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Social Evolution

When Darwin first published *Origin of Species* in 1859, a widespread reaction among intellectuals and religious figures was that his theory of evolution undermined morality. In the place of a divinely ordered world featuring the retribution of the deity who created all forms of life, Darwin's theory of life was entirely materialistic, with no important connection to a deity or a spiritual realm. In the nineteenth century, it was widely supposed that such materialism provided a justification for utilitarianism, socialism, and even communism. Notably, Karl Marx agreed with this assumption. He regarded Darwinism as a valuable support for his dialectical materialism. Charles Darwin himself held no such view. Although liberal in his politics, he was very far from being a revolutionary.

The central issue was whether evolution was corrosive or supportive of morality, law-abiding behavior, and political stability. At first it seemed as if Darwinism was an excellent justification for unbridled competition, a laissez-faire society of dog-eat-dog, and conflict between economic classes. That was the type of social behavior that was expected to evolve with Darwinian selection. But decades of evolutionary and ecological research have shown that there is no universal tendency to rapacious social behavior; it is a possible outcome, but not a necessary one. In many situations, the evolution of social behavior tends to produce what humans consider moral behavior. This surprising reversal of intuitive expectations for the evolution of behavior is the concern of this chapter.

Biologists have used three main ideas to explain why evolution has favored the evolution of restrained social behavior. These ideas are group selection, kin selection, and strategy selection. Our main theme is *why evolution has favored seemingly ethical behavior in so many animals,* despite the Darwinian benefits that seem to come from selfish behavior, on first appraisal.

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GROUP SELECTION

20.1 Biological altruism is critical for social evolution

At the core of many debates about social evolution is the phenomenon of **altruism**. In evolutionary biology, unlike human politics or psychology, altruism is conceived in relation to the consequences of behavior for the Darwinian fitness of defined individuals. Typical examples of biological altruism include one animal aiding another—supplying food, perhaps—or helping another animal fend off an attack from a predator. Scientists have often noticed this type of behavior among both birds and mammals. Groups of younger male chimpanzees sometimes cooperate to harass couples that are mating. Once they have chased off the copulating male, they take turns mating with the female left behind. In scrub jays *(Aphelocoma coerulescens)*, older offspring help the parents feed their younger siblings. Cooperative behavior like this is often reminiscent of humans helping each other, within families and within combat units during wartime.

> *Typical examples of biological altruism include one animal aiding another—supplying food, perhaps—or helping another animal fend off an attack from a predator.*

Some of the most dramatic forms of altruism are found among the **social insects**: group-living insect species such as honeybees, colonial wasps, ants, and termites. In these insects, most members of the group do not reproduce. Honeybee **workers** live out their lives supplying resources to the small subset of males and females that do get to reproduce—especially the **queen** of the hive, which may be the only reproductive female (Figure 20.1A). In social insects, the sterile castes of worker and **soldier** behave as if their lives are of no importance. They do not hesitate to put their bodies in harm's way to stop predators from threatening the hive. They will also attack potential prey with abandon, even when those prey might be dozens of times larger than the ants or termites that attack them.

Altruism is a problem for evolutionary biology because we expect that natural selection will oppose behavioral tendencies that might lead to death or sterilization. The logic of natural selection suggests that individual animals are selected to survive and reproduce. Yet some individuals behave in ways that predictably reduce their fitness. The problem of altruism is sketched in Figure 20.1B for the issue of restrained aggression in conflicts between members of the same species. It is not only sterile honeybees that are a puzzle. The lack of aggression between animals that need the same resources to survive and reproduce is also anomalous.

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FIGURE 20.1A A Honeybee Queen Attended by Sterile Female Workers

FIGURE 20.1B The Problem of Altruism

Group selection can prevail over individual selection 20.2

In **group selection,** entire populations are sometimes selected in the same way that individuals are selected in individual selection. Group selection then works by the extinction and propagation of populations. The extinction of a population is the equivalent of the death of an individual in individual selection. Propagation occurs when new populations are founded by emigration from another "reproducing" population. When the populations of a species are well defined, many features of group selection are comparable to selection acting on individual members of an asexual species. This does not mean that populations are always structured this way, nor does it mean that group selection can work only under such conditions. But it is one scenario in which group selection might work.

How might the concept of group selection explain altruism? The connection between group selection and social behavior is that **selfish behavior** might foster individual fitness, yet undermine the survival of the group as a whole. Group selection might act to prevent overgrazing by deer, for example, even though each deer might benefit from eating more. If group selection did not act in this way, then herbivores like deer might be at risk of eating all their food, causing the population to go extinct. Individual selection should, at first sight, favor just such selfish behavior on the part of deer and other animals. The more the deer eat, the better their health and the more they should be able to reproduce, ignoring the consequences of overgrazing for the ecology of the local habitat.

When the process of group selection for altruism is modeled using computer simulation or mathematics, the results show that group selection can work under some conditions, even when individual selection favors selfish behavior. But the conditions under which altruism is increased in the population are extreme. For instance, selfish behavior must be very disruptive in its effects on group, or population, survival. Groups must go extinct frequently when selfish behavior is common, or they must have reductions in their ability to colonize new habitats.

(*Module continues on next page.*)

Michael J. Wade has argued that an important determinant of the power of group selection is the pattern of population propagation. The more propagation is itself a "group" process, as in the ocean crossing of the *Mayflower* colonists who founded New England, the more likely it is that group selection will succeed in increasing altruistic behavior. This effect can be characterized in terms of two extreme alternative scenarios for propagation—the migrant pool scenario and the propagule scenario.

Figure 20.2A shows the **migrant pool** scenario. In this scenario, the migrants that found new populations are drawn from all surviving populations. Somewhat as in the melting pot of latter-day American immigration, all migrating individuals are mixed together to found new populations. These populations then grow in numbers, so long as the number of selfish individuals is not too high. Populations with a lot of selfish individuals tend to go extinct. In this type of group selection, populations are not formed by well-defined groups, though the fate of a population depends on its mix of altruistic and selfish individuals.

Figure 20.2B shows the **propagule** scenario. In this scenario, the migrants that found new populations all come

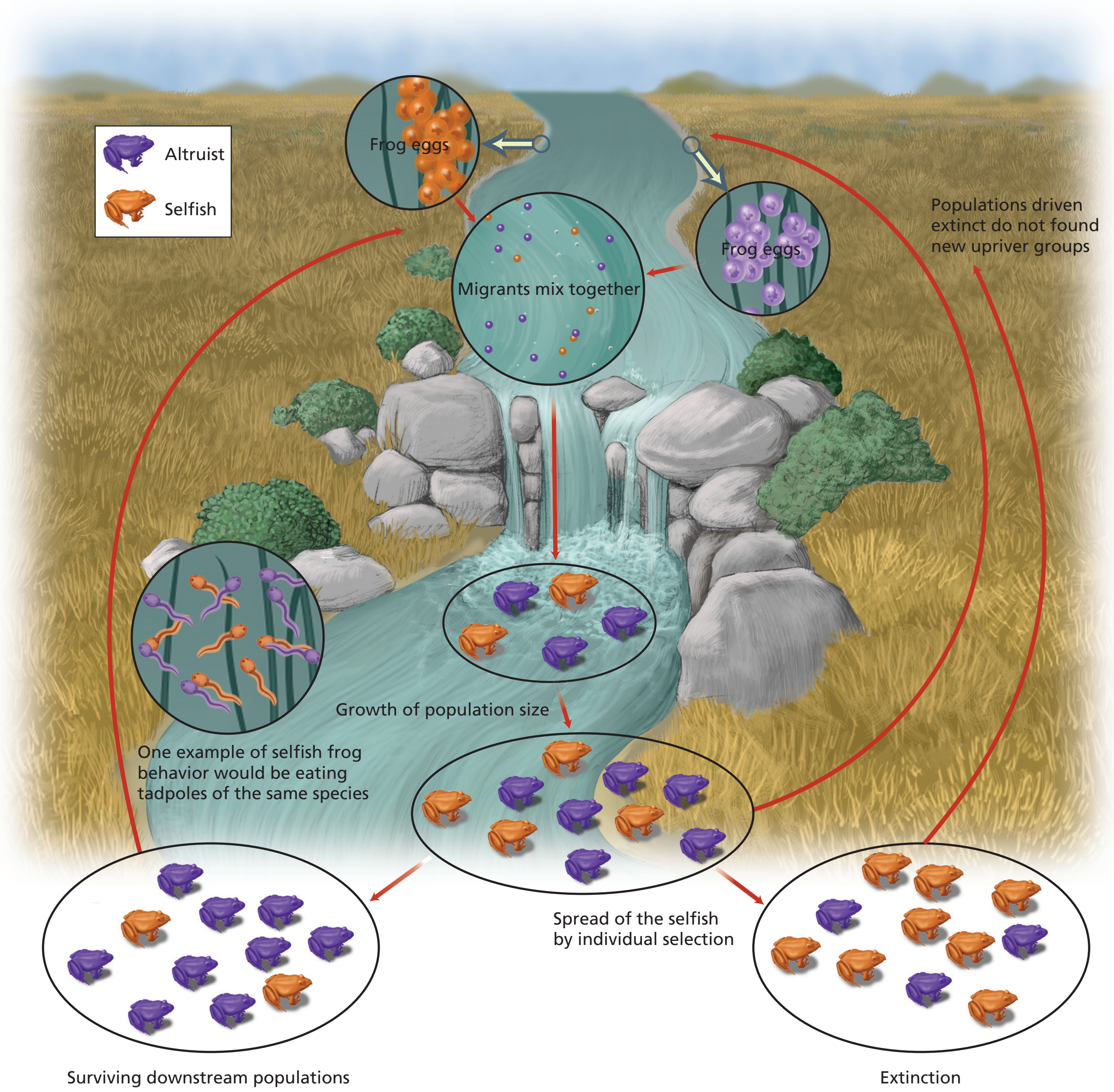

FIGURE 20.2A Migrant Pool Model for Group Selection In this model, new populations are founded by mixing individuals from different populations.

from the same ancestral population. There is no mixing of migrants to found new populations. However, once the new groups are founded, their ecology and evolution are the same as they are in the migrant pool scenario.

Theoretical work shows that the propagule scenario (Figure 20.2B) is much more likely to lead to successful selection for behavior that benefits the group. This occurs because the mixing of migrants in the migrant pool scenario (Figure 20.2A) dilutes the impact of the group selection process. Group selection can work with either model, but it is far more difficult for group selection to overcome individual selection with migrant pool mixing. This may occur because unlike the propagule scenario, the group structure of the migrant pool is partly broken down by the mixing of migrants.

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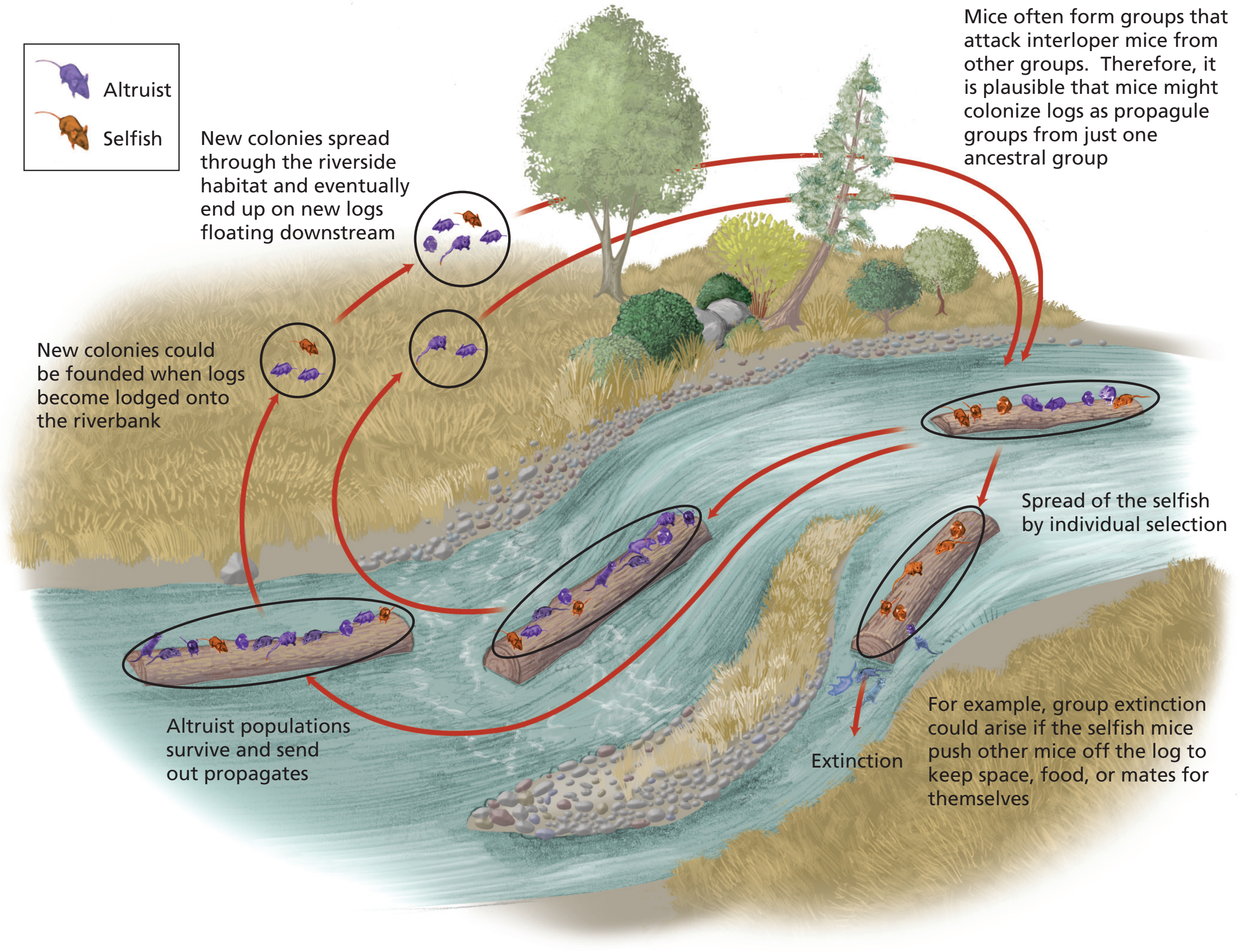

Mice often form groups that attack interloper mice from other groups. Therefore, it is plausible that mice might colonize logs as propagule groups from just one ancestral group

New colonies spread through the riverside habitat and eventually end up on new logs floating downstream

New colonies could be founded when logs become lodged onto the riverbank

Spread of the selfish by individual selection

Altruist populations survive and send out propagates

Extinction

For example, group extinction could arise if the selfish mice push other mice off the log to keep space, food, or mates for themselves

FIGURE 20.2B Propagule Model for Group Selection In this model, each new population is founded by individuals that come from only one established population.

20.3 Group selection may be the best explanation for some cases of biological altruism

Theoretical analysis of group selection shows that it is possible for altruism to evolve through group selection, as we have just seen. But are actual animal populations likely to evolve altruism as a result of the process of group selection? Two kinds of information help us to answer this question. The first consists of laboratory experiments that mimic theoretical models. The second is the natural history of populations, insofar as that natural history can shape group selection in nature.

Figure 20.3A summarizes an experiment testing the power of group selection in a laboratory population of the flour beetle, *Tribolium*. Flour beetles are one of the major agricultural pests, primarily consuming stored grain. If you eat baked goods regularly, you have eaten a fair amount of flour beetle. Flour beetles eat more than grain. They also eat each other—the adults eat eggs and juveniles, the larvae eat eggs, and so on. This cannibalism is obviously selfish behavior, raising the question of whether it is possible to devise a group selection experiment to reduce its impact.

Suppose that flour beetles are kept together in vials, as groups of several dozens in size. If they are given a fixed period for population growth, the more altruistic beetles should reach larger population sizes, because they will not be eating each other. Following our previous discussion of patterns of group selection, Michael J. Wade propagated group-selected populations in discrete propagules, without migration, so there was no mixing of migrants. When Wade imposed group selection, only the vials with large populations were allowed to start additional populations, as shown in Figure 20.3A.

When this procedure was performed over multiple generations, the results were clear. Group selection led to the maintenance of higher population sizes, compared to controls that were not group selected. This experiment verifies our theoretical analysis: Group selection *can* work, when the conditions are right. One of these conditions is that groups found new populations using discrete propagule groups, without mixing of migrants.

But how likely is it that conditions favoring group selection will occur in nature? A key point is that most species are very unlikely to undergo group selection. Species that do not live in groups are unlikely to undergo group selection. Many species of animals, plants, and microbes occur sporadically in the wild, having little contact with others of their species. Species that have unstructured populations are also unlikely to undergo group selection. Some species live in groups; but these groups exhibit little subdivision for group selection to act on, and they do not propagate themselves as groups. Large colonies of communally nesting birds, large herds of ungulates such as deer and antelope, and human populations all fit this pattern. These points are summarized in the box, "Group Selection in Nature: How Common?"

But certain species might well undergo group selection. Pathogens that infect hosts as single propagule groups, with-

Group Selection in Nature: How Common?

Unlikely to show group selection	Possible cases with group selection
• Animals with large, randomly mating populations without local breeding (e.g., most herd mammals; flying insects)	• Pathogens that infect as propagule groups (e.g., lethal viruses)
• Plants that distribute pollen over a wide area (e.g., most conifers and grasses)	• Animals that migrate as small social bands with mating restricted to the band (e.g., some of the social mammals)

out multiple infection, are an example. In such cases, group selection might favor benign pathogens that do not kill the host too quickly by selfishly reproducing too fast. Some biologists think that the **myxoma virus** that infects rabbits has evolved from being highly lethal to being relatively benign, particularly in Australia, where the virus was deliberately used to kill off rabbits. (See Chapter 13 for more detail about myxoma virus.) Indeed, when the virus was first introduced it killed off rabbits at a great rate. Now the virus is not so deadly. On the other hand, the rabbit has evolved greater resistance to the virus.

There are other cases in which group selection may have been important. Some rodents, such as house mice, live in well-defined groups that rarely interbreed. There is some evidence that these small breeding populations of mice undergo group selection against selfish alleles, particularly alleles that disrupt the genetic system.

But these two cases do not suggest that group selection can explain the vast range of species that exhibit benign social behavior. Most altruistic species probably undergo little group selection. So group selection is not a general explanation for biological altruism, even it favors the evolution of altruism in some species.

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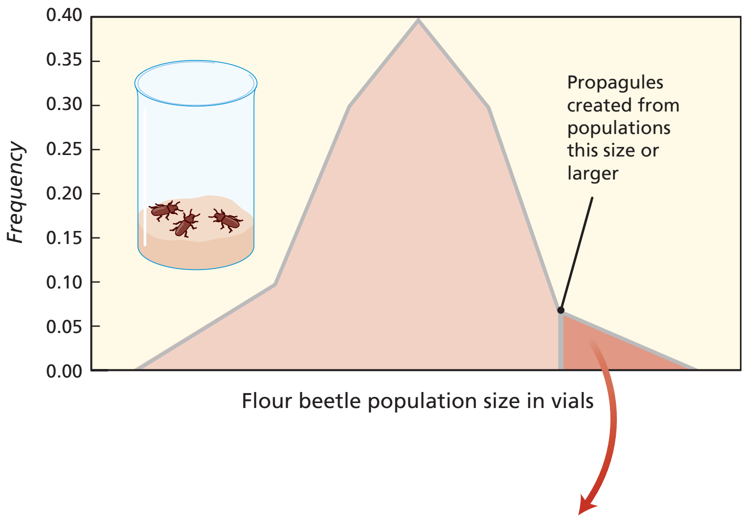

Each selected population is used to start enough new propagules to regenerate the complete set of populations for the next round of selection.

FIGURE 20.3A **Experimental Group Selection on Population Size** The inference from this experiment was that group-selected populations had a slower spread of selfish behavior.

KIN SELECTION

20.4 Selection can act on families

As already mentioned, the most spectacular examples of biological altruism come from the social insects. Soldier ants and soldier termites give their lives defending their colonies, even though they will never be able to reproduce. Indeed, their bodies are often greatly modified even from those of their fellow workers. Their mandibles are often much larger. Some ant soldiers have modified abdomens for spraying toxic fluids at other insects—a natural form of chemical warfare. And then there is the wide range of worker types, which also do not reproduce, yet go about building hives and mounds, gathering food, tending the young, and so on. In a bizarre way, these social insects resemble the social economies of human communities. But they take it farther, in that their "royalty" of queens and **kings** are the primary reproducers. (Figures 20.4A to 20.4C illustrate the lives of the social insects.) Not even human societies are so extreme.

These facts were well known to Darwin and others in the nineteenth century. Darwin devoted some thought to how such organisms could have evolved. One question was how a single species could have such different morphological forms and behavioral patterns among its members. This is not a profound difficulty. It is common enough to have males and females that differ substantially in morphology and behavior, and not all gender determination is genetic. Some of it is environmental. In reptiles, gender is often determined by the temperature at which the turtle or lizard matured. Within the single life spans of moths and butterflies, different life stages have very different morphologies and behaviors. So the production of sterile workers and soldiers by changes in nutrition and other manipulations is not a violation of biology.

The more pertinent difficulty is why some individuals within social insect species—specifically workers and soldiers—do not reproduce. Because these insects are organisms bearing genes, natural selection would be expected to favor the copying of their genes into the next generation. The natural conclusion is that sterile honeybees should be selected to reproduce—unless, perhaps, group selection has favored restraint.

But there is another possibility: **selection among families,** or "kin selection." This is a common principle in plant and animal breeding, as Darwin knew. Plant varieties may be selected because of the flowers or fruit of sterile members of a family, even though the propagation of the variety takes place using the fertile members of the family. In the cultivation of fruit, for example, the seedless fruit may go to the market while the fruit having seed is used for cultivation, because people do not like to bite or swallow seeds. In meat production, breeders may choose bulls and cows according to the carcass of their slaughtered offspring, even though the slaughtered will never be able to reproduce. In these cases, the entire family is being selected by the breeder.

FIGURE 20.4A **Life Inside an Ant Colony**

In nature, when family groups function together ecologically, the same principle can still apply. Insect families that produce more fertile offspring than other families may do so by having some members of the family take on nonreproductive roles. We will consider the case of social insects in more detail shortly. But for now, the basic concept of kin selection is our provisional explanation for biological altruism when organisms function together as families. **Kin selection** is based on the transmission of an organism's genes into the next generation by means other than the production of immediate descendants. There is kin selection when one sister helps another sister raise the second sister's offspring. Kin selection also occurs when grandparents raise their grandchildren, or help their children do so. Kin selection also occurs when one first cousin dies to save the life of another first cousin. Note, however, that kin selection does not provide an explanation of biological altruism between unrelated individuals.

One way to think of this is that individual selection is about the survival and reproduction of an individual, and kin selection concerns *all other* means by which individuals can help their relatives so that copies of the helper's genes find their way into the next generation. Group selection is a process that occurs at another level from that of the family. Natural selection includes all forms of selection, including group selection. However, these are just terminologies. The differences between the levels of selection arise no matter what they are called.

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FIGURE 20.4B Life Inside a Beehive

FIGURE 20.4C Life Inside a Termite Colony

20.5 Altruism toward relatives is favored when the cost is less than the benefit times relatedness

All the essential features of kin selection can be understood in relation to one story. This will enable you to understand the evolution and ecology of biological altruism in the family setting. Suppose that a chimpanzee finds a supply of bananas that no other chimpanzee has found. He eats his fill of bananas, and leaves the rest for later. He is walking away with an uneaten banana and comes upon another chimp. Should he give the banana to the other chimp?

This decision is diagrammed in Figure 20.5A. The chimp with the banana, the potential donor, will lose some nutrition that might aid the donor's fitness if it does not give up the banana. Call that cost C. The fitness of the hungry chimp will benefit from the banana by an amount B. The key parameter is r, the degree of **consanguinity** (which means "same-blooded"), or the number of genes the chimps have in common. For **identical twins,** r is 1; all their genes are in common. For unrelated individuals, r is 0. Note that r is sometimes called the **coefficient of genetic relatedness**.

If the benefit is greater than the cost, so $B > C$, and the two chimps are twins, then the chimp with the banana should give it up. He would be helping his own genes get into the next generation more by donating the banana, probably because he doesn't need much more banana, while his hungry twin might be starving. But if the other chimp is unrelated, then the logic of kin selection says that the chimp with the banana should not give it up. In short, the donation of a banana is entirely dependent on the relative costs and benefits to donor and recipient, respectively, weighted by how much they are in fact kin—r, the degree of consanguinity. In other words, according to the theorist W. D. Hamilton, altruism can evolve when $Br > C$. (It doesn't always evolve, but at least it becomes possible.)

Unrelated individuals and identical twins are the simplest cases, as well as the most extreme. In between are the usual types of kin: siblings, nieces, nephews, grandparents, and so on. The r values for these relationships are shown in the box, "Some Coefficients of Genetic Relatedness." In these relationships, the degree of consanguinity constrains the evolution of biological altruism between any two individuals. The value of r between the children of diploid parents provides a convenient benchmark. Each parent gives the child half its genes, leaving aside sex chromosomes, so $r = \frac{1}{2}$. A child has half the genetic makeup of the parent, from the standpoint of consanguinity. Then it is also logical that r between grandparent and grandchild should be $\frac{1}{4}$. The grandparent is two reproductive events removed from the grandchild. In this way, we expect r values to be larger for individuals who are closely related, and smaller for "distant relatives."

Bear in mind that the benefit and cost parameters (B and C) are important too. In organisms where it is unlikely that an organism will have much to give to, or do for, its relatives, then there may be few opportunities for biological altruism to evolve. Because biological altruism is not that common, this may often be the situation.

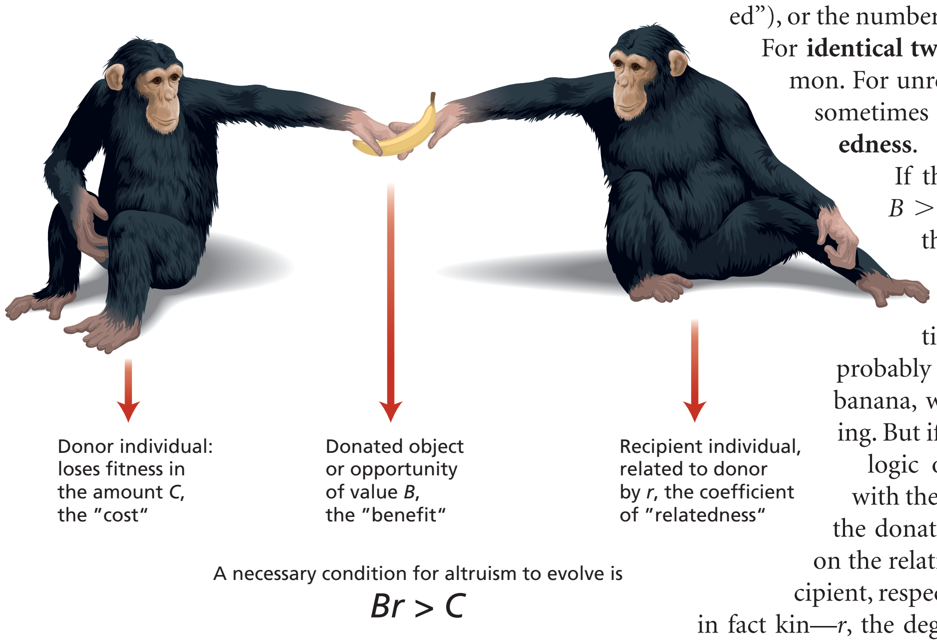

FIGURE 20.5A The Essential Features of Altruism One chimp can help another chimp by donating a banana. Under what conditions will natural selection favor such an act of altruism?

Some Coefficients of Genetic Relatedness

If there is inbreeding, the individuals of a social group may have very high degrees of genetic relatedness.

But if we assume no inbreeding, and thus random mating, we have the following values for r in human populations:

Identical twins	1
Genetic clones	1
Full siblings	1/2
Parent-child	1/2
Half-siblings	1/4
Uncle-nephew	1/4
Aunt-niece	1/4
Uncle-niece	1/4
Aunt-nephew	1/4
Grandparent-grandchild	1/4
First cousins	1/8
Husband-wife	0
Unrelated individuals	0

Insects with closely related sisters evolve complex social systems dominated by females

20.6

With the basic rules of kin selection under our belts, especially the requirement that *Br* be greater than *C*, let us return to the high level of biological altruism among social insects. It is an extremely powerful example of the importance of kin selection in the evolution of social behavior. Social insects have evolved most often in the Order Hymenoptera, which includes all the ants, the bees, and the wasps. Not all hymenopterans are social, but many are. **Hymenoptera** have an unusual form of **sex determination** called **haplodiploid sex determination**. Unfertilized eggs, which are haploid, become male, as shown in Figure 20.6A. Fertilized eggs become female, and are diploid.

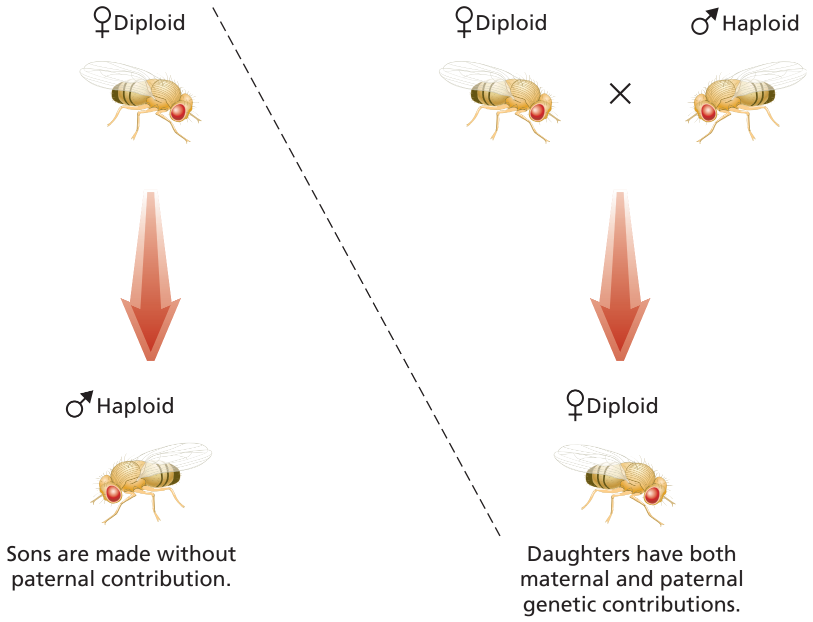

FIGURE 20.6A Haplodiploid Sex Determination Unfertilized eggs grow up to be sons, while fertilized eggs grow up to be daughters.

This unusual system of sex determination transforms the genetic relationships among the members of hymenopteran families. As shown in the box, "Genetic Relatedness in Hymenoptera," females are typically more related to each other than males are to other members of the family. The father-son relationship no longer exists. Notably, full sisters have at least a $^{3}/_{4}$ level of genetic relationship, because the half of their genome that comes from their haploid father is always identical and the half that comes from the diploid mother is identical half the time. (If there is inbreeding, this consanguinity value may be even higher than $^{3}/_{4}$.) Remarkably, this value is higher than that between mothers and their offspring. In effect, hymenopteran females can spread their genes more by "producing" sisters than by producing children, at least in theory.

What actually happens in nature is a demonstration of the power of a genetic system to shape social relationships. The societies that hymenoptera evolve are female dominated. Their characteristic pattern is one of sisters helping each other to reproduce. In the most elaborate cases, such as honeybees and ants, there is a queen that does all the reproducing. The queen is tended by her numerous sterile daughters, so that more daughters can be produced—sisters to the sterile workers. In some social hymenoptera, the sterile daughters are specialized for combat, as soldiers, to defend the colony from potential invaders. Males are pushed to the margins of this animal society, supplying little work beyond fertilizing the queen.

The hymenopteran system of sex determination alters normal genetic relationships, transforming the organization of these insect societies. Note in particular that the sister-sister value for *r* is higher than that between all relatives in species with normal sex determination, leaving aside identical twins. There is a dramatic correspondence between genetic relationship and degree of biological altruism in hymenopteran females and males, which suggests that kin selection is indeed fundamental to the explanation of social behavior in such societies.

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Genetic Relatedness in Hymenoptera

Genetic relatedness involving males:	
Father-son	0
Mother-son	1/2
Brothers	1/2
Brother-sister	1/4
Genetic relatedness without males:	
Mother-daughter	1/2
Full-sib sisters	3/4
Half-sisters	1/4

The figure for half-sisters assumes that their fathers are unrelated. If the fathers are related to each other, then the coefficient of genetic relatedness of half-sisters will increase.

Males are less related to other hive members than females are, with sisters less related to brothers. This will tend to produce matriarchal societies, with peripheral males.

20.7 Kin selection led to the evolution of the burrowing societies of termites and naked mole rats

If the hymenopteran genetic system gives rise to a gender-biased social system, then a genetic system that is symmetrical between the genders should lead to the evolution of animal societies that are not biased with respect to gender. What do we find in nature?

The best-known examples of such societies are those of another social insect, termites, from the Isoptera. Termites feed on underground, woody, plant material, roots being an important item in their diet. This is an unusual ecological niche. Much of termite nutrition is dependent on breaking down cellulose, a polymer built by plants from molecules of glucose. The glucose molecules in cellulose are linked together by a chemical bond that most animals cannot break during digestion, so cellulose makes woody material indigestible for most species, including humans. Cellulose is roughage for us for that reason. But some microbes can digest cellulose. Termites maintain populations of these microbes in their guts and are nourished by the digestive action of these microbes. This dependence gives termites the problem of maintaining these microbe populations, which they solve by eating each other's vomit or feces. Not a pretty thought, but the microbes of the termite gut are absolutely fundamental to its way of life.

This dependence on ingesting each other's microbes greatly influences the social calculus of termite life. A termite that has lost its microbes stands to benefit to a high degree merely from the excreta of a termite that still has some of the microbes. This means that termite families can aid each other to a remarkable extent by staying together. This increases the value of B in the inequality $Br > C$. In addition, because they live underground and need to remain together, inbreeding is higher in termites than in other organisms, elevating r. Finally, because vomit and feces are not exactly hard to produce, the cost factor, C, is likely to be small. All these factors together explain why termite societies show so much biological altruism.

An important feature of termite societies is that they are symmetrical between genders, as diagrammed in Figure 20.7A. There are both male and female sterile

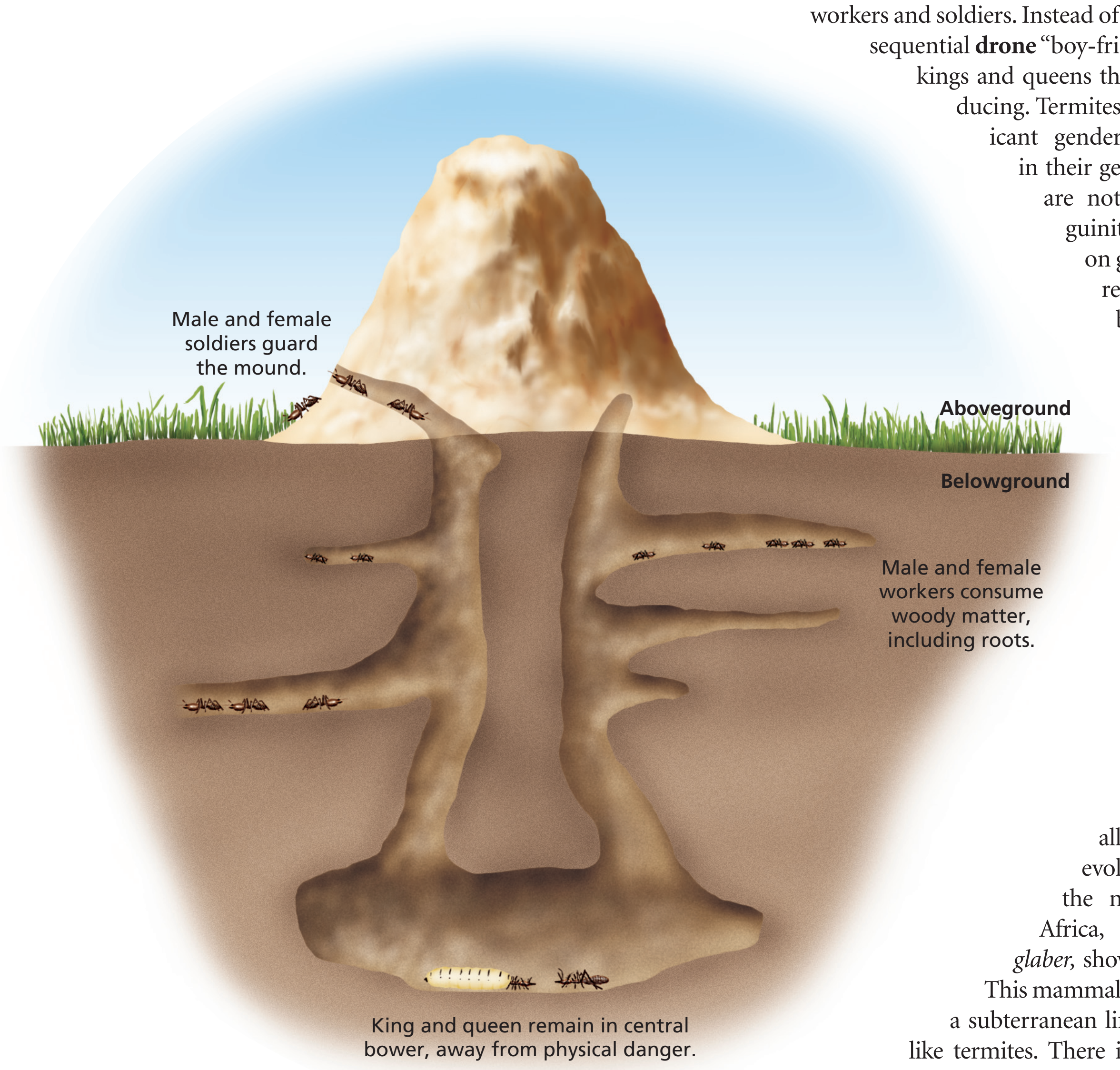

FIGURE 20.7A **The Ecology of Termite Societies**

workers and soldiers. Instead of queens with inconsequential **drone** "boy-friends," termites have kings and queens that do all the reproducing. Termites do not have significant gender-based asymmetry in their genetic system. Males are not haploid. Consanguinity does not depend on gender. Sisters are as related to their brothers as they are to their sisters. This leads to an expectation of symmetry between the sexes, according to kin selection theory. Indeed, the termite social system fits the expectations of evolutionary theory in its symmetry between genders.

A intriguing parallel to termite social evolution is afforded by the naked mole rat of Africa, *Heterocephalus glaber,* shown in Figure 20.7B. This mammalian species also lives a subterranean life in family groups, like termites. There is a primary reproducing couple, the king and queen, along with nonreproductive males and females. This gender-role symmetry corresponds to the symmetry of the mammalian genetic system, where both males and females are diploid. Like the termites, naked mole rats depend on a microbe in their guts to digest woody material, making them exceptionally dependent on each other for reinfection. Termites and naked mole rats provide a remarkable example of parallel evolution, in which the ecology of a species determines its social evolution.

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FIGURE 20.7B The naked mole rat is a mammal with an ecology like that of a termite.

EVOLUTIONARY GAMES

20.8 Animals balance aggression and peaceful behavior as if social interaction were a game

As we have seen, group selection is unlikely to establish cooperative social behavior in most species, while kin selection fosters altruism primarily between biological relatives. What about interactions between nonrelatives?

The basic paradox of restrained aggression remains to be resolved. As we noted earlier, there is no obvious reason why animals should not exhibit unlimited aggression toward nonrelatives, if there is a conflict over who should have some resource. Yet violent combat is rare among animals of the same species. It does occur in some situations, such as fights between lion males for sexual access to the females of a pride, as rendered in *The Lion King*. But these situations are rare. Much more common are fights that are **ritualized**—where antlers, fangs, and claws are not used with complete ruthlessness. Instead, animals seem to hold back their aggression. Often they are literally making more noise than they are fighting—as seen in animals ranging from chirping birds to roaring stags. Why do they do this? Attacking a nonaggressive opponent should lead to victory, as shown in Figure 20.8A, and the good things of life.

Animals don't bargain with district attorneys, and they don't play schoolyard games . . .

The key step that led to the resolution of the paradox of restrained aggression came from the application of **game theory**. Game theory was originally a branch of mathematics applied to human economic and criminal behavior. Game theorists dealt with problems of cooperation among intelligent human strategists.

A classic problem of traditional game theory is called the **Prisoner's Dilemma**. This game arises when two criminals are arrested for a crime, but there is not enough evidence to convict either one. The two criminals are quite likely to know enough to incriminate each other. If one crook plea-bargains for a reduced sentence in exchange for implicating the other criminal, then the implicating crook ends up ahead, *provided* the other prisoner does not do the same. If each crook implicates the other, then the court can send both to prison for the full term; this is because plea bargains normally protect the indicted from self-incrimination, but they do not protect them from evidence that comes from other sources. This situation has the matrix of outcomes shown in Figure 20.8B.

In conventional game theory, the two prisoners should incriminate each other when they cannot coordinate their actions, because that is the only decision that each prisoner can make to improve his or her outcome. If prisoner 1 incriminates prisoner 2, but 2 does not incriminate 1, then prisoner 1 is freed. And vice versa. But if the prisoners are incriminating each other, they are both

going down for a long sentence anyway. Therefore, the best move is always to incriminate.

This theory seems paradoxical, but it arises from the nature of games. The results of your action depend on the choices of your opponent. In football, for example, if the defense assumes that the offense will pass, it will "defend the pass," which is a less effective strategy against a running play. And vice versa. The success of the offense will depend on choosing to do the opposite of what the defense expects. Still another example is the Rock-Scissors-Paper game, in which any choice may lose, win, or tie, depending on the opponent's choice. (For those of you who haven't played this game, Rock beats Scissors, Scissors beats Paper, and Paper beats Rock. You have to make your choice without knowing your opponent's choice.) Game outcomes depend on the choices of all players.

Animals don't bargain with district attorneys, and they don't play schoolyard games, so how does game theory apply to animal conflict? There is a key element in common—the consequences of aggression and cooperation depend on the actions of other animals, just as they do in humans. This realization led J. Maynard Smith and others to develop evolutionary game theory, the key to understanding the evolution of animal conflict between unrelated individuals.

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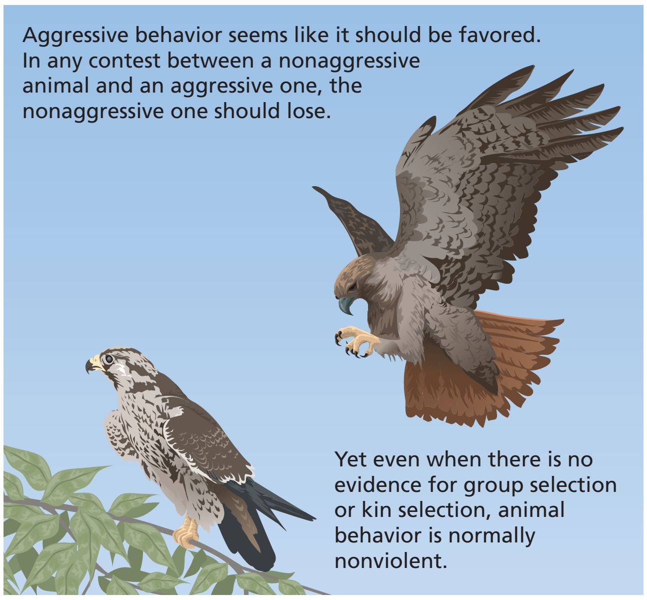
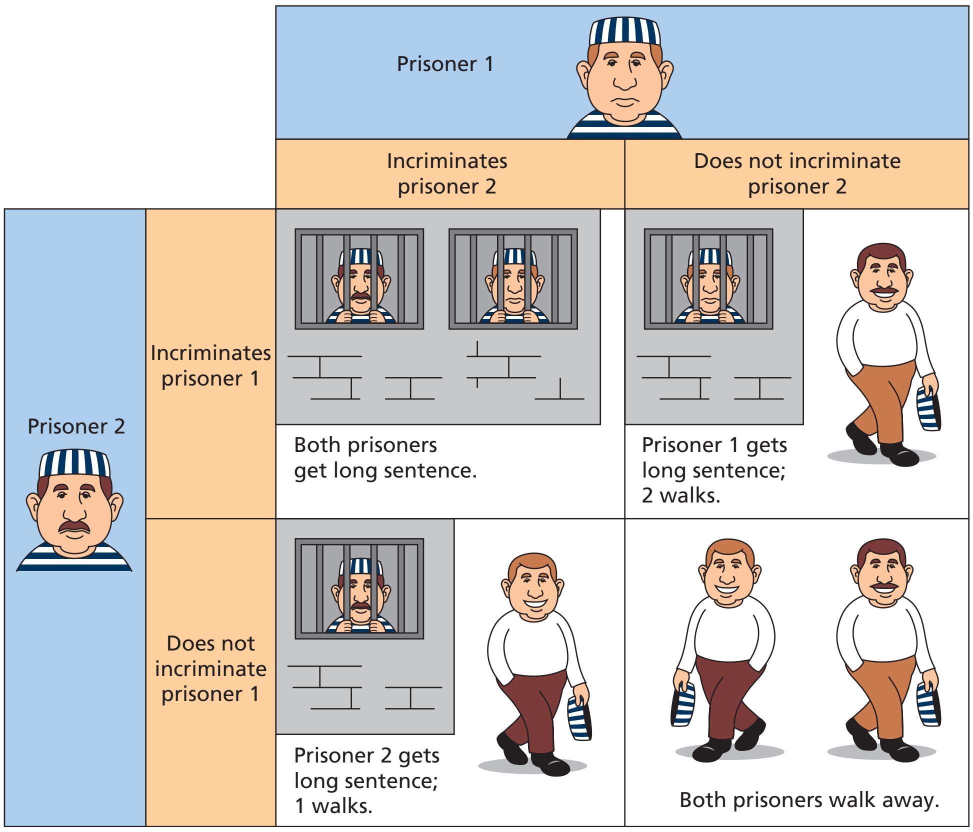


Aggressive behavior seems like it should be favored. In any contest between a nonaggressive animal and an aggressive one, the nonaggressive one should lose.

Yet even when there is no evidence for group selection or kin selection, animal behavior is normally nonviolent.

FIGURE 20.8A The Basic Paradox of Animal Social Behavior



		Prisoner 1	
		Incriminates prisoner 2	Does not incriminate prisoner 2
Prisoner 2	Incriminates prisoner 1	Both prisoners get long sentence.	Prisoner 1 gets long sentence; 2 walks.
	Does not incriminate prisoner 1	Prisoner 2 gets long sentence; 1 walks.	Both prisoners walk away.

FIGURE 20.8B The Prisoner's Dilemma When criminals are arrested together, the goal of the police is to get them to incriminate each other. When the crooks do so, they both end up in prison. When they don't incriminate each other, they can both go free.

20.9 Fitness depends on strategies that specify an animal's behavior in its conflicts

Animals do not behave like humans. Individual animals rarely, if ever, adopt idiosyncratic social strategies previously unseen in their species. Humans do. Therefore, the kind of behavioral flexibility assumed in normal game theory is not appropriately assumed in evolutionary game theory. Instead, animals behave in a stereotypical manner, within a very limited range of options, or **strategy selections**.

This idea of a defined strategy can be applied to animal conflicts in a straightforward way. Suppose that two animals want the same food item, mate, or territory. These animals could be birds, mammals, or even insects. At each moment, they have three alternative behaviors: Attack, Retreat, or Display. An **Attack** may allow the attacker to drive off its opponent. Or the attacker could be injured by the opponent. In that case, it will probably **Retreat**. Or the animal could

Evolutionary Game Strategies

An evolutionary game strategy describes what an animal will do in its social behavior whenever there is a conflict.

There are two extreme strategies:

Hawk—Attack whenever there is conflict, continuing the attack until victory is achieved or injury (including fatal injury) forces a retreat.

Dove—Display (twitter, flap wings, open mouth, engage in electoral politics) until you or your adversary give up because other pursuits have become more interesting (looking for water, getting out of the sun, etc.). Also, if Attacked, immediately Retreat before injuries occur.

just Retreat, abandoning the conflict and letting the other animal take the prize. To **Display** means to make enough noise, or other fuss, that the other animal knows that the prize is still disputed, but there is no direct aggression. Honking a car horn is a human display. Birdsong is a Display, as the flapping of insect or bird wings may be.

In a conflict situation, two extreme strategies are easily identified: Hawk and Dove. Hawks always attack until they either get the prize or are injured and forced to retreat. The **Hawk strategy** embodies the nineteenth-century idea of the type of morality that people supposed Darwin's theory of evolution would foster—unrestrained ferocity. Doves, by contrast, only Display; they never attack. If another individual tries to attack them, the **Dove strategy** is to immediately retreat. Contests between Doves are decided when one or the other gives up out of boredom or fatigue. The Hawk and Dove strategies are summarized in the box, "Evolutionary Game Strategies."

What are the consequences of conflicts involving Hawks and Doves? Three cases are shown in Figure 20.9A. Let the fitness value of winning a conflict be V. Let the cost of being injured be W, which will normally be greater than V. Let the cost of a protracted period of display between two Doves be T (for time), where T is much less than V or W.

With these parameters, the *average* benefit that Hawks derive from a conflict with each other is $(V - W)/2 < 0$, as part (i) of Figure 20.9A shows. That is, Hawks beat up on each other. The average benefit that two Doves derive from a conflict with each other is $V/2 - T > 0$, as part (ii) of Figure 20.9A shows. That is, Doves resolve their conflicts at a lower cost than Hawks do. But contests between Hawks and Doves are resolved entirely in favor of Hawks, which always receive the prize, V. Doves, however, get out of trouble quickly, receiving 0. Part (iii) of Figure 20.9A shows this situation.

All this information defines animal conflicts in relation to alternative evolutionary strategies. Next, let's consider how these strategies actually fare in the arena of social evolution.

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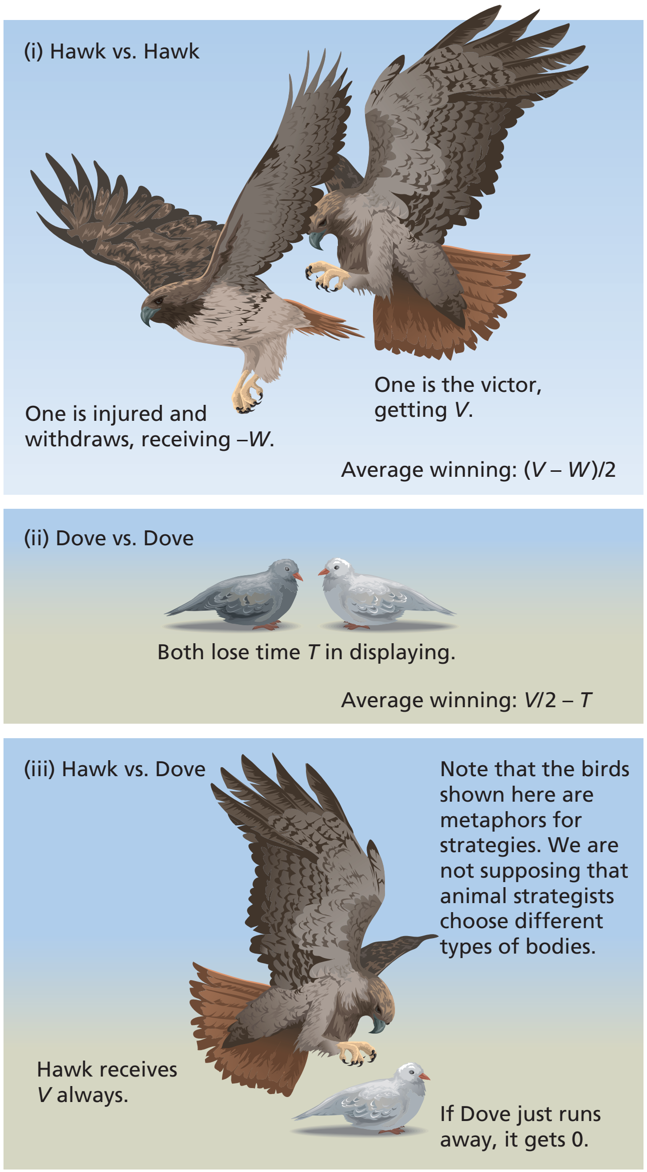


(i) Hawk vs. Hawk

One is injured and withdraws, receiving $-W$.

One is the victor, getting V.

Average winning: $(V - W)/2$

(ii) Dove vs. Dove

Both lose time T in displaying.

Average winning: $V/2 - T$

(iii) Hawk vs. Dove

Note that the birds shown here are metaphors for strategies. We are not supposing that animal strategists choose different types of bodies.

Hawk receives V always.

If Dove just runs away, it gets 0.

FIGURE 20.9A Conflicts Between Hawks and Doves There are three basic conflict possibilities: (i) Hawk vs. Hawk, (ii) Dove vs. Dove, and (iii) Hawk vs. Dove.

20.10 Violent behavior is rare if the costs of injury are greater than the benefits of victory

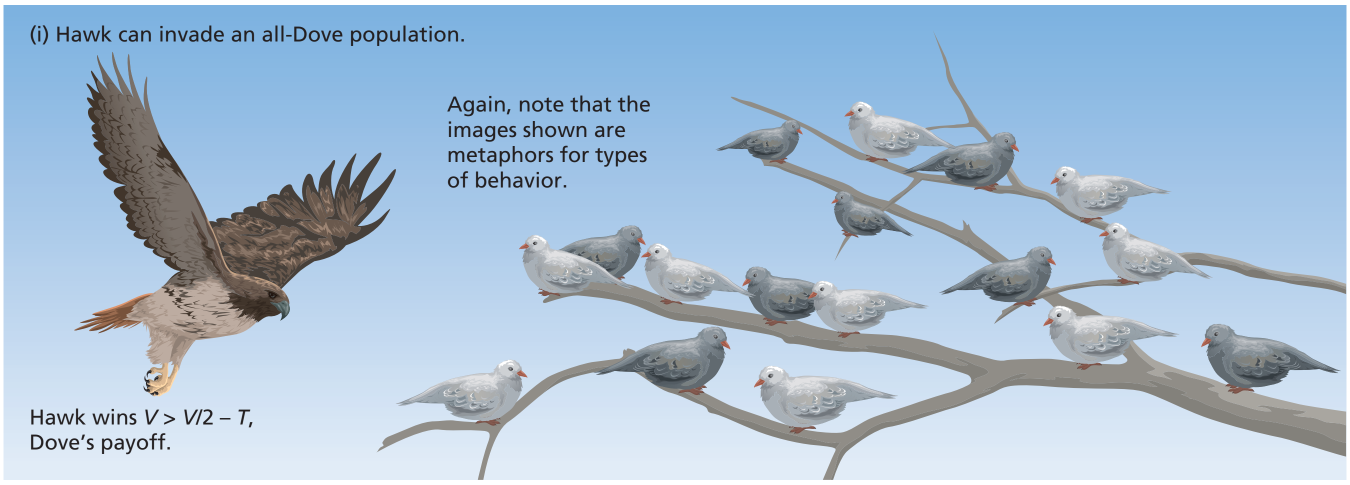
So what are the conditions for the evolution of peaceful social behavior? If the costs of injury are small, then violent aggression is selectively favored precisely because it is not actually that violent. Losers in conflicts do not lose heavily. This situation is reminiscent of the saying that the fighting was protracted because the stakes were so small, often applied to squabbling children and academics. In a sense, this implies that social evolution tolerates violence if it is ineffectual, and so not particularly deadly.

What happens when the costs of injury are considerable, greater than the benefits of victory in a conflict? Consider first the success of a Hawk invading a population that otherwise consists only of Doves, as shown in part (i) of Figure 20.10A. The only type of opponent that the Hawk faces is Dove, so the Hawk wins all its contests. It will be evolutionarily successful, establishing itself in the population and reproducing frequently. This suggests that Hawks should always be able to invade populations of Doves.

Consider a Dove invading a Hawk population, as shown in part (ii) of Figure 20.10A. This Dove will be retreating in every conflict situation, because it repeatedly faces aggression from the Hawks that it encounters. It receives nothing whenever there is a conflict. But Hawks, as pointed out earlier, receive less than nothing from most of their contests. Most of the contests involving Hawks are with other Hawks, when the Dove is first invading. Hawk contests with each other, Hawk vs. Hawk, net them an average payoff of $(V - W)/2$, which is less than zero. This arises because one of them will be injured, and we are considering the case with costly injury. As a result, Dove can always invade populations made up of Hawks.

Neither Hawk nor Dove can prevail when the cost of injury is greater than the benefit of victory. What will happen under these evolutionary conditions? The best way to understand the evolutionary outcome is in relation to the **evolutionarily stable strategy**, or **ESS**. The ESS is defined as an **unbeatable strategy** if almost all members of the population

(i) Hawk can invade an all-Dove population.



(ii) Dove can invade an all-Hawk population.

FIGURE 20.10A **When Injury Is Very Harmful, Neither Hawk nor Dove Will Be an ESS**

adopt it. The meaning of *unbeatable* is explained in the box, "Evolutionarily Stable Strategies." If a population has evolved an ESS, then it cannot be successfully invaded by any alternative strategy that is appropriate to the species. (For example, a strategy of using a high level of intelligence might win the day for a competing insect, but evolution does not allow large brains in insects. They're too small.) ESSs are patterns of social behavior that should dominate social evolution. Hawk and Dove, though, are not ESSs, which raises the question, what strategies are?

◆

Evolutionarily Stable Strategies

An evolutionarily stable strategy is also called an ESS.

A strategy S is an ESS **if**, when S is nearly 100 percent of the population,

S against S does better than all other strategies do against S.

or

If there is another biologically appropriate strategy, say M, that does just as well against S as S does,

then

the S strategy does better against M than M does against M.

20.11 Natural selection may favor the Retaliator strategy, which is peaceful unless attacked

Consider the evolution of a "peaceful" Hawk with a sense of "justice." Suppose this Hawk does not have the reflexive aggression of a normal Hawk, but instead tries to act like a Dove. When a Dove displays at it, it displays back, settling the conflict as if it were no different from a Dove. Then it would receive $V/2 - T$, on average, because it would win only half the time, but always pays the cost of display. But if this peaceful hawk is attacked by a normal Hawk, it gets mad and fights back. Indeed, it fights just as hard as a regular Hawk. Then it would receive $(V - W)/2$ from such conflicts—less than zero. This "peaceful Hawk" can be called a '**Retaliator**,' because that is its behavioral pattern. Its behavior is summarized in Figure 20.11A and the box, "Why Retaliator Is an ESS against Hawk Strategies."

Are Retaliators evolutionarily stable strategies, or ESSs? Can Hawks invade them? Hawks do as well against Retaliators as Retaliators do against Hawks. But in a mixed population of Hawks and Retaliators, the Retaliator-Retaliator contests are settled much more peacefully. Under these conditions, over all the contests that Hawks and Retaliators have, the Retaliators do better. They have a system of resolving conflicts that does not involve violent combat. It is better evolutionarily to behave peacefully, when others are peaceful and the cost of injury is great. But when they come after you, you have to fight back. At least that is what the theory seems to say.

What about social behavior in nature? Do animals use Retaliator strategies? In a few cases, we have some direct evidence that they do. For example, the well-studied rhesus monkey, *Macaca mulatta*, uses ritualized combat to settle its conflicts, somewhat like wrestling. The loser accepts bites from the victor's incisors to conclude the combat. Incisor bites are fairly harmless, like "love bites." Such interactions are like those between Dove and Dove. But if the victor of this mock combat bites the loser with its canines, which are much more dangerous teeth, the "loser" then responds with an aggressive counterattack. Apparently, the canine bites are perceived as significant aggression, which brings out a Retaliator response.

There is circumstantial evidence for Retaliator strategies in many animal species. The best evidence of this kind is the many forms of weaponry that animals have but do not normally use in their conflicts with other members of their species—that is, fangs, claws, antlers horns, and so on. If all the species equipped for violence behaved only as Doves, they would have no need for these structures, except for defense against predators or capturing prey. How often such weapons have evolved solely for predator–prey interactions is unclear. Yet many animal species are well equipped to destroy their fellows, but rarely do so. This finding suggests that Darwinian evolution has led to less aggression than might have been intuitively expected in most animal species. ❖

Why Retaliator Is an ESS against Hawk Strategies

We can get an ESS if

$$\text{Payoff (Retaliator playing Retaliator)} > \text{Payoff (Hawk playing Retaliator)}$$

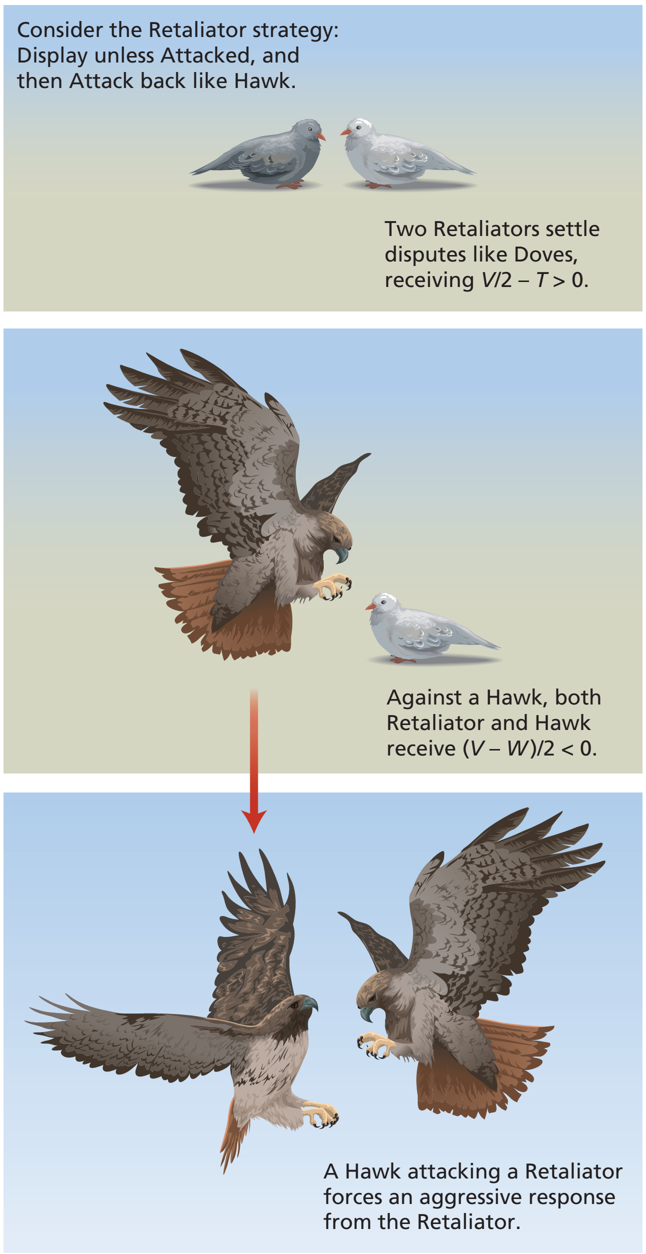
which is

$$V/2 - T > 0 > (V - W)/2,$$

assuming that the costs of display are small and the costs of injury in combat are great.

The biological meaning of this ESS is that the Retaliators have a system of resolving disputes that does not cost them too much, while the Hawks pay a steep price for their violence.

How can peaceful behavior be an ESS?



Consider the Retaliator strategy: Display unless Attacked, and then Attack back like Hawk.

Two Retaliators settle disputes like Doves, receiving $V/2 - T > 0$.

Against a Hawk, both Retaliator and Hawk receive $(V - W)/2 < 0$.

A Hawk attacking a Retaliator forces an aggressive response from the Retaliator.

FIGURE 20.11A Retaliator Is an ESS Against Hawk

20.12 Bourgeois settles conflict using ownership

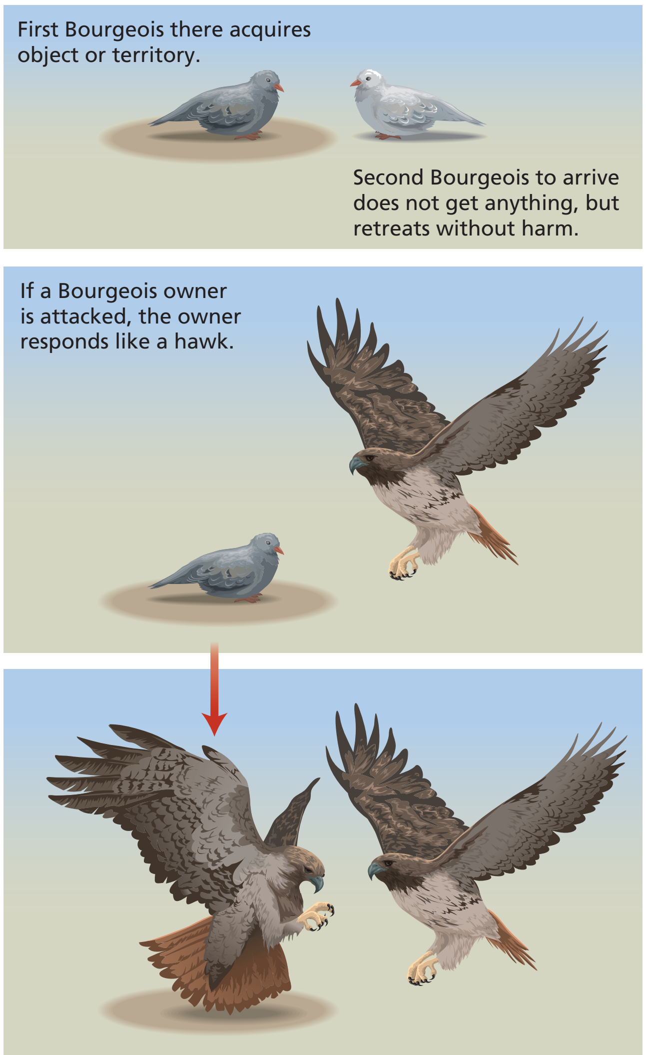
One of the most surprising things about animal behavior is that many species seem to have some sense of ownership, or **territoriality**, even of marriage. Birds will avidly display against other birds, even humans, who wander into particular parts of their habitat. They behave as if they have a deed to the territory, as if it is their property. Similarly, males and females of many species behave very aggressively toward conspecifics that attempt to have sex with the individual they have been having sex with, even when they may not have had sex with their "mate" for some time. Even more amazing, many of the interlopers themselves act as if they have done something wrong and back off in the face of the protest of the "owner" or "spouse."

A simple evolutionary game strategy can be used to explain this type of territorial behavior: Bourgeois. The **bourgeois strategy**, summarized in Figure 20.12A, is to defend a territory or other item if it is discovered first, but give it up if there is already an owner. Two Bourgeois animals will normally know which of them is owner and which is interloper, and the interloper will not fight or squabble with the owner. This allows them to settle their disputes more efficiently than Doves do, and at little risk of injury. Should a Hawk attempt an **invasion** of a territory, the Bourgeois fights back, much like a Retaliator. But if Hawk gets there first, Bourgeois concedes the territory to them right away. Therefore Bourgeois fights less than Retaliator and spends less time displaying than Dove.

Bourgeois is an ESS, because invading Hawks pay a penalty due to their violent fights with Bourgeois defending their "property." Doves settle their contests less efficiently than the Bourgeois do. Bourgeois strategy makes excellent sense theoretically, and seems to fit the behavior of many animal species. (See the box, "Why Bourgeois Is an ESS against Hawk Strategies.")

But is Bourgeois actually the strategy that territorial animals use? This hypothesis has been tested using an elegant experimental strategy—duping two animals into thinking that each is the owner. Male Hamadryas baboons, *Papio hamadryas*, keep specific females as mates, and other baboons normally respect such relationships. However, if two males are kept with the same females on alternate days, and never see each other with their shared mates, they will fight violently when they encounter each other in the presence of "their" females. Experiments with other species, including insects, have also found this pattern. If two animals from a bourgeois species both think they are owners, they will fight each other vigorously.

Bourgeois Strategy: If first to find territory or object, Attack if Attacked, like Hawk. If second to find territory, cede to owner and Retreat.


First Bourgeois there acquires object or territory.

Second Bourgeois to arrive does not get anything, but retreats without harm.

If a Bourgeois owner is attacked, the owner responds like a hawk.

FIGURE 20.12A Bourgeois Is an ESS Against Hawk

Animal behavior strangely conforms to many of the dictates of human morality—retaliation against aggressors, ownership of territory, even "marriage." Yet this behavior is predictable on the basis of evolutionary game theory. There is no overwhelming tendency to violence "red in tooth and claw" in evolution, even though it sometimes occurs within animal societies, just as it does among humans. Twentieth-century research on the conjunction of evolution, ecology, and behavior has laid to rest nineteenth-century anxieties about Darwinism's implications for animal behavior. The remaining question is the implications of Darwinism for *human* behavior, the subject of Chapter 21.

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Why Bourgeois Is an ESS against Hawk Strategies

We can get an ESS if

$$\begin{aligned}&\text{Payoff (Bourgeois playing Bourgeois)}\\ &> \text{Payoff (Hawk playing Bourgeois)}\end{aligned}$$

which is

$$V/2 > V/2 + (V - W)/4,$$

Bourgeois ceding the territory to Hawk half the time and fighting for it half the time, because Hawk will find the territory first half the time. As before, we take $(V - W)/2$ less than zero, assuming that the costs of injury are great.

The biological meaning of this ESS is that the Bourgeois have a system of resolving disputes that does not cost them too much, while the Hawks pay a steep price for their violence.

SUMMARY

1. An outstanding problem in evolution and ecology is biological altruism: one animal aiding another, supplying food, perhaps, or helping another animal fend off an attack from a predator. Some of the most dramatic forms of altruism are found among the "social insects." Altruism is a problem for evolutionary biology because we expect that natural selection will oppose behavioral tendencies that might lead to death or sterilization.

2. In group selection, entire populations are selected in the same way that individuals are selected in individual selection, by the extinction and propagation of populations. The connection between group selection and social behavior is that "bad" behavior might foster individual fitness yet undermine the survival of the group as a whole. When individual selection and group selection are opposed, it is theoretically possible, but difficult, for group selection to prevail. One factor that affects group selection is the pattern of population propagation. The more propagation is itself a "group" process, the more likely it is that group selection will succeed in increasing altruistic behavior. Although group selection can be made to work in the laboratory, there are few cases in nature for which group selection is the most likely explanation of social evolution. These cases include pathogens that infect hosts as single propagules and mammals that live in small, well-defined groups.

3. How can we explain sterile worker insects, like honeybee and ant workers? Insect families that produce more fertile offspring may do so by having some members of the family take on nonreproductive roles. Kin selection is based on the transmission of an organism's genes into the next generation by means other than the production of immediate descendants. Individual selection is about the survival and reproduction of an individual, and kin selection concerns *all other* means by which individuals can help their relatives so that copies of the helper's genes find their way into the next generation. Kin selection favors aid to relatives when the cost of such aid is less than the benefit times the degree of consanguinity. We expect *r* values (the degree of consanguinity or genetic relatedness) to be larger for individuals that are closely related and smaller for "distant relatives."

4. Haplodiploid social insects have high consanguinity between sisters, with full sisters having a $^3/_4$ coefficient of genetic relatedness, which often leads to the evolution of a complex social system dominated by females. In the most elaborate cases, such as honeybees and ants, a queen does all the reproducing. Males are pushed to the margins of this animal society, supplying little work beyond fertilizing the queen. The correspondence between genetic relationship and degree of biological altruism in hymenopteran females compared with males is one of the most important scientific findings in the field of social evolution. In the burrowing societies of termites and naked mole rats, individuals aid each other by supplying each other with endosymbionts for digesting woody material. Such societies are symmetrical between genders. There are male and female sterile workers. Instead of queens with inconsequential drone "boyfriends," termites have kings and queens that do all the reproducing.

5. Animals seem to "hold back" their aggression against other members of the same species. Often they literally make more noise than they fight; this behavior is seen in animals ranging from chirping birds to roaring stags. The key to resolving the paradox of restrained aggression comes from evolutionary game theory. Evolutionary games are based on the concept of behavioral strategies that specify an animal's behavior in its conflicts. This idea of a defined strategy can be applied to animal conflicts in a straightforward way. When two animals want the same food item, mate, or piece of territory, two extreme strategies are easily identified—Hawk and Dove. Hawks always attack until they either get the prize or are injured and forced to retreat. Doves only Display. Violent Hawk behavior may not evolutionarily dominate if the costs of such violence are greater than the benefits of victory; but if the costs of injury are small, aggression will be selectively favored.

6. If the costs of injury are large, natural selection may favor the Retaliator strategy, which settles conflicts peacefully unless the Retaliator is attacked. Over all the contests that Hawks and Retaliators have, the Retaliators do better. It is better evolutionarily to behave peacefully, when others are peaceful. But when they attack, you have to fight back. There is at least circumstantial evidence for Retaliator strategies in many animal species. Bourgeois is another successful strategy for settling conflict without aggression. An animal using this strategy defends a territory or other item if it has been discovered first, but gives up the item if there is already an owner. Two Bourgeois animals will settle their disputes more efficiently than Doves will, and at little risk of injury. Invading Hawks pay a penalty because of their violent fights with Bourgeois animals defending their "property." Many animal species appear to use the Bourgeois strategy.

REVIEW QUESTIONS

1. What occurs when group selection and individual selection favor the same characteristics?
2. Are there any fly species that could be called 'social insects'?
3. Name a species in which you think group selection is occurring, and explain why you chose that species.
4. What is the difference between kin selection and group selection?
5. Analyze the evolutionary prospects for Anarchist, a strategy in which animals concede ownership to the next animal to find a territory.
6. Is kin selection important in the organization of human societies?
7. Do you think that group selection has ever been important in human evolution?
8. Are birds more or less likely to undergo group selection?
9. Why are male lions so violent when they compete for "ownership" of a pride?
10. Does the evolutionary analysis of social behavior suggest that animal behavior will be more or less violent than you first supposed?

KEY TERMS

altruism
Attack
Bourgeois strategy
coefficient of genetic relatedness
consanguinity
Display
Dove strategy
drones
Evolutionarily Stable Strategy (ESS)
evolutionary game theory
game theory
group selection
Hamilton, W. D.
haplodiploid sex determination
Hawk strategy
Hymenoptera
identical twins
invasion
king
kin selection (selection among families)
Maynard Smith, J.
migrant pool
myxoma virus
Prisoner's Dilemma
propagule
queen
Retaliator strategy
Retreat
ritualized conflict
selection among families (kin selection)
selfish behavior
sex determination
social insect
soldier
strategy selection
territoriality
unbeatable strategy
Wade, M. J.
worker

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