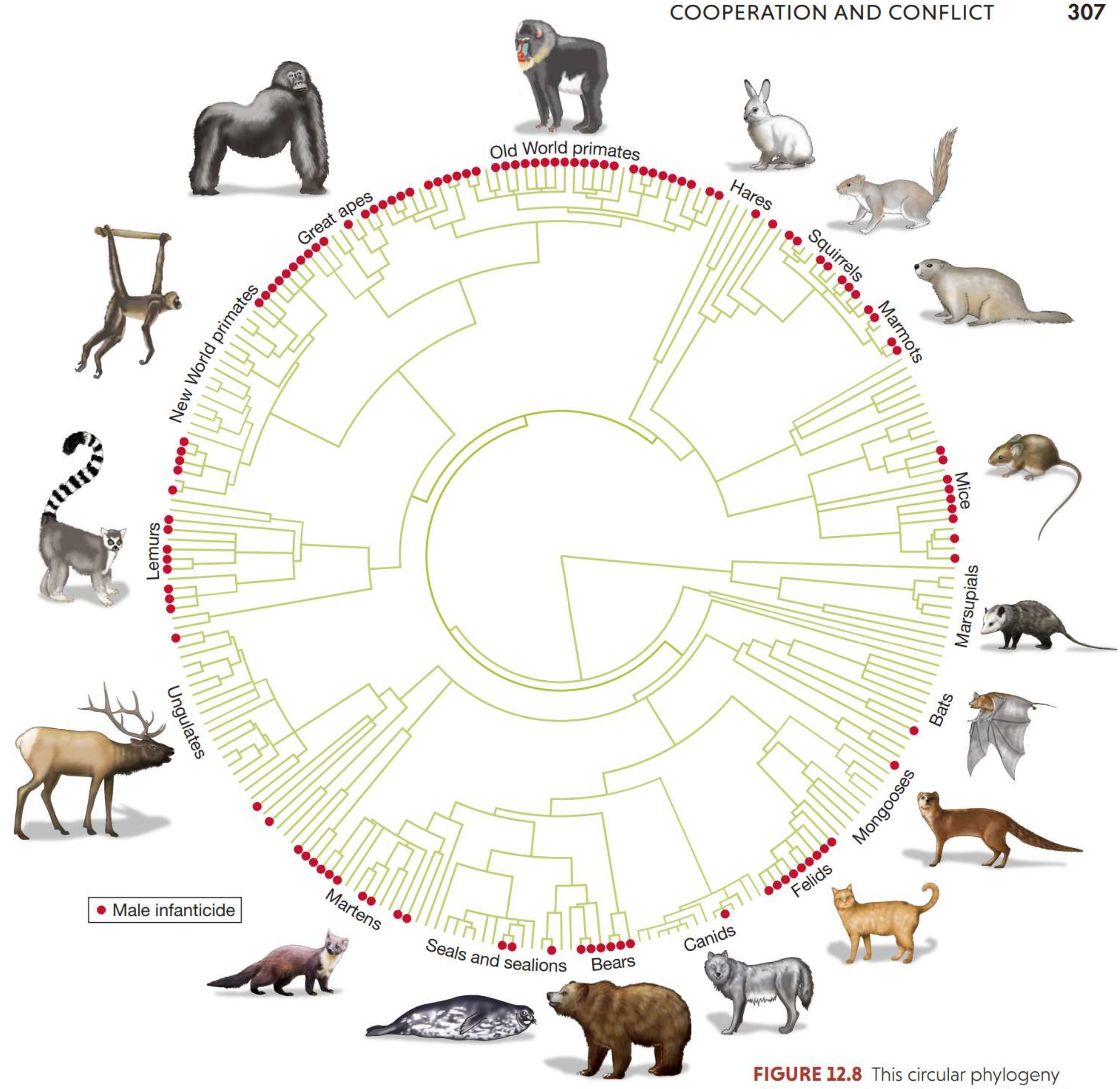


**FIGURE 12.8** This circular phylogeny of mammals shows that male infanticide occurs in many species (branches with red circles at the tip). It is most prevalent in social species, less prevalent in solitary species, and least common in monogamous pair-bonding species. (After [48].)

if food is scarce or the litter is too large—behavior that increases the chance that the female will have more offspring in the future. Plants often abort many of their offspring (seeds) and reallocate their limited resources to fewer but larger seeds that have a greater chance of survival.

Aggregation can increase competition among kin for food and other resources [27, 60]. Siblings in a brood may actively fight for resources, and larger individuals may kill smaller siblings. This behavior, called siblicide, is the norm in some species of eagles and boobies. Females lay two eggs, but one of the nestlings always kills the other (**FIGURE 12.9**). The second egg may be the female's evolutionary insurance in case the first is inviable.

The ways in which animals such as these behave toward their family starkly illustrate the point that natural selection lacks any form of morality.

## *Parent-offspring conflict*

Natural selection typically favors different behaviors in parents and offspring [33, 75]. An offspring can gain indirect fitness benefits by increasing the survival of its siblings, to which it is related by $r = 0.5$. But it has even more to gain by increasing its own survival: an individual is related to itself by $r = 1$. Selection favors an offspring to take more resources from its parents, even if that harms them and decreases the number of other offspring they have, so long as the gain in its direct fitness is larger than its loss of indirect fitness. On the other side of this interaction are the parents. Selection on their inclusive fitness favors them to maximize the number of offspring they have, not to divert extra resources to selfish ones. The result is **parent-offspring conflict**. What is best for a parent conflicts with what is best for an offspring.

**FIGURE 12.9** Siblicide in the brown booby (*Sula leucogaster*). The parent is sheltering a large chick that has forced its sibling out of the nest. The parent ignores its dying chick (foreground). (Photo by John Alcock.)

In humans, parent-offspring conflict plays out even in the womb [35]. Early in the development of the placenta, cells from the embryo invade the specialized arteries of the mother that supply the embryo with blood. Once there, the cells break down the smooth muscle and nerves in the arterial walls. This prevents the mother from constricting the arteries, and so increases the supply of nutrients to the embryo. In short, the embryo has evolved to extract more resources from its mother than the mother is favored to give.

Further conflicts in the womb involve the father as well as the offspring. A gene called *IGF2* that is expressed in the fetus produces a factor that enhances fetal growth by obtaining more nutrition from the mother. Strangely, only one of the two alleles carried by the fetus is expressed, and it is the one inherited from the father. The product of a second gene, *IGF2R*, degrades the growth factor, and at this locus only the allele inherited from the mother is expressed in the fetus. The expression level of the growth factor in the fetus is therefore determined by the opposing effects of the alleles it inherited from its mother and its father.

The leading hypothesis to explain these observations starts with the idea that the father gains no fitness benefit from the mother's future reproduction if she mates with a different male. Selection therefore favors paternal genes in the fetus that enable it to get more from the mother, even if that decreases the mother's future reproduction. In response, females have evolved to suppress the tactics used by the mates' genes to exploit them. Unfortunately, this war between genes can inflict collateral damage in the form of infant pathologies [29].

## *Eusocial animals: The ultimate families*

The most extreme altruism is found in **eusocial** animals. These are species in which some individuals do not reproduce much or at all themselves, and instead rear the offspring of others, usually their parents. The most familiar examples are found among the ants, bees, and wasps (all in the order Hymenoptera). Eusociality is also found in all species of termites (Isoptera), in several other kinds of arthropods, and in a few species of naked mole-rats (**FIGURE 12.10**) [9, 18, 44, 85].

Eusociality has evolved independently many times in Hymenoptera. In all cases, the ancestors were solitary species in which a single mated female provisioned or reared her offspring by herself [40]. In the eusocial species, reproductive females are called queens, and most of their eggs develop into workers, which are the nonreproductive females that maintain the colony. Some eggs develop into reproductive queens and some into reproductive males. In most species, whether a female becomes a queen or a worker depends on her diet, which is often controlled by the workers, and on how the workers behave toward her.

How did eusociality originate? In some species of bees, some females rear offspring with help from older offspring, while other females are solitary and receive no help. Compared with the reproductive fitness of single females, the inclusive fitness of daughters that help their mother is higher in some cases but lower in

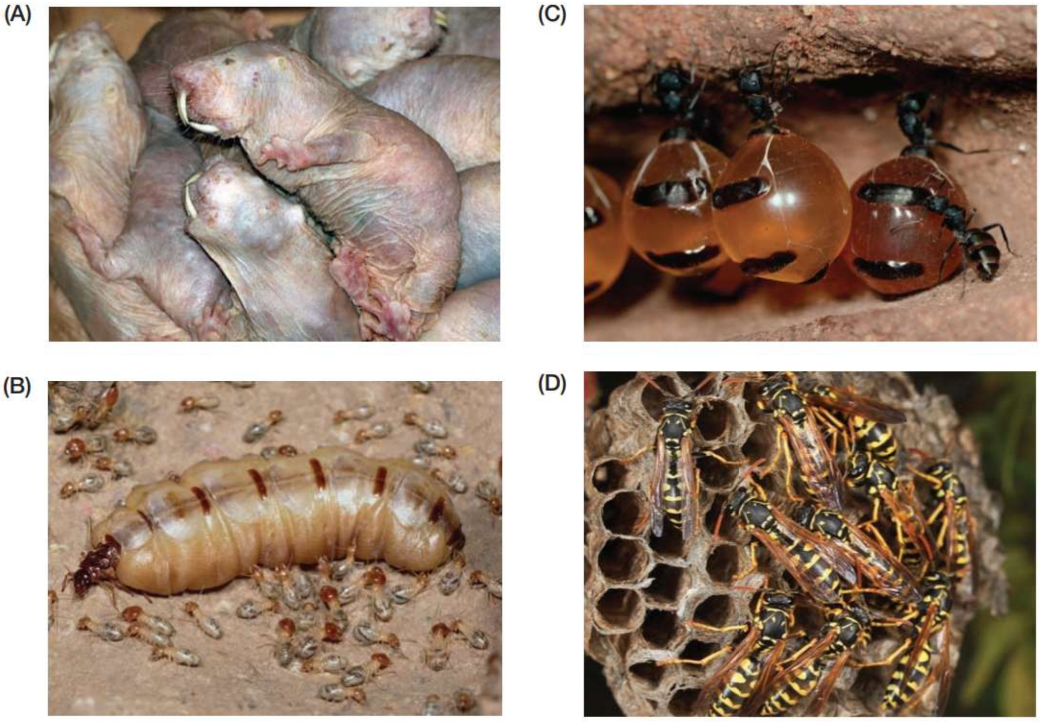


**FIGURE 12.10** Some eusocial animals. (A) Several species of naked mole-rats, here *Heterocephalus glaber*, are the only known eusocial mammals. (B) This queen termite is attended by small, sterile workers and large-headed, sterile soldiers. (C) Australian honeypot ants (*Camponotus inflatus*), engorged with nectar, hang from the roof of their nest's larder. These "repletes" regurgitate nectar on demand to their worker nestmates. (D) Paper wasps (*Polistes gallicus*) at their nest.

others (e.g., [43, 86]). So some origins of hymenopteran eusociality may well have been facilitated by kin selection. But ecological and behavioral factors were also important [61, 63]. Eusociality probably evolved frequently in Hymenoptera (compared with other insects) because single females of solitary wasps and bees construct a nest such as a burrow, which requires hard work but provides shelter for the young, and the offspring are helpless larvae that the mother must feed. These hymenopterans were predisposed to sociality because they already had the habit of caring for offspring and because the nest provided a safe place—a fortress—for grown offspring to stay and to interact with their mother and younger siblings [61]. In the case of other eusocial insects, such as termites that live in dead wood, the fortress is also the food source. Another advantage of having helpers is that some can defend the larvae while others forage for food; a single female cannot do both. Moreover, dispersing from the natal nest and constructing a new nest is very risky, and the great majority of young mated females do not succeed. Thus, even a slight increment in inclusive fitness from rearing siblings may have made it advantageous to stay and help mother instead of leaving home.

Kin selection explains many aspects of cooperation and conflict in eusocial hymenopterans [7, 8, 64, 70]. These species are *haplodiploid*: fertilized eggs are diploid and develop into females, while unfertilized eggs are haploid and develop into males. A queen can decide the sex of an offspring by releasing sperm, or not, that she stored when she mated early in life. As a result of this strange genetic system, the coefficients of relationship among relatives differ from those in diploid species. Comparing the family trees in Box 12B, we see that in diploids, $r = 0.5$ between parent and offspring and between full siblings. In haplodiploid species, however, a female is more closely related to her sisters ($r = 0.75$) than she is to her sons and daughters ($r = 0.5$), and she is even less closely related to her brothers ($r = 0.25$). If a colony has only one queen that mated with only one male, workers are rearing brothers and sisters, some of which may become queens.

In a colony of hymenopterans, there is evolutionary conflict over which individuals should reproduce. A worker can gain more fitness by raising her own sons (related to her by $r = 0.5$) than by helping to raise the queen's sons (the worker's brothers, related to her by $r = 0.25$). But the queen gains more inclusive fitness through her own sons (related to her by $r = 0.5$) than through her daughters' sons (related to her by $r = 0.25$). Queens of many species therefore destroy their workers' eggs, and in some species (including honeybees, *Apis mellifera*) workers destroy the eggs of other workers [64, 78]. This is one of the best examples of *policing* of noncooperators in social species, and it illustrates that kin selection can underlie the evolution not only of altruism, but also of selfishness.

There is also conflict between queens and workers about how many males and reproductive females the colony should produce. A queen's fitness is maximized by a 1:1 sex ratio, since she is equally related to her daughters and sons. But workers can control the sex ratio among the larvae destined to be males or queens, by feeding some more than others, or even by killing some of them. In a colony with a single queen, a worker's inclusive fitness is maximized by rearing young queens and males in a 3:1 ratio, because a worker is related by $r = 0.75$ to her queen sisters, but only by $r = 0.25$ to her brothers. In colonies with multiple queens, however, workers should favor a sex ratio closer to 1:1 (because not all females are full sisters and so $r < 0.75$). Data support these predictions [18, 61]. Within some species of ants, wasps, and bees, some colonies have a single queen that mated with a single male, and others have colonies with either multiple queens or a single queen that mated with multiple males. A review of studies of species with this kind of variation found that the prediction about sex ratio was upheld in 18 of the 19 species [61].

## Levels of Selection

The basic principle of evolution by natural selection is simple: the entities that make more copies of themselves increase in frequency through time. Usually, the "entities" in question are alleles. But the same principle applies to anything that can replicate—bits of DNA, mitochondria, entire chromosomes, even groups of individuals. In this section we will see how Darwin's concept of natural selection can be applied at these different levels to understand important features of the natural world.

### *Selfish DNA*

Meiosis is a remarkably democratic affair: the two alleles carried by an individual at a locus usually have an equal chance of being passed to an offspring. But consider a mutation that can tilt the odds in its favor so that its chances are greater than 50 percent. Any mutation that can do so will enjoy an evolutionary advantage, a situation called **segregation distortion**. It can spread in the population even if it actually decreases survival or reproduction. Given the strong evolutionary incentive to cheat at inheritance, it is surprising how fair meiosis usually is.

There are, however, mutations that do cheat [47b]. Meiosis is fundamentally different in males and females, and so the ways that mutations are able to break Mendel's laws are quite different in the two sexes (**FIGURE 12.11**). Alleles that cause segregation distortion in males are known from diverse groups, including mammals, insects, and fungi. Some alleles at the *t* locus in the house mouse (*Mus musculus*) are transmitted to about 95 percent of a heterozygous male's sperm. Sperm that carry of these alleles gain an advantage by secreting a toxin that kills other sperm in the testes. These sperm are themselves immune to the toxin because they carry a resistance allele at a second locus. This transmission advantage causes the selfish alleles at the *t* locus to spread, even though they reduce the fertility of males. A killer allele must be inherited together with the resistance allele, or else sperm with the killer allele will commit gametic suicide. That explains why in mice and other species with this kind of segregation distortion, the two loci are always tightly linked, and are often found in regions of the genome with reduced recombination (such as the sex chromosomes).

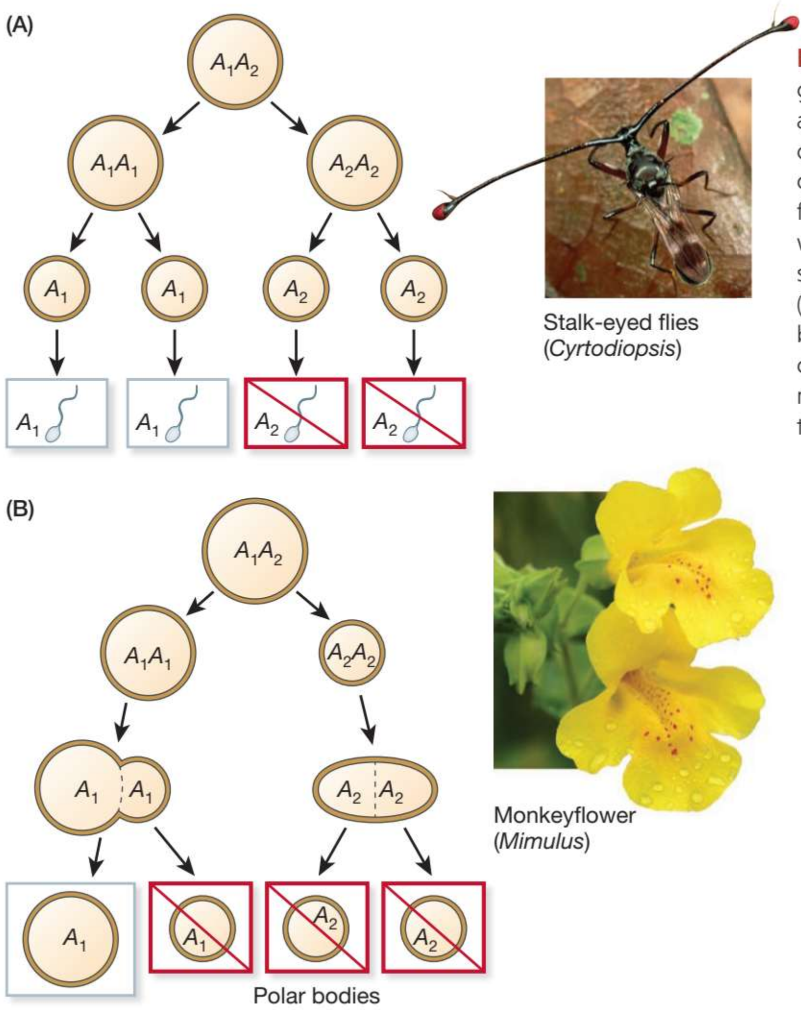


**FIGURE 12.11** In the battle to be passed on to the next generation, some mutations gain an advantage by cheating at the laws of inheritance. The diagrams at left show how a cheating $A_1$ allele is transmitted during the two meiotic cell divisions and then to the gametes. (A) In males of stalk-eyed flies (genus *Cyrtodiopsis*), segregation distortion results when the sperm that carry an allele (shown as $A_1$) kill other sperm in the male's testis that do not have that allele [59]. (B) In monkeyflowers (genus *Mimulus*), some chromosomes benefit from segregation distortion [24, 26]. During meiosis, chromosomes with certain DNA sequences in their centromeres (shown as $A_1$) are more likely to enter ovules, while their rivals end up in polar bodies, which die. (After [47b].)

The loss in male fertility generates a strong evolutionary advantage to mutations at yet other loci to suppress the allele causing segregation distortion. Many distorter systems arise and are then shut down by countermeasures that evolve elsewhere in the genome [10]. This genetic conflict can contribute to speciation (see Chapter 9). Consider a population in which a distorter system arose and then was suppressed by other loci. Now individuals from this population meet and mate with others from a population that does not have the distorter or the suppressor. Some hybrids will inherit the distorter but not the suppressor, reactivating the distorter and once again depressing male fertility. In some taxa, this may be an important source of genetic incompatibilities between populations and species [58].

In females, alleles cheat the laws of inheritance in other ways. Only one of the four products of meiosis in plants and animals becomes a gamete (see Figure 12.11B). Any allele that can increase its odds of ending up in the gamete will enjoy an evolutionary advantage (see Figure 12.11B). Centromeres have the opportunity to do just that [39]. During meiosis, each pair of chromosomes segregates when their centromeres attach to microtubules and then pull themselves toward opposite poles of the cell. The DNA sequence of the centromere and the proteins that bind to it affect how quickly a chromosome moves toward the pole. Depending on the species, chromosomes that segregate more quickly or more slowly have the best chance of ending up in a gamete. This can drive the rapid evolution of the position and genetic sequence of the centromere, and of proteins that interact with it.

Mosquitoes transmit some of the world's most important infectious diseases, including malaria. The secret to controlling these diseases may come from manipulating the rules of inheritance in the mosquitoes. If mutations that make mosquitoes

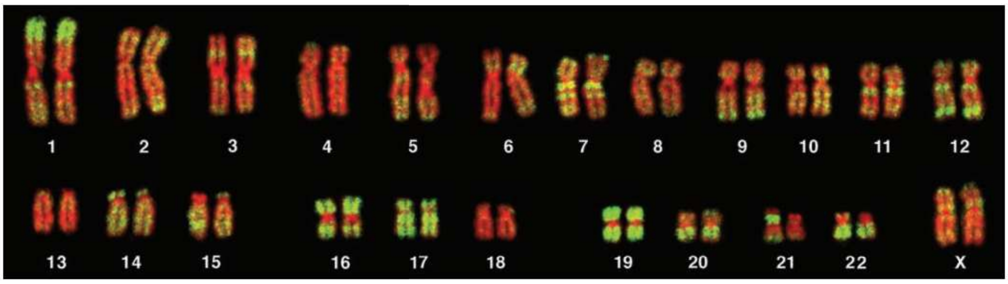


**FIGURE 12.12** In this photograph of the chromosomes that make up the human genome, regions that are rich in the *Alu* transposon fluoresce in green. More than 1 million copies of this element are embedded in the genome. *Alu* is only one of many transposons that together make up half of our DNA. (From [6].)

resistant to malaria could somehow be introgressed into natural populations, it might be possible to eradicate the disease. "Gene drive" may now make that possible [30]. A resistance mutation has been genetically engineered that transmits itself from a mosquito to its offspring nearly 100 percent of the time, rather than the usual 50 percent. While this is an exciting prospect for public health, it will be important to evaluate the potential risks of genetically manipulating natural populations.

Transposable elements, or **transposons**, are a type of selfish DNA that is closer to home—they make up almost half our genome (**FIGURE 12.12**). Transposons are short sequences of DNA that are able to insert additional copies of themselves in the genome [49]. They are genetic parasites that do not leave their host, and in fact one hypothesis for their origin is that transposons began as viruses. Transposons have been spectacularly successful, particularly in eukaryotes. Like other parasites, transposons are typically bad for their host. A transposon generates a mutation when it inserts itself into a new place on a chromosome, and many of these mutations are deleterious. Organisms have evolved a variety of mechanisms to combat transposons.

Transposons do not exist to improve the fitness of their host. Instead, they exist simply because selection on the transposons favors those that leave more descendant copies of themselves. Transposons are explored further in Chapter 14, where we will see that they are one of the most important factors in the evolution of genome size in eukaryotes.

Many other kinds of selfish genetic elements have been discovered. A small extra chromosome called PSR (for "paternal sex ratio") in the wasp *Nasonia vitripennis* is transmitted through sperm but not through eggs [79]. When a sperm carrying PSR fertilizes an egg, all the other chromosomes inherited from the father disintegrate, leaving only the maternal set of chromosomes intact. Because diploid eggs develop into females and haploid eggs into males in wasps, the degeneration of male chromosomes converts the female into a male, and PSR is passed to the next generation through his sperm. As PSR spreads in a population, the sex ratio becomes more and more skewed toward males, which in principle could even drive a population to extinction. Natural selection does not always favor traits that make species more likely to survive.

### *Selfish mitochondria*

Thyme is an herb used in cooking that comes from a plant (*Thymus vulgaris*) with an unusual breeding system (**FIGURE 12.13**). Most plants are hermaphrodites—their flowers have both male and female parts. Some individuals, however, are sterile in their male function and reproduce only as females [14]. Sterility is caused by a mutation that is inherited through the cytoplasm, not the nucleus, so it is called *cytoplasmic male sterility* (or *CMS*). Sterility is caused by the $CMS^+$ allele of a mitochondrial gene. Hermaphrodites carry the sterility allele, and also an allele called $R^+$ at a nuclear locus that restores male fertility. In some other species, remarkably, all individuals are hermaphrodites and carry both $CMS^+$ in the mitochondrion and $R^+$ in the nucleus. Why should one gene exist, only to be counteracted by another?

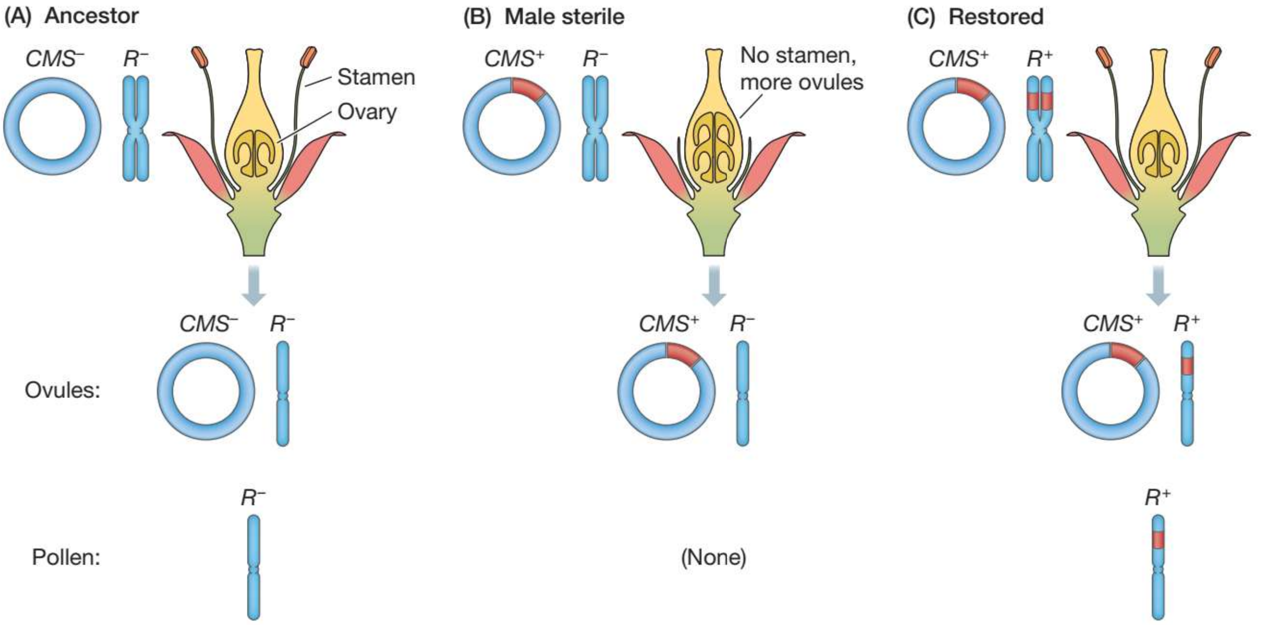


**FIGURE 12.13** *Cytoplasmic male sterility* (*CMS*) in thyme plants (*Thymus vulgaris*) illustrates genetic conflict. Next to each flower is a schematic showing the mitochondrion (the circle) with its genotype at the *CMS* locus, and a pair of nuclear chromosomes that carry the *R* restorer locus. Mitochondria are transmitted only through ovules. (A) Plants that are $CMS^-$ and $R^-$ produce both ovules and pollen. The ovules transmit both the *CMS* and *R* loci, while the pollen transmits only the *R* locus. (B) Plants that are $CMS^+$ and $R^-$ are male sterile. Pollen production is eliminated, which increases the ovule number because the plant reallocates energy and resources from pollen to ovules. This increases the number of copies of the $CMS^+$ allele passed to the next generation, causing male sterility to spread. (C) Plants that carry the $R^+$ allele have their male fertility restored, which causes that allele to spread in populations with the $CMS^+$ allele. A population fixed for alleles $CMS^+$ and $R^+$ may be phenotypically indistinguishable from the ancestral population that was fixed for $CMS^-$ and $R^-$.

Mitochondria are maternally inherited. Natural selection therefore favors any mutation in mitochondria that increases the number of ovules that females produce. The effect on male reproduction does not matter in the slightest to the mitochondria, since they are not transmitted through pollen. When the $CMS^+$ allele knocks out male reproductive function, resources are diverted from making pollen to making more ovules. This gives the $CMS^+$ allele a fitness advantage, and it spreads in populations of thyme.

But selection on nuclear genes favors a very different outcome. Recall from Chapter 10 that selection on those genes favors a 1:1 ratio of males to females (or male to female gametes). The spread of the $CMS^+$ allele leads to an excess of females in the population. That in turn favors the spread of any mutation in a nuclear gene that cancels the action of the $CMS^+$ allele. The result is an evolutionary arms race between genes on the mitochondria and genes in the nucleus.

Genes that are inherited cytoplasmically often conflict with nuclear genes, as thyme plants illustrate. Mitochondrial mutations that harm males are not selected against [32, 42]. This explains why mitochondrial mutations that cause male-specific diseases are common in humans, fruit flies, and other species (see p. 19).

## *Group selection*

In most situations, competition between individuals for survival and reproduction leads to the evolution of traits that increase each individual's fitness. Under the right conditions, however, selection operating on the phenotypes of *groups* of individuals can lead to the evolution of traits that are not favored by selection acting on differences between individuals within each group [84]. These traits can include altruistic behaviors.

A classic experiment with the flour beetle *Tribolium castaneum* shows that group selection can cause large evolutionary changes [76]. Three treatments were established, each with 48 small populations (groups) that were maintained in vials of flour. After the beetles reproduced, the population size in each vial was censused. In the first treatment, beetles from the vials with the largest populations were used to establish a new set of 48 vials. In the second treatment, only beetles from the vials with the smallest population sizes were used as founders for the next generation. The third treatment was a control in which all populations contributed equally to the next generation. This procedure was followed for nine generations. A key point is that the experimental selection imposed by the treatments acted only on a property of the group—the population size of the vial. In addition to the group selection imposed by the experiment, individual selection was also at work, favoring individuals that left more offspring within each group.

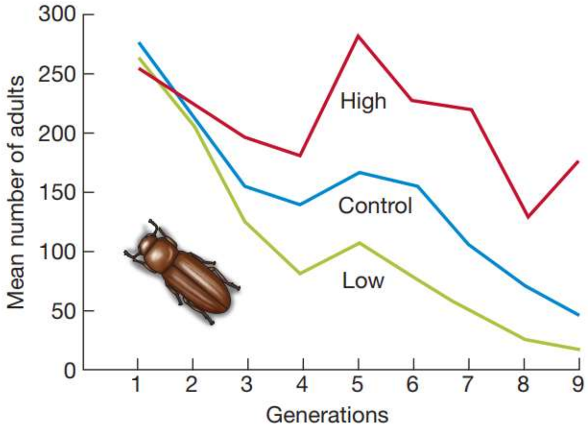


**FIGURE 12.14** Evolution of group size in response to group selection among and individual selection within populations of the flour beetle *Tribolium castaneum*. After nine rounds of selection, populations under group selection for high population size (red line) were on average nine times larger than those under group selection for low population size (green line). Individual selection within groups caused the population sizes to decrease in all three treatments. (After [76].)

The results show two striking trends (**FIGURE 12.14**). By the end of the experiment, there were nine times more beetles per group in the treatment that selected for high population size than in the treatment that selected for low size. Clearly group selection had a very strong evolutionary impact. The second pattern is that population size declined in all three treatments. Further research revealed the causes [77]. Larval and adult beetles sometimes eat eggs and pupae. Cannibalism is advantageous to the cannibals, and it increased in frequency as the result of individual selection within each vial. In the treatment that selected for high population size, cannibalism rates were lower, which can be thought of as the evolution of an altruistic behavior. In short, the trend of population size through time in each treatment resulted from an interplay between group selection and individual selection.

To be clear, evolution by group selection results from changes in allele frequencies, just as when selection acts on individuals. The difference between group selection and individual selection is that group selection results from a difference between the rates of survival or reproduction of groups, rather than of individuals. Group selection is closely related to kin selection, and in fact many evolutionary biologists do not distinguish between the two [5, 27, 80]. Although the individuals in each group of beetles were not immediate family members, they were more genetically related to each other than they were to the beetles in other groups. In effect, selection that favors certain groups is favoring certain extended families.

One setting in which group selection has clearly played an important role is the evolution of virulence in pathogens [11]. Each host contains a group of pathogens. Selection on pathogens favors traits that increase the number of hosts that they infect (see Chapter 13). Pathogens face an evolutionary trade-off. If they multiply rapidly within the host, they are more virulent (that is, they kill their host faster), but they infect new hosts more quickly. The influenza virus does this: millions of viral particles can be spewed out in a single sneeze, and infect many unfortunate people nearby. The viral genotypes within a host that replicate fastest are the most likely to infect another host, and so are favored by individual selection. Other pathogens reproduce much more slowly. This prolongs the life of the host, which for these pathogens increases the number of other hosts that they infect over the long term, and so these pathogens are relatively benign. Whether selection favors low or high virulence depends on the biology of the pathogen and the host—for example, on how frequently the pathogen has an opportunity to infect a new host.

A dramatic but entirely accidental "experiment" shows that virulence can evolve rapidly by group selection. In 1950, the myxoma virus was introduced into Australia to control a population explosion of European rabbits (*Oryctolagus cuniculus*) which (ironically) had themselves been introduced earlier [45]. Initially, the virus was lethal and killed more than 99 percent of infected rabbits. But in the years that followed, fewer and fewer rabbits died. The rabbits evolved greater resistance, and the virus evolved lower virulence. The evolution of the virus was studied in laboratory experiments that used a population of rabbits that had never been exposed to the virus. Virulence was measured on a scale from most virulent (= 1) to least virulent (= 5). Between 1952 and 1955, the two most virulent classes made up about 33 percent of the viral isolates. Twenty-five years later, the most virulent classes had declined to about 5 percent of the isolates. This pattern was repeated when the virus was introduced to control rabbits in France in 1952. For the myxoma virus, group selection for decreased virulence was more powerful than the selection among viruses within each rabbit favoring increased virulence. The virus therefore evolved to become more benign.

## Cooperation and Major Evolutionary Transitions

The fitness of most parasites and pathogens depends on **horizontal transmission**, that is, infecting other hosts that are not the offspring of their current host (**FIGURE 12.15A**). Parasites and pathogens transmitted this way are sometimes selected to become highly virulent if that increases the probability they will infect a new host.

**Endosymbionts** are mutualists that live within the cells of their hosts. Some, like mitochondria, are passed by **vertical transmission**, that is, they infect the offspring of their current host (**FIGURE 12.15B**). Here the evolutionary fates of the

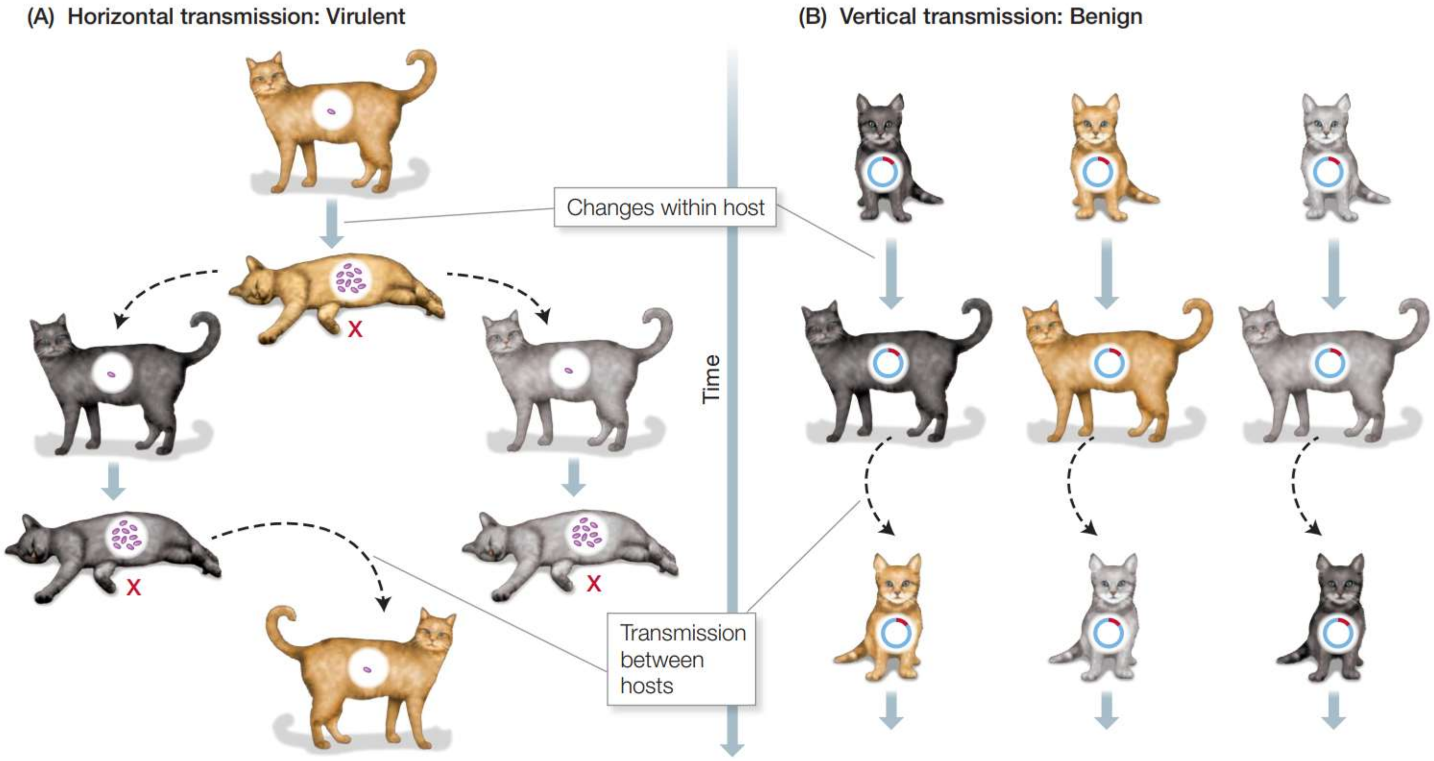


**FIGURE 12.15** Selection pressures on pathogens and endosymbionts depend on their mode of transmission. (A) Pathogens such as the influenza virus maximize their fitness by multiplying rapidly within their host, which increases their chance of being transmitted horizontally to another host. The rapid replication of the virus can harm and even kill its hosts. (B) Endosymbionts such as mitochondria are transmitted vertically from mothers to their offspring. This kind of endosymbiont maximizes its own fitness by increasing the survival and reproduction of its female hosts.

endosymbiont and host are chained together. The endosymbiont's fitness depends entirely on the fitness of its host. Selection for high proliferation *within* the symbiont population occupying each host is strongly opposed by selection *among* the populations of symbionts that occupy different hosts. On balance, selection at the group level favors mitochondria (and other maternally-transmitted symbionts) that maximize the number of female offspring that their hosts leave to the next generation. In the extreme case, the symbiont may become an essential part of the host, forming a new collective entity [56].

This is what happened in one of the *major transitions* in the history of life on Earth: the evolution of eukaryotes [51]. The key event was the symbiotic union of a bacterial endosymbiont and a host cell, probably an archaean, about 1.5 billion years ago. The bacterium evolved into the mitochondrion [12]. This was the first of many symbioses that formed major new collective entities. A second was the incorporation of blue-green bacteria (cyanobacteria) into a one-celled eukaryote. That enabled the eukaryote to photosynthesize, and it became the ancestor of the green algae and plants. The common interest of the endosymbiont and host genomes resulted in the evolution of a new kind of collective entity, and a higher level of organization.

A third major transition occurred with the origin of multicellular organisms [27, 51, 54]. These organisms are more than just groups of cells. For example, dividing bacteria that remain loosely attached but physiologically independent of each other do not constitute an organism. The cells of a multicellular organism cooperate in ways reminiscent of the ants in a colony: they differentiate into tissues specialized for different tasks that contribute to the fitness of the group (that is, the individual they belong to). Why should unicellular ancestors, in which each cell had a prospect of reproduction, have given rise to multicellular descendants, in which some cells sacrifice their own reproduction?

The fundamental answer is kin selection. If the cell lineages in a multicellular organism arise by mitosis from a unicellular egg or zygote, the genes of cooperative cells that sacrifice reproduction for the good of the cell "colony" are propagated by closely related reproductive cells. However, the coefficient of relationship is reduced if genetically different cells invade the colony, or if mutational differences arise among cells. A mutation that increases the rate of cell division has a selective advantage *within* the colony, but unregulated cell division usually harms the organism, as in cancer. Selection at the level of whole colonies of cells—organisms—therefore opposes selection among cells within colonies.

As a result, mechanisms of policing have evolved that regulate cell division and prevent renegade cell genotypes from disrupting the integrated function of the organism. In animals, selection has resulted in the evolution of a germ line that is segregated from the soma early in development. This organization prevents deleterious mutations in somatic cells from being transmitted by the gametes. Selection for organismal integration may be responsible for the familiar but remarkable fact that almost all multicellular organisms begin life as a single cell, rather than as a group of cells. This feature increases the relatedness among all the cells of the developing organism, reducing genetic variation and competition within the organism and increasing the heritability of fitness. The result, then, has been the emergence of the "individual," and with it, the level of biological organization at which so much of natural selection and evolution take place.

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

# SUMMARY

- Many biological phenomena result from conflict or cooperation among organisms or among genes. The evolution of most interactions can be explained best by selection at the level of individual organisms or genes.
- Altruism benefits other individuals and reduces the fitness of the actor, while cooperative behavior need not reduce the actor's fitness. Cooperation can evolve because it is directly beneficial to the actor, although the benefit may be delayed. It can also evolve by reciprocity, based on repeated interactions between individuals in which the fitness interests of the associates are aligned. Cooperative interactions can be maintained in part by "policing," or punishment of cheaters.
- Altruism can evolve by kin selection. An allele's inclusive fitness is the sum of its direct fitness (the average number of copies that a carrier leaves to the next generation) and its indirect fitness (additional copies left by the carrier's relatives as the result of the carrier's behavior). Hamilton's rule describes the conditions for the increase of an allele for altruistic trait in terms of the benefit to the recipient, the cost to the actor, and the coefficient of relationship between them.
- Conflict and kin selection together affect the evolution of many interactions among family members. The genetic benefit of caring for offspring is an increase in the number of current offspring that survive. The genetic cost is the number of additional offspring that the parent is likely to have if she or he abandoned the offspring and reproduced again. Parental care is expected to evolve only if its fitness benefit exceeds its fitness cost. Whether or not one or both parents evolve to provide care can depend on the ratio of fitness costs and benefits for each parent.
- Evolutionary conflicts between parents and offspring are widespread. A parent's fitness may be increased by allocating some resources to its own survival and future offspring rather than to its current offspring. Selection acting on the offspring, however, often favors taking more resources from its parents than is optimal for the parents to give. This principle may be one of several reasons why in some species, parents may reduce their brood size by aborting some embryos or killing some offspring.
- The most extreme examples of cooperation and altruism are in eusocial species, in which some individuals reproduce little or not at all, and instead help relatives rear their offspring. In eusocial insects, nonreproductive workers rear reproductive queens and males, as well as other workers. Many social interactions in these colonies are governed by kin selection and policing by workers.
- Under some conditions, selection acting on groups can cause the evolution of altruism. This form of group selection can be viewed as a type of kin selection. Group selection acting on a pathogen sometimes favors the evolution of decreased virulence when increased host survival increases the number of new hosts that the pathogen infects.
- Conflicts may exist among different genes in a species' genome that are inherited by different pathways. Selection acting on loci that are transmitted through only one sex favors alleles that alter the sex ratio in favor of that sex. The changed sex ratio creates selection at other loci for suppressors that restore the 1:1 sex ratio.
- Kin and group selection explain three of the major transitions in the evolution of life on Earth. Eukaryotes evolved by the union of two organisms, in which the fitness of each depends on the other. The union of such a eukaryote with cyanobacteria produced photosynthetic eukaryotes: algae and plants. Multicellular organisms could evolve only because their cells are nearly genetically identical, and so cooperate due to kin selection.

## TERMS AND CONCEPTS

**altruism**
**conflict**
**cooperation**
**direct fitness**
**endosymbiont**
**eusocial**
**evolutionarily stable strategy (ESS)**
**game theory**
**group selection**
**Hamilton's rule**
**horizontal transmission**
**inclusive fitness**
**indirect fitness**
**kin selection**
**mutualism**
**parent-offspring conflict**
**reciprocity**
**relatedness**
**segregation distortion**
**selfish**
**sexually antagonistic selection**
**spite**
**transposon**
**vertical transmission**

## SUGGESTIONS FOR FURTHER READING

*An Introduction to Behavioural Ecology* (Wiley-Blackwell, Oxford, 2012) by N. B. Davies and colleagues is an outstanding introduction to that field. A more general introduction to animal behavior is *Animal Behavior: An Evolutionary Approach* by J. Alcock (Sinauer Associates, Sunderland, MA, 2013).

The evolution of social behavior and its implications for major transitions in evolution are comprehensively treated by A. F. G. Bourke in *Principles of Social Evolution* (Oxford University Press, Oxford, 2011). An excellent set of essays on many aspects of cooperation and conflict is *Levels of Selection*, edited by L. Keller (Princeton University Press, Princeton, NJ, 1999). J. A. R. Marshall's *Social Evolution and Inclusive Fitness Theory* (Princeton University Press, Princeton, NJ, 2015) is a comprehensive synthesis of that topic.

Genetic conflict and selfish genes are reviewed in a book by A. R. Burt and R. Trivers, *Genes in Conflict: The Biology of Selfish Genetic Elements* (Harvard University Press, Cambridge, MA, 2006). Much shorter but excellent are the review articles by J. H. Werren, "Selfish genetic elements, genetic conflict, and evolutionary innovation" (*Proc. Natl. Acad. Sci. USA* 108: 10863–10870, 2011) and W. R. Rice, "Nothing in genetics makes sense except in light of genomic conflict" (*Annu. Rev. Ecol. Evol. Syst.* 44: 217–237, 2013).

The evolutionary "battle of the sexes" is an area of active research. We recommend *Sexual Conflict* by G. Arnqvist and L. Rowe (Princeton University Press, Princeton, NJ, 2005). A concise overview that focuses on genetic aspects is the article by R. Bonduriansky and S. F. Chenoweth, "Intralocus sexual conflict" (*Trends Ecol. Evol.* 24: 280–288, 2009).

The topic of group selection has a rich history. One of the most important contributions to this subject is the famous book by G. C. Williams, *Adaptation and Natural Selection* (Princeton University Press, Princeton, NJ, 1966), which has stimulating thoughts on many other topics as well. More recent discussions include a book by E. Sober and D. S. Wilson, *Unto Others: The Evolution and Psychology of Unselfish Behavior* (Harvard University Press, Cambridge, MA, 1988), which takes a positive view of group selection, and an article by S. A. West and colleagues ("Evolutionary explanations for cooperation," *Current Biology* 17: R661–R672, 2007), who instead emphasize kin selection.

## PROBLEMS AND DISCUSSION TOPICS

1. Many species of animals make alarm calls, which warn others in their group that a predator is approaching. Alarm calls also attract the attention of the predator, making it more likely that the individual making the call will be eaten. Why might natural selection favor the evolution of alarm calls in a species? How might you test that hypothesis?
2. Darwin argued that natural selection would never cause a trait to evolve in one species that benefitted another species at a fitness expense to the first species. A study of egrets in Florida found that parents eject their own chicks from their nests, and this behavior feeds alligators living in the swamp below the nests. This steady supply of food improves the health and condition of the alligators. In view of Darwin's logic, what are two hypotheses that might explain why the egrets perform behaviors that benefit alligators?
3. Kin selection explains why organisms provide benefits to relatives. Is there a conflict between the principle of kin selection and the evolution of siblicide?
4. Explain why we expect mitochondria to have more mutations that are harmful to males than to females.
5. What differences do you expect to see in how females behave toward their brothers in haplodiploid species (such as ants) compared with diploid species (such as beetles)?
6. Many clonal marine invertebrates (such as corals and sponges) exhibit fierce competition for space, sometimes leading to death among competitors. At other times, two expanding colonies will merge to form a single, larger colony. What factors might account for decisions either to attack or to fuse with another colony?
7. Some pathogens, such as HIV, can be transmitted both vertically and horizontally. How do you expect their virulence to compare with that of pathogens that are transmitted only horizontally or only vertically?