8

Sociobiology

Issues

- What is sociobiology? How is it different from sociology?
- Why does sociobiology have so many critics? Who is objecting, and what are they objecting to?
- Is most behavior learned or inherited?
- What are the differences between instincts and other innate behaviors?
- How do learned behaviors relate to evolutionary change?
- To what extent can social behavior be modified?
- Why do the sexes behave differently in so many species?
- How different are humans from other species in social behavior? To what extent can findings in other species be extrapolated to humans?

Biological Concepts

- Evolutionary change (variation, natural selection, nonrandom mating, specialization and adaptation, human evolution)
- Population ecology (populations, regulation of population size)
- Learning and instinct (interaction of genotype and environment)
- Reproduction (asexual reproduction, sexual reproduction, mating systems, sexual dimorphism, reproductive strategies)
- Behavior (social behavior, communication, courtship and mating)

Chapter Outline

Sociobiology Deals With Social Behavior

Learned and inherited behavior
The paradigm of sociobiology
Research methods in sociobiology
Instincts

Social Organization Is Adaptive

Advantages and disadvantages of social groups
Simple forms of social organization
Altruism: an evolutionary puzzle
The evolution of eusociality

Reproductive Strategies Can Alter Fitness

Asexual versus sexual reproduction
Differences between the sexes
Mating systems

Primate Sociobiology Presents Added Complexities

Primate social behavior and its development
Reproductive strategies among primates
Some examples of human behaviors

8 Sociobiology

Behavior that influences the behavior of other individuals of the same species is called ***social behavior****. Examples of social behavior in animals include cooperative feeding, cooperative defense, aggression within the species, courtship, mating, and various forms of parental care. People also practice many forms of social behavior: nurturing their young, helping their neighbors, defending their possessions, and providing both material help and emotional support to their loved ones and to others. The population crisis discussed in Chapter 9 is a direct result of reproductive behavior. Some types of social behavior are often termed 'antisocial' behavior and result in problems for society. Examples include violence, crime, racist acts, sexist acts, and child abuse and neglect, all of which are social behaviors because they affect the behavior of other individuals.* ***Sociobiology*** *is the comparative study of social behaviors and social groupings among different species. The study of social behaviors in complex human societies is a separate discipline called sociology.*

Can behaviors that cause problems be changed easily? Can beneficial behaviors (however defined or recognized) be substituted for destructive behaviors? Is most behavior rigid and unchangeable, or plastic and easily molded? Are we governed more strongly by our genetic background (nature) or by our upbringing (nurture)? The debate is very old. In Shakespeare's Tempest (4:1), Caliban is described as "a born devil on whose nature / Nurture can never stick." If human behavior were strongly determined by genes, then cultural influences, including education and training, would have only limited power to bring about changes in human behavior. Social reformers of all kinds usually support the opposite viewpoint, that human behavior can be modified almost at will, subject to few if any restrictions. Debates about alcoholism or homosexuality are often unproductive because some people assume that these are behaviors that could easily and voluntarily be changed, while others assume that these are permanent and deeply rooted in biological differences that may or may not be genetic. Differences in behavior between the sexes are likewise seen by some researchers as genetically constrained and by others as culturally controlled and easily changeable.

Although the most heated discussions arise from attempts to apply sociobiology to humans, sociobiology is a broad field of study and humans are but a single species. Most research in sociobiology focuses on nonhumans. Altruism, for example, poses a major research question in the sociobiology of all species. Among other broad-spectrum issues within sociobiology are the advantages of sociality itself, the kind of social organization found in each species, and the manner in which it evolved. Another issue is that of social relations between the sexes of each species, including the concept of reproductive strategies; in this chapter we show that parental care, infanticide, adultery, and altruism can all be viewed as components of reproductive strategies. The evolution of these strategies is an important field of investigation for sociobiology. In this chapter we examine the sociobiology paradigm and some of the major issues within the paradigm.

Sociobiology Deals With Social Behavior

Sociobiology means different things to different people. To scientists working in sociobiology, it is a field of study that deals with social behavior and its evolution. Sociobiologists usually explain behaviors in evolutionary terms. Although sociobiologists are more interested in the inherited components of behavior, they all acknowledge that much of behavior can also be modified by learning. They also acknowledge that natural selection can act only on those components of behavior that are inherited. One of the important research goals of sociobiology has therefore become the investigation of the relative importance of learned and inherited influences on particular behaviors. Sociobiology also has a number of critics who challenge the emphasis on inherited behavior patterns. These critics prefer to emphasize learning, including cultural learning in humans, as a strong influence on behavior. We will examine both viewpoints.

CONNECTIONS
CHAPTERS 5, 9

Learned and inherited behavior

Many behavioral patterns may be strongly influenced by experience in dealing with the environment, i.e., by **learning**. Nearly every behavior that has been carefully investigated also has some genetic component. Learned behavior may increase fitness, but only the genetic components (or predispositions) underlying the behavior can be influenced by natural selection (see Chapter 5). Natural selection can operate on the capacity for learning particular kinds of things, such as how to find one's way through the maze of one's surroundings. The character favored by selection in such cases is not the behavior itself, but rather the capacity to learn the behavior.

This is true of the ability to run through mazes, one of the most often studied types of learned behavior. Rats were tested for their ability to learn certain mazes, and the number of training sessions that it took the rats to learn the mazes was recorded. Their littermates, who were never tested themselves, were then selectively bred for several generations. Breeding the littermates of fast maze-learners resulted in a strain in which the average number of training sessions needed was low, while a strain of slow learners was bred from the littermates of individuals who needed more repetitions. The use of littermates in this experiment eliminated learning experience or other influences as determinants of the differences between the two selected strains. Notice that the behavior was not fully determined by inheritance; it still had to be learned. This behavioral trait is determined by many genes and environmental influences acting together. The *difference* between the two strains resulted from the buildup of gene combinations, which was only possible because some portion of the variation between groups was heritable.

Furthermore, to say that variation between groups is heritable *does not mean that the behavior is inherited as a fixed and unchangeable trait*. There are extremely few behaviors in any species (and none at all in humans) that are not subject to modification through learning. For example, nobody learns to play basketball like Michael Jordan or to play the cello like Yo Yo Ma without years of practice. Nobody can become even a mediocre basketball or cello player without lots of practice—a period of learning. However, some innate talent and ability are surely needed, or else any of us would be able to become a great basketball star or a world-renowned cellist simply by practicing enough.

Thus, it is important to emphasize that the oft-posed question of learned versus inherited behavior is a false dichotomy. Every learned behavior is based in part on some inherited capacity to learn, which may include the capacity to learn certain kinds of behaviors and not others, to respond to some stimuli and not others, to learn up to a certain level of complexity, and so on. Similarly, most behavior patterns with an inherited component can be modified to some extent by learning. These observations give rise to the testable hypothesis that *nearly every behavior pattern is at least partly learned and at least partly inherited*. Behaviors that do not require learning are called **innate**, and innate behaviors are assumed to have an inherited component. No behavior is 100% learned, and few are 100% inherited in any species (Figure 8.1). The methods used to distinguish between learned and innate components of behavior are described later in this chapter.

CONNECTIONS CHAPTER 1

The paradigm of sociobiology

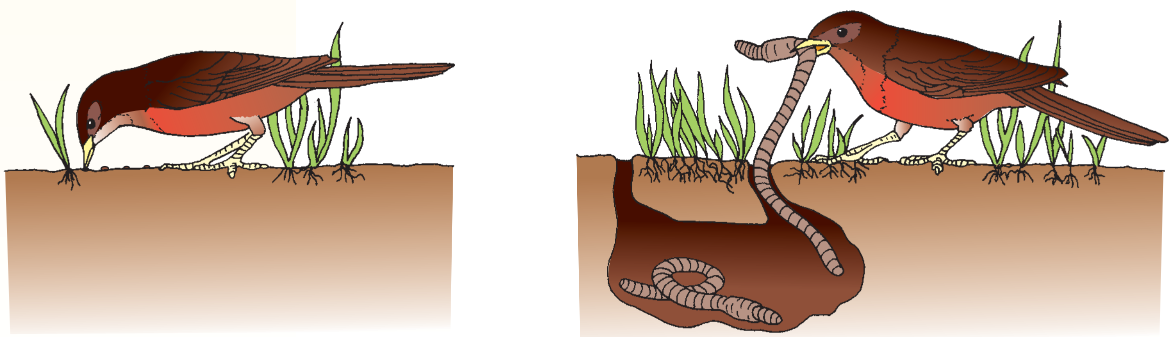
Sociobiology, the study of social behavior among different species, uses a scientific paradigm of the kind described in Chapter 1: one or more

Figure 8.1

Learned versus innate behavior patterns.

Nursing and suckling behaviors have strong innate components in most mammals (but this doesn't prevent bottle-feeding of many human infants).

Novel behaviors can be learned by many species.



Most forms of behavior show both learned and inherited components. Robins and many other birds innately peck at certain stimuli and thereby gain learning experiences about how to hunt more effectively and how to distinguish food objects from other objects.

theories, plus a set of value-laden assumptions, a vocabulary, and a methodological approach (Box 8.1). The formulation of sociobiology as a paradigm dates from the publication of the book *Sociobiology: the New Synthesis*, by the American evolutionary biologist Edward O. Wilson (1975). Many of the ideas of this paradigm can be traced to Charles Darwin's writings. What was new in 1975 was the way in which these ideas were put together to form the paradigm.

If people outside the paradigm had viewed sociobiology as no more than the study of social behavior, few objections would have been raised to it. However, sociobiology was frequently criticized for its focus on inherited behavior. As the many critics of sociobiology have emphasized, much of behavior is learned, and nearly all behavior can be modified by learning, particularly in mammals. Also, human behavior is strongly influenced by both language and culture, so many scientists who are otherwise sympathetic to sociobiology have cautioned against extrapolating sociobiological findings from other animals to humans.

Some nonscience critics of sociobiology are fearful of genetic determinism, the assertion that our individual characteristics are determined before birth and cannot be changed. As we discussed in Chapter 7, genetic determinism is feared because throughout history people in power have sought to control other people (other social classes, other races, and women) by teaching that existing inequalities were 'natural,' based on innate and unchangeable differences. Also, many people fear that the mere claim that a behavior is innate will discourage people from trying to change that behavior through education or similar means. The claim that behavior is innate can be particularly threatening to social reformers who pin their hopes for the future on the ability of people to modify their behavior.

CONNECTIONS CHAPTER 7

Among biologists, those who believe in genetic determinism are decidedly in the minority. Most biologists, especially those who study animal behavior, are impressed with the degree to which behavior can change in response to environmental circumstances, including the behavior of other individuals. There are genetic constraints on what can and cannot be learned, but, within these limits, behavior is remarkably changeable (or 'plastic') in most animal species. No behavior is fully 'determined' either by genetics or by environment—almost every behavior is influenced by both of these factors throughout the lifetime of the individual.

We now examine the research methods used by sociobiologists.

Research methods in sociobiology

No behavior can be analyzed by any method until it has been adequately described. Sociobiology therefore includes a great many observational field studies of animals. How does one distinguish between the learned and innate components of a particular behavior? Sociobiologists use the following methods to investigate these components.

Rearing animals in isolation. A classic type of experiment is to raise an animal in isolation, in a soundproof room with bare walls and minimal opportunities for learning, including no opportunity to learn behavior from others. Behavior that the animal exhibits under these conditions is assumed to be largely innate. Experiments of this sort cannot ethically be done on humans.

BOX 8.1 The Sociobiology Paradigm

Research activity in science is often organized around paradigms (see Chapter 1). Here, in brief outline form, are some of the major points of the sociobiology paradigm:

1. Behavior is interesting to observe and to study. (This is a value judgment; people who do not share it will never be attracted to the paradigm.)

2. Much of the interesting behavior influences the behavior of other individuals, and is called 'social.' (This is a definition with an implied value judgment that people within the paradigm are expected to share.)

3. Social behavior has evolved and continues to evolve. (This is a central theory whose rejection would bring down the entire paradigm.)

4. The evolution of social behavior takes place by natural selection, along the lines outlined by Darwin: variations occur, and the variations that increase fitness persist more often than those that do not. (This is again a theory; it includes theoretical concepts such as 'fitness' and 'variation.')

5. Behavior is often modified by individual experience ('learning'). However, this learning takes place within limits set by the biology of the organism: the eyes limit what can be seen (likewise with other sense organs); the muscles and skeleton limit the possible responses; the structure of the brain limits the learning capacity, and so on. There are also many preexisting predispositions to respond to certain types of stimuli, to react in certain ways, and so on. These predispositions may have been learned at an earlier time, but *at least some of them* precede any learning and may be called 'innate.' (This is a central tenet of the paradigm, forming the basis for its further research.)

6. In the evolution of behavior, learned modifications are not directly inherited. Learned behaviors can contribute to fitness, but cannot be inherited. Only the innate predispositions and their biological underpinnings can be inherited, and only these inherited components can evolve. Natural selection can only work on the inherited aspects of behavior. (These ideas follow in part from the ways in which 'learned' and 'innate' are defined, and in part from the findings of evolutionary theory.)

7. It is therefore important to distinguish the learned and innate components of behavior, and to focus attention on the latter. This is a value judgment about the aims of research within the paradigm. It does not mean that learned behaviors are unimportant; it just means that sociobiologists would rather identify what is learned so that they can ignore it and spend the rest of their time studying the innate components. *It is this preference for studying the innate components of behavior that makes the sociobiology paradigm so controversial; most critics of sociobiology have the opposite preference*.

8. We can use modified Darwinian methods of investigation to study those components of behavior that evolve. One method is to measure variations in fitness by observing many individuals and studying the number of viable offspring successfully reared by each. Another method is to study the results of past evolution by comparing social behaviors among different populations or different species. (These are the basic research methods.)

9. Before comparisons can be made, however, there must first be an often lengthy period of observation and description. However, we realize that the presence of observers might modify the behavior that we wish to study. Because we are interested in behavior under 'natural conditions,' it follows that we should conduct most observations at a distance and interfere as little as possible. (These are more research methods.)

Rearing animals under different conditions. If the behavior is performed in the same way by animals or humans reared under strikingly different circumstances, then the behavior is largely innate. If, in contrast, the behavior varies according to the circumstances of rearing, then the variation can be attributed to environmental influences, although this does not rule out inherited influences, which may also be present. Cross-cultural studies are used to compare the behaviors of people raised in different societies or under different customs; innate behaviors are expected to be constant across various cultures, while learned behavior patterns are expected to vary.

Studying behavior in different genetic strains. If different strains or breeds of a species differ behaviorally in a consistent and characteristic way, then a strong inherited component exists. (This does not rule out learned components, which might also be present.)

Conducting adoption studies. If two populations differ in a particular behavior, it may be useful to study individuals from one group who are adopted early in life and raised by the other group. Under these conditions, behavior consistently resembling the population of birth demonstrates an inherited influence, while behavior resembling the population of rearing demonstrates a learned influence. Mixed or inconsistent results may indicate that both influences are present.

Conducting twin studies. If a trait is under strong genetic control, then identical twins should usually both exhibit the trait whenever either one does, while fraternal twins more often exhibit differences. Twin studies in humans are frequently criticized because the effects of learning cannot easily be separated from those of inheritance unless the twins are reared separately in families randomly chosen, conditions that are rarely even approximated. Some studies compare identical twins reared together to those reared apart, an experimental design that attempts to get around some of these difficulties.

Instincts

A subset of innate behaviors are called **instincts**. Instincts differ from other innate behaviors in being complex behavior patterns that are under strong genetic control. The classical test for whether a particular behavior is an instinct is whether the behavior appears at the appropriate time of life in an animal reared in isolation since birth or hatching. For example, if a songbird reared in a soundproof room sings the song of its species and sex upon reaching maturity, then the song is considered to be instinctive. By this test, many behaviors that have been studied in fishes, birds, and many invertebrates (including insects) have been shown to be largely instinctive. Behaviors related to courtship and mating usually have strong instinctive components in most species. Other behavior patterns that are frequently instinctive include automatic ‘escape’ behavior, nest-building behavior, orb-weaving in spiders, and various threat gestures. When instinctive behavior leaves a lasting product, such as a nest or a spider’s web, these products are often so distinctive that they can be used to identify the species that created them.

Mammals generally rely more on learned behavior than on instinct. Among primates especially, many behaviors that are instinctive in other species have strong learned components. These behaviors may vary greatly among human societies.

Advantages of instincts. Short-lived animals rely heavily on instincts. For example, mayflies (insects of the order Ephemeroptera) have an adult life span of less than 24 hours. During this brief period they do not feed but have just enough time to find a mate, copulate, lay their eggs, and die. There is no time for learning to take place, nor is there any time for mistakes. The mayflies that accomplish their mission successfully are those that can perform their behavior correctly on the first try; they will probably never get a second chance. Selection over millions of years has therefore produced a series of adult behaviors that are instinctive and automatic, allowing no room for diversity or innovation. This is typical of instincts generally: behavior is instinctive in contexts in which uniformity and automatic response are adaptive and where innovation and diversity might be maladaptive. A greater complexity of behavior is possible with a simpler brain if the behavior is instinctive; learned behavior of equal complexity requires a more elaborate nervous system and also a long learning period during which many mistakes are made.

Mating behavior. Mating behavior includes both courtship (attracting a mate and becoming accepted as a mate) and the actual release or transfer of gametes. Mating behavior has a strong instinctive component in nearly all species, except in higher primates. Scientists can demonstrate the instinctive component of most forms of mating behavior by raising individuals in isolation until they are sexually mature, then testing them to see whether they can perform the behavior typical of their species.

Natural selection favors uniformity in mating behavior rather than diversity. Such unvarying behavior (called **stereotyped behavior**) is used for mate location and recognition in many species. The behavior that evolved in each species matches the type of signal that each is able to sense, so that visual mating signals are used by species with good vision, chemical signals by species with good chemical reception, and sounds by species with good sound discrimination. Many species of birds, frogs, and insects use sounds as mating signals, and the noncalling sex (usually female) responds only to mating calls of the proper pitch, duration, and pattern of repetition. Both the mating signals and the behavioral response to them are instinctive. Members of each sex know exactly what to listen for in the other sex and usually avoid nonconformers who deviate from the instinctive pattern. Sexual selection thus penalizes the nonconformers, who generally fail to mate and therefore leave no offspring. The flashing patterns of fireflies, though visual, are sexually selected in the same way. Because of sexual selection, mating calls or visual displays are precisely controlled within a narrow range for each species. Closely related species often differ in their mating calls and courtship patterns. Differences in mating calls and other courtship displays often serve as reproductive isolating mechanisms that prevent interbreeding between species (see Chapter 5).

CONNECTIONS CHAPTER 5

Male birds of many species display conspicuously colored parts during courtship. Mating rituals that include beautiful, ornate displays evolve as a consequence of sexual selection in those species where the discriminating sex (the one doing the choosing) consistently prefers the most conspicuous displays. Peacocks, lyre-birds, and birds-of-paradise are renowned for their beautiful and ornate male plumage (Figure 8.2). Male birds of species with less conspicuous plumage may concentrate instead on building an elaborate nest. The South Pacific bowerbirds build their nests within a large framework (a bower) that also serves as a place of mating. A few species even build an 'avenue' lined with colorful stones leading to the entrance of the bower. Generally, bowerbird species with ornate plumage do not build elaborate bowers, and the species that build impressive bowers do not have elaborate plumage.

Figure 8.2

An example of a conspicuous mating display in a peacock. Females of this species prefer males with the most conspicuous displays.

Territorial behavior. In many species, one or both sexes may show territorial behavior by defending a territory, either throughout the year or only during the mating season. The defense of a territory against intruders of the same species is common in many animal species. In some species, only males are territorial. Territorial behavior spaces individuals apart and encourages the losers to strike out in search of new territory, thus extending the range of the species wherever possible. Each territory must have sufficient food resources for a mating couple and their offspring, places for hiding and refuge, and at least one suitable nest site. Males without any territory are usually unable to attract mates and thus leave no offspring in that particular season. The specific boundaries of a territory and one's status as a territory holder or a trespasser are learned, but the general tendency to establish territories is instinctive in certain species (or sexes or seasons).

Territorial species may use gestures to threaten territorial rivals. Mammals who establish territories may mark their territory with their own scent. The intimidation of rivals by gestures or by the presence of odors serves to space individuals apart without causing injury or loss of life. Such ritualized forms of territorial defense are much more common than any form of fighting in which injuries are likely.

Nesting behavior. The choice of a nesting site may be an important part of territorial behavior. In some bird species, the male builds the nest and then offers it to the female as part of the mating ritual. In other species, male and female may cooperate in building the nest together as part of the mating ritual. Females may incubate the eggs alone, but males may provide other forms of assistance by bringing food or by defending the area against predators. In other species, the males and females take turns in guarding the nest and sitting on the eggs. Feeding the hatchlings may similarly be either a solitary or a shared task.

The behaviors just described are performed by individuals. Behaviors can also be performed by groups of organisms, a subject that we take up in the next section.

THOUGHT QUESTIONS

1. Does 'antisocial' behavior (such as assaulting others and causing them injury) fit the definition of social behavior? Do you think the definition should be modified? In what way?
2. Is sociobiology a subject area with room for many viewpoints, or is it a single viewpoint that enshrines both genetic determinism and sexism? Can sociobiology be studied without the assumptions of genetic determinism?
3. Can the methods used for gathering or analyzing data in sociobiology be the same for different species? To what extent do size (small versus large animals) or habitat (above ground, underground, underwater, in trees, etc.) require differences in field methods? What special problems in methodology arise when humans are being studied? Can the methods used for other species be applied to humans?

Social Organization Is Adaptive

Very few animal species consist of solitary individuals that spend all their time alone. Even in species whose members are solitary much of the time, individuals must come together for sexual reproduction. Most species, however, are far more social than this, and species that form social groups greatly outnumber those that consist primarily of solitary individuals. Social groups vary greatly in both size and cohesiveness. Simple pairs and family groups have only a few individuals. Larger social groupings include antelope herds, baboon troops, and fish schools, all of which may include up to a few hundred members. Still larger are the colonies of social insects, which may include many thousands or in some cases millions of individuals. Some social groups are loosely organized, with individuals staying together but seldom interacting, while others are organized into social hierarchies within which interactions are complex, as they are among humans and social insects.

Advantages and disadvantages of social groups

There are clear disadvantages to living in a social group. Chief among these is the competition for food and other resources (mates, hiding places, nesting sites), and this competition is made more intense by the fact that members of the same species generally have exactly the same ecological requirements (they seek the same foods, nesting sites, etc.). In those cases where food comes in portions small enough to be monopolized by a single individual, social groups are often small or non-existent. Social groupings also foster the spread of parasites and infectious diseases, and they may make the group easier for a predator to spot. Species that rely on camouflage avoid forming densely clustered social groups.

Despite these disadvantages, we find that species in which there are social groups far outnumber the species formed by solitary individuals. Clearly, there must be some great advantages for social groups.

Some advantages of social grouping are related to the obtaining of food. A large group of individuals searching for food together has a higher probability of finding it than a single individual. If food tends to be discovered in quantities much greater than a single individual needs, selection favors the formation of social groups.

Finding a mate is made easier if there are social groups. Indeed, many species that are solitary throughout most of the year come together on occasion, often during a particular season, and form social groups and mate. The risk of inbreeding increases if social groups are small and remain closed to the introduction of new genes; this risk is usually minimized by mechanisms for the exchange of genes or of individuals between populations.

Other advantages of social grouping relate to defense against predation. Social groups can often defend themselves more effectively than individuals can. Musk oxen, for example, respond to threats by standing close together with individuals facing outward in different directions (Figure 8.3). Even in species that do not practise group defense, members of a group may warn one another by giving alarm signals, or simply by fleeing as soon as a predator is spotted. Thus, belonging to a group gives all group members the advantage of greater (and earlier) alertness against predator attacks. For this reason, large but loosely organized flocks, schools, or herds are common among birds, fishes, and ungulates (hoofed mammals such as wildebeest and zebra) (Figure 8.4). Other advantages to group membership arise from the sharing of risks: a predator attacking the entire herd may capture one of its members at most, while the rest escape, so that each individual in a herd of 500 is exposed to only 1/500 of the risk of capture faced by a solitary individual. Actually, the risk may be even smaller because predators can more easily capture solitary individuals. Most herd animals taken by predators are individuals that have strayed from the herd.

Figure 8.3

Musk oxen in a defensive formation. When musk oxen stand close together and face in different directions, no predator can surprise them.

Simple forms of social organization

Social organization refers to the ways in which social groupings are structured. The fact that social organization sometimes varies among closely related species suggests that social organization evolves. Studies on the inheritance of social status (dominance) within organized social groups point to a complex interplay of learned and inherited behavioral components in the establishment of social organization.

Groups without dominant individuals. Perhaps the simplest form of social organization is shown by brittle stars (see Figure 6.17, p. 192), marine organisms distantly related to sea stars. On encountering one another, brittle stars tend to stay together in clumps, even though there is no evidence of any more complex interaction.

CONNECTIONS CHAPTER 6

The schooling behavior of fish is another very simple form of social organization. There are hydrodynamic advantages to schooling—swimming is made slightly easier by certain changes in water pressure caused by the swimming of the other fish—but these effects are small. The major advantage to schooling behavior may be that the fish hide behind one another in such a way that most escape predators. Most fish school closer together when a predator is nearby (see Figure 8.4). When attacked, schools of fish or flocks of birds tend to scatter in every direction, a reaction that confuses many predators and that gives the individuals a chance to escape.

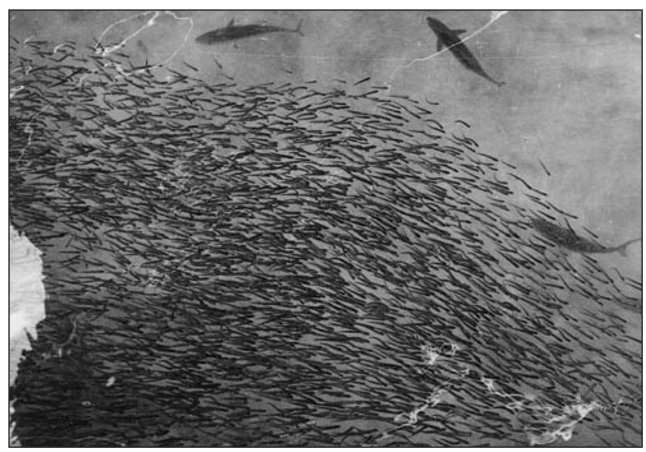
The size of social groups can vary greatly, often in response to ecological factors. For instance, the weaver birds live in many parts of Africa and Asia. In humid, forested regions, most weaver birds nest in pairs and feed on insects, while those species inhabiting grasslands and other drier habitats build large communal nests and eat a diet rich in seeds.

Groups with dominant individuals. One form of social organization is called a linear dominance hierarchy or 'pecking order.' Such hierarchies are found among domestic fowl and certain other captive animals (Figure 8.5). The top-ranked individual, usually a strong male, can successfully bully or threaten all the other individuals in the group, literally pecking at them in the case of birds. The second-ranked individual can intimidate all others except the top-ranked individual. The third-ranked individual can intimidate all except the first two, and so on. Occasionally, two closely ranked individuals may be tied for status, so that neither can dominate the other. For the most part, however, this type of organization results in the biggest bully getting whatever he wants, the second biggest

Figure 8.4

Social groups in various species.

Pelicans



Minnows schooling in the presence of predators

Wildebeest on the plains of Africa

Gannets on the coast of Quebec

getting whatever he wants as long as he steers clear of the top-ranked individual, and so on. Some feminist critics of sociobiology suggest that such male-dominated forms of social organization exist more in the minds of male sociobiologists than in the animals that they study. In at least some studies, pecking orders may reflect the artificial conditions of captivity and confinement.

Altruism: an evolutionary puzzle

Efforts to solve human social problems such as pollution often call for individuals or corporations to sacrifice their own interests for the common good, a practice called **altruism**. Altruistic behavior exists in many other species as well. As an example, consider the 'broken wing' display of certain female birds such as nighthawks. When guarding her nest against a predator, a female nighthawk may lead it away from the nest location, distracting its attention by limping or pretending to have a broken wing. Once she has drawn the predator sufficiently far from the nest, she flies away, leaving the predator confused. While protecting her young, she has increased her own danger. In evolutionary biology, altruism is defined as behavior that *decreases* the fitness of the performer while it increases the fitness of another individual. In this example, the female bird has decreased her own fitness by putting her life at risk for the sake of her offspring. Remember that fitness is defined as the relative number of fertile offspring produced by an individual (see Chapter 5). Only changes that increase fitness are perpetuated by natural selection.

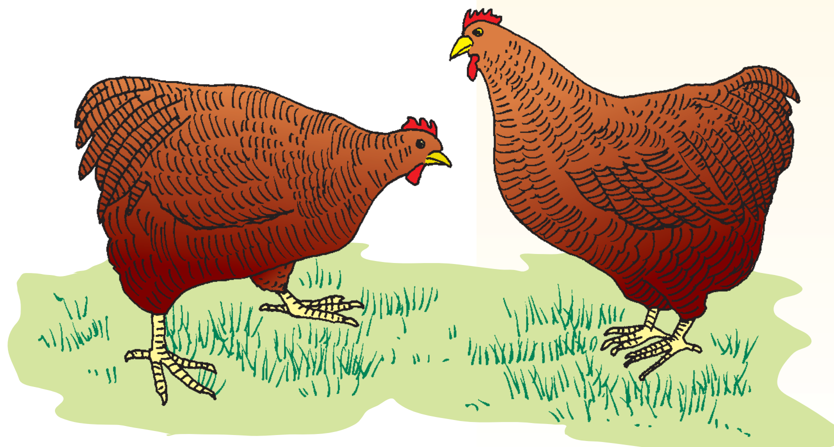


Figure 8.5

Domestic fowl showing a pecking order.

CONNECTIONS CHAPTER 5

Altruistic behavior poses a problem in evolutionary theory because natural selection might be expected to work against it. How could altruism evolve if it decreases fitness? Various hypotheses have been developed to explain this. In this section we examine several hypotheses that act at different levels of selection.

Selection at the species level. One early hypothesis for the evolution of altruism is that it benefits the species as a whole. However, careful examination of this hypothesis shows it to be unsatisfactory. If a species had both altruists and selfish individuals ('cheaters'), and if some part of this behavioral difference were controlled genetically, then selection would work against the altruists and in favor of the cheaters. Altruism may benefit all recipients of another individual's altruistic behavior, but the advantage is greater to selfish individuals than to other altruists. Under these conditions, natural selection should favor selfishness and eliminate altruism from the population.

Group selection. Another possible explanation for the evolution of altruism was proposed by the British ecologist V.C. Wynne-Edwards. If a species is subdivided into populations or social groups, then selection among these groups (group selection), may favor one group over another. In particular, a group containing altruists is favored *as a group* over other groups composed of selfish individuals only.

As we explained earlier, the defense of territory prevents excessive population density by spacing individuals apart and limiting population size. Wynne-Edwards describes the losers of territorial disputes as altruists who forgo mating for the benefit of the group as a whole. He argues that the mating of individuals without territories would lead to overpopulation, increased mortality, and a smaller resulting population size. Selection between groups would thus favor altruism. Other biologists who have examined this claim with mathematical models have shown that a loser who cheats (mates anyway) would greatly increase its fitness over one who does not mate, and that cheating behavior would thus be favored over altruism in every territorial species. Similar arguments have been advanced to show that other behaviors that achieve spacing or population control would also not be favored by group selection because cheaters would tend to leave more offspring than altruists.

Kin selection. Many biologists dissent from the group-selection hypothesis, seeking instead a simpler explanation based on individual selection. The currently favored explanation of altruism is based on the concept of **inclusive fitness**, defined as the total fitness of all copies of a particular genotype, including those that exist in relatives. Relatives are listed according to their degree of relationship, symbolized by R. For sexually reproducing organisms with the common types of mating systems, an individual shares half of its genotype ($R = 1/2$) with its parents, its children, and, on average, with its brothers or sisters (who share two parents). Also, an individual shares one-fourth of its genotype ($R = 1/4$) with grandchildren, half-siblings (who share one parent only), uncles, aunts, nieces, and nephews. The inclusive fitness of your genotype is the sum total of your individual fitness *plus* one-half the fitness of your parents, children, and full siblings who share half your genotype, *plus* one-fourth the fitness of those relatives who share one-fourth of your genotype, *plus* one-eighth of the fitness of your cousins who share one-eighth of your genotype, and so on. This concept allows us to define **kin selection** as the increased frequency of a genotype in the next generation on the basis of its inclusive fitness.

The conditions under which kin selection favors the evolution of altruism were specified by the British sociobiologist William D. Hamilton. Assume that altruistic behavior results in a certain reduction in fitness or 'cost' to the altruist, and a corresponding gain in fitness or 'benefit' to another individual who shares a fraction of the altruist's genotype. Hamilton reasoned that natural selection would favor altruism whenever the gain in inclusive fitness to the altruist's genotype exceeds the cost. If I perform an altruistic act that diminishes my individual fitness by a certain cost but raises my child's fitness or my sister's fitness (with whom I share half my genotype) by more than twice that cost, then the net effect on my inclusive fitness is positive. The probability that my genotype will be represented in future generations is increased because the benefit to my relatives (or to the fraction of my genotype that they share) exceeds the cost, so the net result is an increase in my inclusive fitness.

The above explanation, however, gives rise to an interesting prediction: kin selection favors altruism only if close relatives are more likely to benefit from altruistic acts than more distant relatives or nonrelatives. Studies of many species have confirmed this prediction: the beneficiaries of altruism are often close relatives of the altruist, and the frequency of altruistic acts varies in almost direct proportion to the degree of the relationship. In the Florida scrub jay, the offspring of the previous year are not mature enough to mate. Instead, they help the nestlings who are their own brothers and sisters (Figure 8.6). In doing so they contribute to the survival (and thus the fitness) of these near relatives, who share a portion of their own genotype. Ground squirrels emit an alarm call when a predator is spotted. The alarm call decreases the fitness of the caller, but increases inclusive fitness by warning the caller's kin (see Figure 8.6).

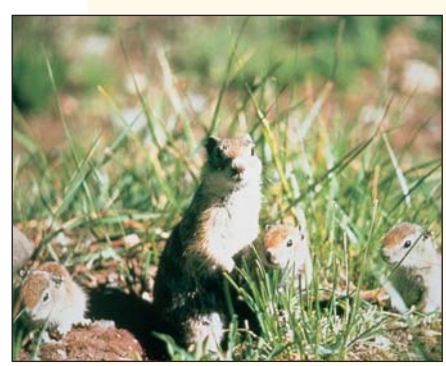
For kin selection to operate, it is not necessary that the altruist be able to distinguish relatives from nonrelatives; it is only necessary that close relatives are more likely to benefit from altruistic acts. Although kin selection does not *require* kin recognition, can animals assess the degree to which other organisms are related to themselves? In some social animals, individual recognition (based on growing up together) can be used. Other species, including mice, use odor cues. The odor of each animal is genetically influenced, and the diversity of genotypes results in a diversity of odors. Mice can detect by odor which individuals are the most closely related to themselves. Mice seem to use odor-based kin-recognition when they establish communal nests. Several females share a nest and nurse each other's offspring. A mother's inclusive fitness is maximized if she nurses only offspring that are closely related to her. Females who share a communal nest are usually related genetically.

Another explanation of altruism, based on game theory, is described on the book's Web site, under Resources: Reciprocal altruism.

Figure 8.6

Two examples of altruism favored by kin selection.

A one-year-old Florida scrub jay (right) assists in the care and feeding of its younger siblings.



A female ground squirrel (*Spermophilus beldingi*) stands guard against predators. If a coyote or hawk is spotted, the guard female emits an alarm call that attracts the predator and thus endangers the caller, but the alarm also warns the caller's next of kin and thus raises her inclusive fitness.

The evolution of eusociality

The highest degree of social cooperation is developed among the truly social, or **eusocial**, insects. Eusocial species are recognized by the possession of three characteristics: strictly defined subgroups called castes, cooperative care of the eggs and young larvae (cooperative brood care), and an overlap between generations. Eusociality occurs in the insect order Isoptera (termites) and particularly often in the order Hymenoptera (bees, wasps, and ants). A few bird species and one mammal (the naked mole rat, a burrowing type of rodent) approach eusociality in having 'helper' individuals who assist in caring for their siblings, but these helpers do not form a distinct caste.

Humans show some of the characteristics of eusocial behavior, but not to the extent shown by the eusocial insects. Humans have overlapping generations but often do not cooperatively care for their young and do not usually form castes. Assisting in the care of someone else's children (**alloparental behavior**) is, according to the American sociobiologist Sarah Hrdy, an important characteristic of our species (see Figure 1.4, p. 17), but the eusocial insects far surpass us in this behavior.

CONNECTIONS
CHAPTER 1

Eusociality in termites. Termites (order Isoptera) are a group of insects related to the cockroaches. Termite colonies are founded by a single reproductive pair called the 'king' and 'queen.' The queen grows many times larger than the other colony members, her offspring, who continually feed her and raise her additional offspring.

An important termite characteristic central to the understanding of their evolution is their chewing and digesting of wood. Termites can digest wood only with the help of symbiotic microorganisms (mostly flagellated unicellular organisms of the kingdom Protista) that live in their guts. The termites transmit these protists through regurgitated food passed to other members of the colony. This habit not only spreads the wood-digesting microorganisms throughout the colony, it also feeds those members of the colony, such as the queen, who do not feed themselves. In the evolution of eusociality among termites, the chewing of wood led to selection favoring the retention and transfer of the symbiotic microorganisms.

Along with food and microorganisms, termites also pass chemical secretions that communicate social information to other colony members. Chemicals that are used for communication are called **pheromones**. Some of these chemicals are similar to hormones, except that they are secreted by one individual and produce their effects in other individuals. One such chemical, secreted by the termite queen, inhibits most other individuals in the colony from becoming reproductively mature. Thus, the passing of food and symbiotic microorganisms throughout the colony was a precondition that probably led to the evolution of termite eusociality by providing each queen with the means to chemically control the reproduction of other individuals. These other individuals form several types of sterile castes, depending on the species. Many of the nonreproductive individuals are workers that feed the queen, tend her larvae, and enlarge the colony's living space. Other individuals serve as soldiers, fending off potential enemies that pose threats to the colony.

At seasonally timed intervals, winged reproductive individuals of both sexes are produced; these winged individuals emerge from the colony all at once and embark on nuptial flights during which mating takes place. Newly mated pairs become the founders of new colonies. Meanwhile, the original colony persists for the lifetime of the queen, a period of some 10–12 years.

Eusociality in the Hymenoptera. The insect order Hymenoptera (bees, wasps, and ants) has a much larger number of social species, of which an estimated 12,000 are species of ants. The American evolutionary biologist E.O. Wilson, considered to be the founder of modern sociobiology, is a specialist on ants. He has estimated that eusociality has evolved among the Hymenoptera as many as a dozen times and perhaps more. Why has eusociality evolved so many times in this one insect order, and so seldom in other animals? The clue seems to be found in hymenopteran sex determination and in its effects on inclusive fitness.

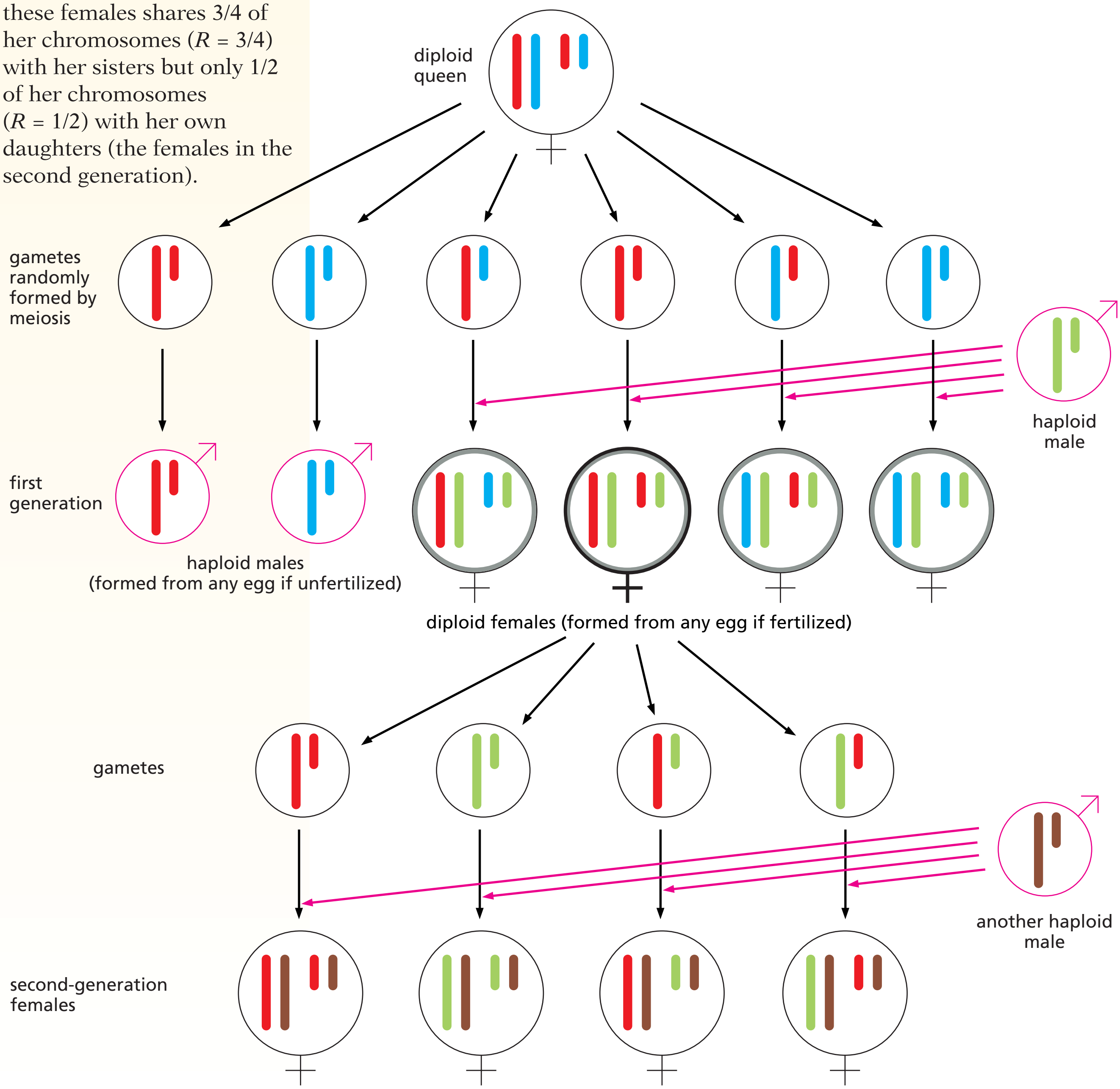
The social Hymenoptera have a unique form of sex determination (called **haplodiploidy**). Eggs that are unfertilized, and therefore haploid, nonetheless develop, but all develop into males. Eggs that are fertilized, and therefore diploid, all develop into females. Reproduction is sexual, but each reproductive female mates only once, for life, with a single male. All cells in the male are haploid, and he contributes the same haploid set of chromosomes to all his offspring. The daughters therefore share all the same alleles from their father. (By contrast, in the more usual form of sexual reproduction found in animals like ourselves, males are diploid and their haploid gametes do not all carry the same alleles; their children do not share all their father's alleles, but each gets a different assortment.)

In both forms of sexual reproduction, each female is diploid, and her gametes carry different alleles following meiosis. Her daughters each get half of her chromosomes, and half of her alleles, but each daughter gets a different sample. For each chromosome that a female receives from her mother, there is a 50:50 chance that her sister will receive the same maternal chromosome. Thus, on average, a female shares half of her maternal chromosomes, and half of her maternal alleles, with each sister (Figure 8.7). As a result, two sisters share all of the alleles from the half of their chromosomes obtained from their father, plus half of the alleles from the half of their chromosomes obtained from their mother. Sisters therefore share $1/2 + 1/4 = 3/4$ or 75% of their alleles, on average (see Figure 8.7). A female, however, only shares half of her alleles with her mother or her daughters. By neglecting her own daughters (who share only one-half of her genotype) and raising her sisters instead (who share three-fourths of her genotype, on average), she is increasing her genetic fitness. For this reason, sex determination by haplodiploidy favors the evolution of eusociality in the Hymenoptera because most females can gain greater inclusive fitness by becoming sterile workers and by helping their mother (the queen) to raise her offspring (their sisters) than by raising offspring of their own. Ancestral Hymenoptera were solitary (and many solitary species still exist), but eusociality has evolved repeatedly and independently in this group of insects (Figure 8.8).

Figure 8.7

Haplodiploidy in a species with a haploid chromosome number of 2. Notice the four females shown with shaded borders in the first generation. Each of these females shares between 50% and 100% of her chromosomes with the others, who are all her sisters. On average, each of these females shares 3/4 of her chromosomes (R = 3/4) with her sisters but only 1/2 of her chromosomes (R = 1/2) with her own daughters (the females in the second generation).

The queen bee or wasp usually secretes pheromones that inhibit the sexual development of other females in the colony. Other mechanisms determine which larvae develop into queens and which into sterile workers. For example, future queens are fed a nutritious 'royal jelly' that contains both nutrients and chemicals that stimulate their reproductive development. Also, whenever new queens emerge, one of them (usually the one emerging first) stings the others to death and thus emerges as the undisputed queen.



Most of the social behavior of eusocial insects is under instinctive control; in fact, the eusocial insects represent the highest complexity that instinctive behavior has ever reached. Antisocial behavior (meaning behavior that decreases the fitness of others) does not exist in these societies because antisocial individuals are quickly eliminated.

Figure 8.8

Eusocial insects.

A colony of ants

Honeybees swarming

THOUGHT QUESTIONS

1. Are the behaviors of individuals within a species more alike than the behaviors of individuals from different species?
2. As noted in this section, individuals share, on average, half of their genotype with their siblings. Refer to the discussion of meiosis in Chapter 2 (pp. 42–44) and explain why this is so.
3. Why should humans be interested in the social behavior of birds, frogs, or insects?

Reproductive Strategies Can Alter Fitness

Natural selection results in some genotypes leaving more copies of themselves in subsequent generations than other genotypes do. The manner in which these copies are produced can be called a reproductive strategy. **Reproductive strategies** include such features as the manner of reproduction (laying eggs or bearing live young), the litter size or number of eggs laid, the presence or absence of parental care, the presence or absence of sexual recombination, and, if there is a mating system, whether it is predominantly monogamous, polygamous, or promiscuous. Sexual behavior is an important part of reproductive strategy in many social species.

Asexual versus sexual reproduction

Reproduction of organisms can be either sexual or asexual. Many species (including all mammals and birds) are exclusively sexual, while bacteria are predominantly asexual, and certain other species (yeasts, aphids, and a variety of plants) can reproduce either way depending on the circumstances.

Asexual reproduction may be defined as reproduction without any genetic recombination. This type of reproduction has certain advantages over sexual reproduction. Within a group of organisms that includes species reproducing sexually and also species reproducing asexually, those reproducing asexually can generally do so faster and with lower energy costs. Asexual reproduction allows reproduction at an earlier age and a smaller body size, and it also avoids the costs associated with sexual reproduction. For an individual that discovers a large but finite or perishable supply of food or some other resource, asexual reproduction is an advantage because more offspring, and more generations of offspring, can be produced in a minimum of time, without any need of finding or courting a mate. Moreover, the numerous offspring are genetically identical to the original parent or founder, ensuring that favorable combinations of genes are perpetuated exactly. (The genetically identical asexual offspring of a single individual are referred to as a **clone**.)

In contrast, **sexual reproduction**, reproduction with genetic recombination, is more costly than asexual reproduction because of the time and energy expended in seeking, finding, and courting a mate, and in transferring or accepting sperm. Energy is also used in synthesizing structures that attract mates, and in the mating act itself. Mate attraction also makes a sexually reproducing individual more visible to predators, exposing that individual to increased risks. A major genetic cost is that of passing only 50% of one's alleles to each child, giving up the other half (during meiosis) to be replaced by those from one's mate. In view of these costs, it is amazing that sexual reproduction would be so widespread in both the animal and plant kingdoms. Sexual reproduction must have some great advantage.

CONNECTIONS CHAPTER 2

The great advantage of sexual reproduction is genetic variety among the offspring. In the most common type of sexual reproduction, males produce sperm cells that contain the haploid number of chromosomes, and females produce eggs that are also haploid. Each sex cell (gamete) produced by an individual carries only half of that individual's genetic material, formed during meiosis by a random choice of one chromosome from each pair (see Chapter 2, pp. 42–44). Because each gamete-forming cell undergoes meiosis independently, the chromosomal choices are different each time, and the gametes thus vary among themselves. The combination of gametes with the gametes of the opposite sex is also random. The result is that *sexually produced offspring vary greatly in all genetically controlled traits*. This may be a disadvantage if tomorrow's (or next year's) conditions are identical to today's—and unchanging conditions do in fact favor asexual reproduction. However, if tomorrow's (or next year's) environmental conditions are uncertain, then the best hedge against this type of uncertainty is to produce many *different kinds* of offspring, and sexual reproduction achieves this very efficiently. What we have just said pertains not only to the common forms of sexual reproduction, but also to other forms, such as the special kind found among the social insects: however much they differ in detail, all forms of sexual reproduction are characterized by greater variation among offspring than any form of asexual reproduction.

The hypothesis that sexual reproduction derives its adaptive advantage from the greater variation among the resultant offspring receives support from the study of certain insect species (such as aphids, also called plant lice) that are capable of producing either sexual or asexual generations. During the summer, when maturing crops offer dependable food supplies for several months in a row, these insects produce several asexual generations in quick succession. At the end of the season, however, these insects reproduce sexually, and the sexually produced eggs overwinter. When they emerge in the following spring, diverse genotypes of offspring find their way to the new stands of plants under new weather conditions, neither of which could have been predicted during the previous fall when the eggs were laid. Many genotypes perish, but a few survive and prosper by reproducing asexually during the new season. The important point is that the genotype that proves most fit in the spring is not necessarily the same one that produced successful offspring asexually during the preceding year. *Sexual reproduction is favored whenever future conditions are uncertain*, and experiments confirm that individuals laying eggs in the fall have more surviving offspring the next year if they reproduce sexually than if they reproduce asexually.

Differences between the sexes

In sexually reproducing species, the two sexes are not necessarily different. Some species, such as the green alga *Chlamydomonas* (kingdom Plantae, phylum Chlorophyta), have male and female haploid gametes that look identical, a condition called **isogamy** (meaning 'equal gametes'). But a pair of gametes may be at an advantage if at least one of them is capable of finding the other over greater distances, thus allowing more mating or mating from a wider choice of potential mates. In some cases there may also be an advantage for the resultant fertilized egg (zygote) if it possesses stored food or protective layers, each of which increases bulk. The advantages of motility and of large size can best be balanced if one of the gametes is large and the other is small and motile, a condition called **anisogamy** (meaning 'unequal gametes'). The larger, nonmotile gamete is called an **egg**, and the smaller, motile gamete is known as a **sperm**.

Males and females. Although it is possible that different-sized gametes could be produced by identical organisms, this does not usually happen. Instead, reproductive anatomy and behavior differ between the sexes in most species of animals and plants, and most of the familiar differences between males and females are explained within evolutionary theory as the consequences of anisogamy. Selection among sperm-producers, or **males**, favors the release of numerous gametes, each of which is of minimal size and maximum motility. The minimal size means that each individual sperm represents a trivial investment (in energy and materials) for the male that produces it. A male can easily produce thousands (or millions) of sperm, and he can compensate for a poor choice of mates by mating more often. Competition among males usually favors whichever one can produce the most gametes that combine successfully with the most eggs.

Selection among egg-producers, or **females**, generally favors a larger investment of parental resources, such as stored food, in each egg. Among numerous eggs, those with the most stored food or the strongest protective layers generally have the best chance of survival. This necessarily limits the number of eggs that a female can produce, and places a premium on egg *quality* rather than number.

Parental investment. There are further consequences of **parental investment**. If male parental investment is low in both energy and material costs, the price that a male pays for mating with a given female is very small. If their offspring are low in fitness (i.e., they have a small chance of survival), the male can simply mate again with other females. Low parental investment produces non-discriminating males.

Females, having fewer eggs, can produce more surviving offspring if they invest more care and protection in each one. This is especially true in mammalian females, which devote much time and energy to gestation, intrauterine feeding, and lactation. Because a female's parental investment is high, each of her offspring is more costly to her. If she mates with a low-fitness male, she greatly reduces her own fitness. She cannot simply make up for a poor choice by mating again because her capacity for repeated mating is generally limited by the large investment she must make in each of her offspring. Females thus have more at stake in each mating, and stand to gain more by choosing a mate who will father offspring who are more fit, or to lose more by choosing a mate who will father offspring who are less fit. In social species in which males vary in social status, a female can generally maximize her fitness by mating with a high-status male who can provide her and her offspring with a greater degree of protection. Selection thus favors females who are more discriminating in their mate choices, both as to social status and genetic fitness.

Mating systems

There are many types of **mating systems** known within sexual reproduction. In species in which care of the young requires the cooperation of both parents, parental investment tends to be high for both sexes. These conditions favor **monogamy**, or mating between one male and one female (Figure 8.9). If the rearing of their common offspring takes a long time, the formation of a permanent pair-bond (i.e., mating for life) is favored.

Another common situation is one in which only females care for the young, but males provide protection to both female and offspring. This situation generally favors the development of one form of **polygyny**, a mating system in which one male mates with several females. Many mammals form polygynous mating units; for example, male fur seals come ashore during the breeding season and establish territories, which they defend against other males (see Figure 8.9). The strongest male defends the best territory, an area where females can rear their pups within easy reach of the sea. Females are attracted to the territory (rather than to the male himself) and mate with males that hold territories. Males who lose territorial contests go off in search of other suitable territories. If they find none, they will not mate during that season.

Red deer, bighorn sheep, and certain other species of hoofed mammals (ungulates) form polygynous mating units in a different way. Adult males establish a dominance hierarchy, either through ritualized threat displays or through actual fighting. The females are most attracted to the dominant male. The dominant male gathers together as many females as he can, forming a 'harem.' Male social status in harem-forming species often correlates with fighting ability and with the size of horns, antlers, or other conspicuous features, so females can see at a glance which male is dominant. Females can ensure better protection against predators for themselves and their offspring by following and mating with the dominant male. Any genetic component of the characteristics correlated with social dominance is passed on to their offspring, who will thus inherit such characteristics as fighting ability, size, and the size of horns or other weapons. Nondominant (subordinate) males have fewer mating opportunities than dominant males. Many subordinates are simply young adults who will get their turn to become dominant the following year.

In addition to monogamy and polygyny, other types of mating systems include **polyandry**, an uncommon type in which one female mates with multiple males. The term 'polygamy' is sometimes used to include both polygyny and polyandry. Another mating system is **promiscuity**, in which members of both sexes mate with multiple partners and generally avoid forming permanent partnerships (see Figure 8.9).

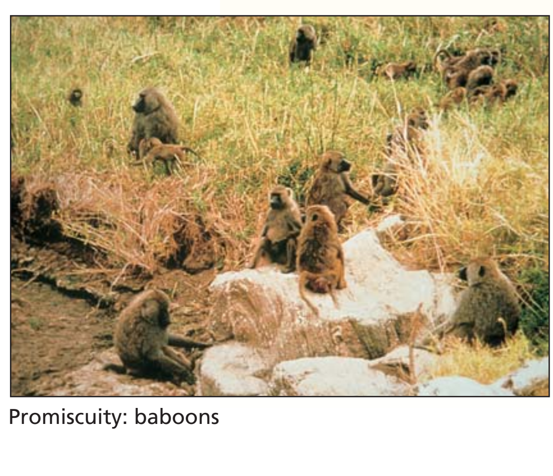
We have seen that reproductive behaviors, as well as other social behaviors, vary greatly between species. We have primarily looked at examples from the animal kingdom, but even bacteria show some social behavior. When bacteria grow in groups, they make different proteins than when they grow singly. Bacteria in groups can, for example, influence one another in the timing of their cell cycles and metabolic events. This type of social behavior is called quorum sensing. Plants show other social behaviors, including the secretion of chemicals that inhibit the nearby growth of other individuals. Plants also show some ability for kin recognition in that some plants can assess the 'match' between proteins or other molecules derived from the male pollen and the female stigma. In the next section we look more closely at social behaviors and reproductive strategies in primates, including humans.

Figure 8.9

Examples of different mating systems.

Monogamy: a family of Canada geese

Polygyny: a large male fur seal surrounded by females



Promiscuity: baboons

THOUGHT QUESTIONS

1 What are the biological definitions of 'male' and 'female?' How do these compare with cultural definitions of the same words? Do 'male' and 'female' (or 'masculine' and 'feminine') mean different things in different cultures, or at different times in history?

2 In humans and other species, males tend to have greater muscle mass than females. Under what conditions would you expect anatomical differences (in muscle mass, antlers, or size) to evolve? Is there a reason why such differences would be favored by natural selection?

3 Does the difference in gamete size in humans and other mammals tell us anything about our sexual behavior? Are human males 'destined' to be promiscuous?

Primate Sociobiology Presents Added Complexities

Primates are an order of mammals that includes monkeys, apes, lemurs, tarsiers, and humans. Primates are all extremely social animals. They are so interested in interacting with other members of their species that they sometimes go to great lengths to maintain an interaction or merely to look. We can devise an experiment to test this hypothesis. Set up a partition that completely obstructs the view through a window, and provide a lever that raises the partition for a predetermined length of time, affording a temporary view through the window. Most primates will then spend hours repeatedly pressing the lever and looking through the window, then going back to press the lever again for another view almost as soon as the partition falls. The rate of lever-pressing is higher if the window affords a view of moving objects (such as electric trains) rather than nonmoving objects (such as furniture). The rate is higher still if an actively moving animal is visible through the window, and it is highest of all if the view includes other primates of the same species. Is it any wonder that people also spend hours looking through windows at the world around them, especially when other people's movements and interactions are visible? And, in addition to the live action visible through a real window, television provides a virtual window through which we can watch people interact even more.

Primate social behavior and its development

Social skills in both human and nonhuman primates depend strongly on learning that takes place early in life. All parents and future parents should be aware of the paramount importance of early childhood experiences in all later aspects of human life. The lasting importance of learning that takes place very early in life is one of many important areas in which humans and other primates are very similar. Because of the great similarity among all primates, findings based on experiments with nonhuman primates are often used to gain insights into human behavior, although findings in one species should not be uncritically applied from one species to another. However, when we compare the behaviors of different primate species, we usually find many more similarities than differences.

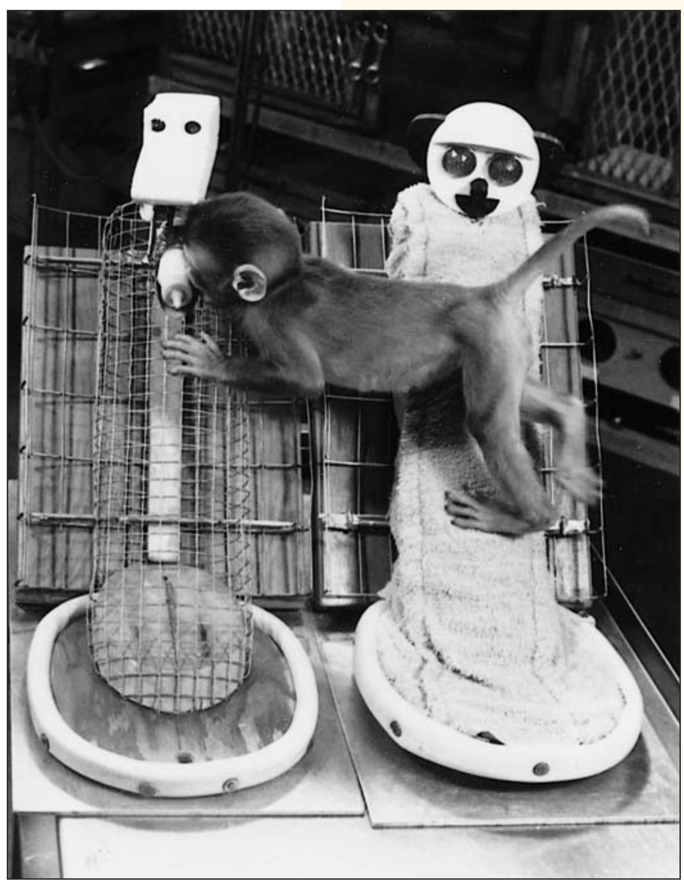
Early development of behavior. As we stated earlier, the standard test for an instinct requires that an animal be raised in isolation. Raising a primate in isolation, however, results in abnormal behavior resembling that of abused children. Sigmund Freud claimed that a baby's attachment to its mother is based initially on its need for nutrition. To test this hypothesis, Harry Harlow of the Wisconsin Primate Research Center raised infant rhesus monkeys (*Macaca mulatta*) with various forms of care but with no live mothers. Instead, dummy 'mothers' with colorful wooden 'heads' held baby bottles mounted in wire frames. Although the infant monkeys drank the milk, their behavior grew progressively more abnormal with time. The infants frequently cowered in the corner and were easily frightened. They formed no emotional attachments and seemed to ignore their 'mothers' except when they were hungry. Freud's hypothesis was falsified because the young monkeys failed to treat the wire model as a mother. Something more than the milk supply was needed for infants to form a bond with their mothers.

Harlow noticed that young monkeys liked the feel of terrycloth towels. He tried wrapping the wire mothers in a few layers of terrycloth to make them soft and clingy. The infant monkeys enjoyed clinging to these cloth-covered dummies, and the terrycloth retained the infant's own body heat during the periods of clinging. Harlow raised infant monkeys with two dummy 'mothers,' with and without terrycloth, one of them holding a baby bottle. Young monkeys spent countless hours clinging to the terrycloth 'mother,' regardless of which dummy held the bottle (Figure 8.10). When exposed to a novel or frightening stimulus, the infant monkeys would run to their terrycloth 'mothers' to cling for reassurance. After clinging for a while, the young monkeys were sufficiently reassured that they became brave enough to inspect the previously frightening stimulus. In many cases, their curiosity finally overcame their fear. Wire dummies, in contrast, never provided the behavior-changing reassurance.

Development of adult behavior. Rhesus monkeys raised with terrycloth 'mothers' seem to function normally until they become sexually mature, at which time behavioral deficits do appear. A normally raised male rhesus monkey 'mounts' a female during her reproductive cycle if she 'presents' to him (Figure 8.11), but the motherless males never mounted any females and seemed not to know how to behave in this situation. Motherless females did come into their reproductive cycles (their genitals swelled up and became bright pink), but they never

Figure 8.10

An infant rhesus monkey raised by two dummy 'mothers,' one made of bare wire and the other covered with soft terrycloth. Note that the infant maintains contact with the terrycloth 'mother,' even while nursing from the wire dummy.



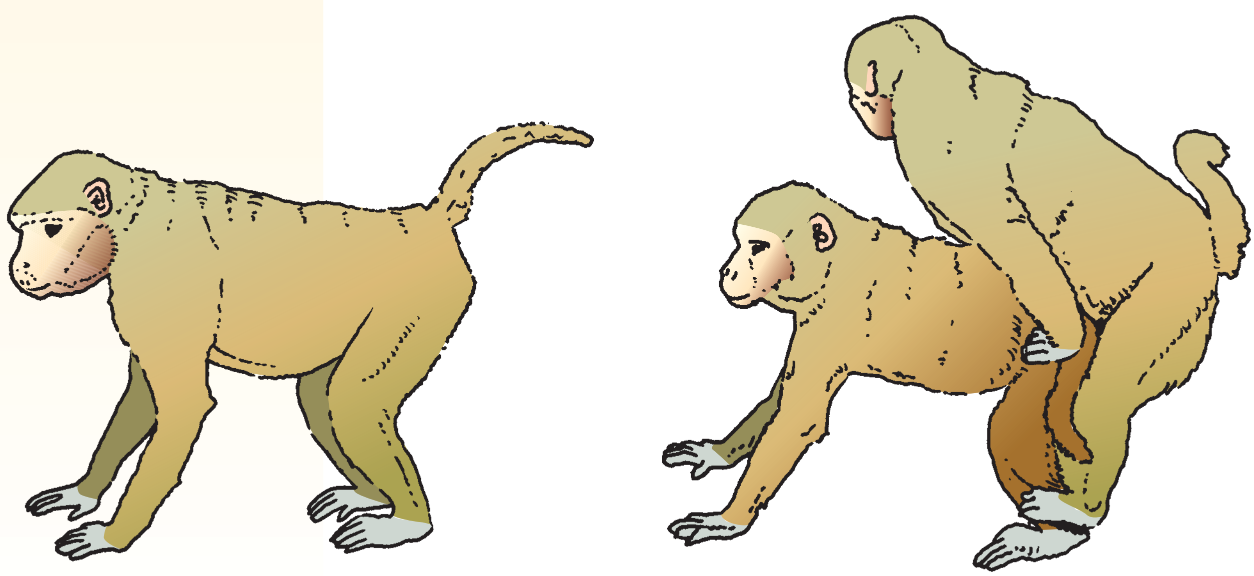
'presented' to any test males, and they consistently rejected all sexual advances. A few such females were artificially inseminated under anaesthesia and became pregnant. When their babies were born, they showed no signs of maternal behavior, such as picking up their infants and holding them to the breast. Instead, they either ignored or rejected their infants, in some cases so forcibly that the infants had to be removed for their own safety. Sexual behavior and maternal behavior had never been learned in these monkeys, even though their behavior had seemed normal up to the time of sexual maturity. Adult social behavior has very strong learned components in rhesus monkeys and in other higher primate species, too.

Harlow continued his experiments, seeking to pinpoint what the motherless monkeys were failing to learn from the terrycloth dummies. Could the young monkeys receive a proper upbringing without a live mother? What conditions were minimally necessary? Remembering that wild juvenile primates associate with one another in play groups, Harlow let some of the young, motherless monkeys play together. He found that motherless monkeys who had opportunities both to cling to a terrycloth dummy and to play with one another developed normal adult social behaviors. By varying the length of the play period, Harlow was able to show that as little as half an hour of play per day was adequate to ensure that young monkeys would acquire normal adult behaviors. Harlow concluded that instincts were not sufficient to produce the proper sexual behavior or maternal behavior in these monkeys, but that a youthful period of social learning was also required.

Rough and tumble play. Most play in primates is "rough and tumble" play in which there is frequent and repeated body contact, including pushing, pulling, and climbing—just watch young children in a schoolyard to see examples. Primate play also includes a good deal of chasing and dodging, usually followed by more rough and tumble play. Although rough and tumble play is neither sexual nor maternal, it seems to teach many lessons, such as how to handle and perhaps restrain other individuals without hurting them. Hurting another individual, whether accidentally or not, brings

Figure 8.11

Normal mating behavior in rhesus monkeys.



an adult female 'presenting'

mounting and copulation

squeals of pain, generally causing adults to intervene and break up the activity. Play also teaches taking turns at different roles: pursuer and pursued, restrainer and restrained, climber and support, etc. In the context of play, the players learn how strong or weak other individuals are, and how much rough play each will tolerate. These lessons are later refined into dominance and submission relationships with other individuals and into sexual behaviors such as those in which male monkeys mount females. Mounting behavior arises during rough and tumble play, without regard to the sex of either individual; only after sexual maturity does it take on an explicitly sexual meaning. The defense and protection of smaller individuals, including picking them up and delicately cradling them, is also learned in play. In large, mixed-age social groups, there is usually an opportunity for subadult animals to practice the behaviors related to child care.

There are parallels in human behavior. Children learn many lessons in play, including cooperation, turn-taking, role-playing, counting and scorekeeping, setting and following rules, and settling arguments and disputes. They also learn a good deal about each other's personalities: who plays fair, who cheats, who is a bully, who cries if they do not get their way, and so forth. Children often imitate adult roles in play, practicing many of the skills that they see adults using and that they may themselves use later in life: hunting, digging, child care, food preparation, useful and artistic crafts, and so on. Abused children and those deprived of the opportunities of exploratory and rough and tumble play with other children often fail to develop the proper adult social behaviors, including both marital behavior (which is much more than just sexual) and parental care.

Social organization. Most primates are extremely social, but the size and complexity of social groupings vary greatly. Closely related to the species that Harry Harlow studied are the baboons, monkeys of the genus *Papio*. *Papio hamadryas* is a harem-forming, polygynous species that lives in the rocky highlands of Ethiopia. Male hamadryas baboons are often aggressive fighters, and were revered by the ancient Egyptians for this trait. The other baboons, *Papio cynocephalus* and related species, live on the open, grassy savannas of Africa. The savanna baboons all share a form of social organization different from that of the hamadryas. In the wild, savanna baboons hardly ever fight. They express dominance largely through gestures such as staring at an opponent, showing their teeth, or slapping the ground (Figure 8.12). We can study dominance by observing pairwise encounters (between two individuals at a time) and noting which baboon more often gets what it wants. Dominance status generally follows size and fighting strength, although it is rarely contested and outright fighting is rare. A lengthier description of baboon social organization can be found on our Web site, under Resources: Baboons.

Grooming. Baboons, like other monkeys, are forever grooming one another—picking burrs and parasites from each other's fur (see Figure 8.12). As a gesture of friendliness, grooming is generally reciprocated, with groomer and recipient taking turns. Grooming is a pleasurable activity, and it helps form many social bonds. Infants and juveniles are often groomed by their mothers. Females who are not yet mothers themselves often practice grooming behavior and infant care. This 'mother-in-training' behavior, called 'allomothering' or 'aunt behavior,' is very important in many primate species, including humans. Through such experiences, older juvenile primates of both sexes learn the behavior patterns essential to parenting, while younger primates gain social experiences, learning experiences, and even substitute parents in the event of the parent's death or temporary removal.

Human examples of allomothering include holding and feeding other people's children, playing with children, and, of course, baby-sitting.

Reproductive strategies among primates

Studies of primate behavior before the late 1960s were in most cases written by male scientists and tended to emphasize male behavior and dominance relations among males. Males were often described as making choices, while females were often depicted as either passive or 'coy.' Beginning with the early work of primatologists Jeanne Altmann (American), Phyllis Jay (American), and Jane Goodall (English), relationships among female primates began to receive equal or greater attention. The primatologists of the subsequent generation conducted many important new studies that focused on the social behavior of female primates.

One primatologist who has changed our views of primate sexual biology is Sarah Hrdy, whose sociobiology is influ-

Figure 8.12

Examples of social behavior in monkeys.

Baboons grooming one another

Threat display of a male hamadryas baboon, showing his large canine teeth

Grooming behavior in rhesus monkeys

enced by a feminist outlook. Female primates, according to Hrdy, are much more sophisticated than previous researchers had imagined. Whereas the adult males use rather obvious means to maximize their inclusive fitness, Hrdy discovered that the means used by females were considerably more subtle and usually involved influencing the behavior of the males.

In her work on langur monkeys in India, Hrdy discovered the important ways in which female monkeys, although subordinate in power and strength to males, nevertheless managed to influence male reproductive choices and male social behavior to the female's own advantage. Male primates differ from one another in the number of offspring that they leave, and female primates frequently modify what males must do to achieve reproductive success. Female primates can often maximize their own reproductive success by the ways in which they influence male social behavior. Hrdy identified at least five ways in which female primates can maximize their reproductive fitness:

1. by choosing their mates,
2. by influencing males to support and protect them,
3. by competing with other females for resources,
4. by cooperating with other females (usually close relatives),
5. by increased efficiency in daily activities such as locomotion and obtaining food.

Through the work of these primatologists, we now know that females make important choices of their own and solicit male attention for a variety of reasons, showing that it often pays for them to be flirtatious rather than coy. For example, females of many species can mate with males who are not their usual partners, and they have often been observed to mate at times when they were already pregnant or otherwise unable to produce new offspring. Males can generally increase their reproductive fitness by mating with as many females as they can, indiscriminately. The optimal behavior for a female, however, depends on her own fitness and social status, as well as that of her possible mates. If a female is of high status herself, and is mated to a high-status male, then she has nothing to gain from mating with a lower-ranking male. In contrast, a female of low status, or one mated to a low-status male, could potentially increase her fitness by mating additionally with a high-status male. If he sires one of her offspring, then she has produced a higher-status offspring and raised her own fitness as a result. That is because the offspring of higher-status males have more opportunities to mate; therefore, females can maximize their fitness (leave more grandchildren) if they raise the offspring of high-ranking males. Moreover, even if their mating produces no offspring at all, the high-status male who has mated with her will maximize *his* fitness by protecting any female that he has mated with, as well as her subsequent offspring, because he would be operating under the assumption that these offspring might be his. Thus, females can gain important advantages from liaisons with high-ranking males, even at times when ovulation has not occurred and when subsequent pregnancy and childbirth are not possible.

Hrdy also discovered that male primates are sometimes infanticidal, and that female willingness to mate with powerful males was sometimes a strategy to discourage their infanticidal tendencies. Infanticide may occur among certain primate species whenever a new dominant male takes over a group. The new male can increase his fitness if he kills infants that are not his, especially if their mothers are lactating. Lactation inhibits the female reproductive cycle in most mammalian species; infanticide by the male causes lactation to end. Females enter estrus and the male gains access sooner to reproductive females. Once he has mated and produced offspring, however, the male will maximize his fitness if he defends all his mates and their offspring.

One of the many consequences of primate reproductive strategies is a difference between the sexes in how they pay attention to social rankings. Males in socially ranked species must pay attention to their own rank and status—they must remember who has ever threatened them or been intimidated by them. Females, however, must know much more, because each female must not only know her own status, but also that of every male in the group. In order to know whether one potential mate ranks higher than another, she must pay attention to *all* the social interactions among the males. In social species, females therefore generally take more interest than males in knowing about the social interactions of all other members of the group and in learning the status of all the males. Those who are better at paying attention to male–male interactions and correctly judging each male's social status and genetic fitness are at a selective advantage because they are better able to maximize their fitness by their behavior toward these males.

Both Hrdy and Jane Goodall have observed several instances in which competition between females produced outright hostility, even infanticide. Arguing from a sociobiological perspective, Hrdy explained that competition among unrelated females should be expected when their genetic self-interests are in conflict. A universal sisterhood, in which all females cooperate as a unit, would therefore never evolve. In evolutionary terms, such a sisterhood would not be a stable strategy, because an individual female would always be able to 'cheat' by refusing to cooperate, and by doing so she would raise her fitness and be favored by natural selection. Because evolution would never be expected to produce cooperative sisterhoods among unrelated females, Hrdy suggests that women who share her desire for such cooperative sisterhoods should strive to create them socially. Humans are not prisoners of biological destiny and are able to create social groupings and social behaviors that have not evolved.

Some examples of human behaviors

Much interest has focused on certain human behaviors and on the extent to which these behaviors are learned or inherited. Behaviors disapproved of by large segments of society have generally attracted the most attention. People who wish to change behavior that has a strong learned component generally seek to find *how* it is learned and how an alternative form of behavior can be learned instead. If the behavior has a strong inherited component, it will be more difficult to bring about change through education. Other forms of intervention that might be more appropriate in such cases include trying to identify any genes involved in the behavior. However, most of the behaviors of interest are complex and are probably influenced by many genes, making it harder to identify any of them or to modify them in any meaningful way.

We also hasten to add that political motives are often suspected of those who write about human behavior or who try to apply what we know of other species to the understanding of human behavior. History has taught us that various oppressors have claimed scientific support to justify slavery, political repression, and genocide. (The Nazis come to mind as the most obvious example, but there have been many others.) There is thus reason for caution, but sometimes the reactions have become uncivil and tempers have run high. Some biologists who intended no harm to anyone have been yelled at by disapproving crowds and have had eggs thrown at them. There are people, in other words, who fear that scientific study may again be used to justify unspeakable horror.

Aggression. Konrad Lorenz was a German scientist who studied animal behavior. He first won recognition (including a Nobel Prize) for his studies on imprinting, a form of learning that occurs early in life. In his later years, Lorenz wrote several controversial books in which he claimed that many human behaviors are instinctive. For example, in his book *On Aggression*, Lorenz claimed that aggression is largely instinctive in humans as well as other animals. As evidence, Lorenz argued first that aggression is widespread in many animal species and in various human societies. Second, he argued that the facial expressions and other gestures that accompany aggression and aggressive threats are similar in humans and animals and are also similar across many human societies.

Other scientists, however, have marshalled considerable evidence that aggression in humans has strong learned components.

1. Aggression takes many different forms in different societies, which use different weapons and different fighting traditions. If aggression were entirely instinctive, one would not expect it to be so variable.
2. Aggression is more prevalent in those societies that encourage it, and it generally takes the form that the society encourages. In the many societies that encourage aggression only in males or only in certain age groups, it occurs primarily in the groups in which it is encouraged. In societies that discourage aggression, it is much less common.
3. Within any society, some individuals are more aggressive than others. Individuals trained to be aggressive become aggressive, while most people raised to be less aggressive become less aggressive. We would not expect such large individual differences if aggression were inherited.
4. When aggressive behavior is desired, as in the military or in sports such as boxing and judo, it must be taught and practiced frequently.

Two special forms of aggression that have received a lot of attention are child abuse and rape. Studies examining criminal records in various countries all over the world have shown that child abuse among humans follows the same patterns as infanticide in other primate species. In particular, stepfathers (who are genetically unrelated to the children who live with them) are up to 100 times more likely to abuse or kill the children in their care than are genetic fathers.

Feminist writers such as Susan Brownmiller have portrayed rape, or forcible sexual intercourse, as an attempt by the rapist to dominate and control his victim, and thus as a crime of violence rather than of sex. Against this idea, sociobiologists Randy Thornhill and Craig Palmer argue that rape is very much about sex. They use statistical records from rape crisis centers to show that victims are most often in the prime reproductive age range and that married rape victims feel more heavily traumatized than unmarried ones. They claim that a predisposition to rape persists because rape does occasionally produce children who perpetuate the genes of the rapist. Therefore, these authors argue, rape is natural, though they hasten to add that it is still reprehensible behavior. Their hypothesis does not, however, explain why the overwhelming majority of men are *not* rapists.

Many studies show that most women prefer as mates men who are good-looking, healthy, strong, skillful, kind, respected by others, and high in social status and wealth. Thornhill and Palmer say that "men might resort to rape when they are socially disenfranchised, and thus unable to gain access to women through looks, wealth, or status." According to this hypothesis, the men who become rapists can leave more offspring if they rape than if they do not, because they are usually the men that women are unlikely to choose as mates.

Barbara Ehrenreich, a critic of the Thornhill–Palmer hypothesis, emphasizes that rapists make inferior husbands and fathers, and that the children of rape are thus far less fit than other children. The mothers of these children have been traumatized, and their fathers are in most cases gone, and when present they are neither good fathers nor good role models. Compared with the men that women would choose as mates, rapists are inferior in social standing, inferior in fitness, and inferior in their ability to raise fit children. This may explain why most men are not rapists: they can produce more children, and contribute as fathers to their children's fitness, by cultivating the behaviors that women value. The children of these men and the women who choose to marry them usually attain higher social status and are more socially and psychologically equipped to enter into normal and stable relationships themselves. They tend to leave more future children and are thus far more fit than the children born of rape.

Alcoholism. Alcoholism is a complex form of behavior that seems to have both learned and inherited components. To complicate matters, there are various degrees of alcoholism, and many individuals are classified as alcoholics by some criteria and not others. However, the greatest complication arises from the heterogeneity of the disorder: alcoholism manifests itself differently in men and in women, and it may also have different characteristics in different social classes.

Recent studies show that alcoholism may in fact exist in two or more separate forms. Type I alcoholism, also called late-onset or milieu-limited, typically arises after age 25 and is common in both sexes. It is characterized by psychological or emotional dependence (or loss of control), by guilt, and by fear of further dependence. This type of alcoholism frequently responds well to treatment. By contrast, type II alcoholism, also called male-limited, early-onset, or antisocial alcoholism, typically arises during the teenage years and is common in males only. It manifests itself in alcohol-seeking behavior, in novelty-seeking or risk-taking behavior generally, and in frequent impulsive and antisocial behavior including alcohol-related fighting and arrests. This type of alcoholism responds poorly to conventional forms of treatment.

Adoption studies in Denmark, Sweden, and the United States suggest that a predisposition for type II alcoholism may be inherited. The largest study, of 1775 adoptees in Sweden, found that the rate of alcoholism among the biological sons of type II alcoholic fathers raised in families without alcoholics was nine times the rate among other adoptees, including those adopted into type II alcoholic households. Type I alcoholism, however, shows a much smaller hereditary influence and may instead be subject to strong environmental influences. Some experts suggest that type I alcoholism is still heterogeneous and should be subdivided further.

Studies on alcoholism among twins show a higher rate of concordance in identical twins than in fraternal twins, meaning that, if one twin is an alcoholic, there is greater probability that the other is also an alcoholic if the twins are identical than if the twins are fraternal. (As described in Chapter 3 (pp. 71–72), a rate of concordance is the fraction of individuals who match in a certain trait.) The concordance is greater for type II alcoholism than for type I.

CONNECTIONS CHAPTER 3

Sexual orientation. Some people regard variations in sexual orientation, including homosexuality, as innate and unchangeable, while others view them as learned behavior patterns that are subject to change. The available evidence, which is not very extensive, was summarized and reviewed in two books by the English-born neurobiologist Simon LeVay. Some small differences were observed between the brain structures of homosexual men and heterosexual men, but many of the homosexual men in the study had died from AIDS, so it is uncertain whether these differences resulted from AIDS or pre-dated the onset of that disease. If a difference in brain structure could be demonstrated between homosexual and heterosexual men, other questions would remain to be answered: did the structural difference precede the sexual orientation, or might the structural change have resulted from some aspect of a lifestyle difference? Scientists are only just beginning to examine such questions in homosexual men; studies examining lesbian women are even rarer.

Studies have been conducted on homosexual males who have twin brothers. The rate of concordance is higher for identical twins than for fraternal twins, meaning that, if one twin is homosexual, there is a much higher probability that the other twin is also homosexual if he is an identical twin than if he is a fraternal twin. Such a result is suggestive of at least some genetic influence, but the very real methodological problems of such twin studies makes it very difficult to rule out other possible influences. The biggest shortcoming of twin studies is that the environments in which the twins are raised are never chosen at random and are usually very similar, even in cases of adoption.

THOUGHT QUESTIONS

1 To what extent can sociobiological findings on animals be extrapolated to humans? Are animal studies relevant at all to the study of human behaviors such as alcoholism or homosexuality?

2 How important are fathers in early childhood development? What important *social* skills do children learn from interacting with their mothers? With their fathers? What do children learn from watching their parents interact with one another? What happens in families in which no father is present? What happens when no mother is present?

3 Think of the many ways in which humans learn (and subsequently practice) the social skill of evaluating the social status and motives of others. How much do we learn (or what skills do we exercise and practice) from play, from small-group discussions, from gossip, from novels, or from television? Do males and females participate in these activities in the same way? Why, or why not?

Concluding Remarks

Sociobiology, the comparative study of social behavior and social groups among organisms, is a subfield within evolutionary biology. Much of social behavior is learned, but only those aspects of social behavior that are inherited are subject to natural selection and therefore to evolutionary change. Sociobiology therefore focuses on inherited behaviors or capacities, although all sociobiologists agree that learning can modify those behaviors in many species. Often it is a predisposition for a behavior, or a capacity to learn a behavior, that is inherited, not the behavior itself. Sociobiology can predict when natural selection will favor altruism, social groups of differing sizes, behavior that is stereotyped as opposed to variable, or behavior that differs between the sexes. Many such hypotheses have already withstood repeated testing.

In humans, even though some components of behavior are inherited, every behavior can also be modified by learning. Twin studies, adoption studies, cross-cultural studies, and studies of other species can all provide important clues to the understanding of human behavior patterns. Many human behaviors vary across cultures; many are also strongly influenced by early childhood experiences. One of the most effective and cost-efficient ways in which we can improve human society is to provide each and every child with a safe childhood full of experiences from which to learn.

Chapter Summary

- **Sociobiology** is the evolutionary study of **social behavior** and **social organization** among all types of organisms.

- Organisms live in social groups because it affords such advantages as group defense, help in finding and exploiting food resources, and greater reproductive opportunities.
- **Altruistic** behavior is favored if it contributes to **inclusive fitness** through **kin selection**.
- Inclusive fitness has also favored the evolution of social cooperation and **eusocial** species**.**
- Among **reproductive strategies**, **asexual reproduction** is favored by natural selection in situations in which a quickly produced series of uniform offspring are advantageous, but **sexual reproduction** is favored whenever future conditions are uncertain and a greater variety of offspring is a greater advantage.
- Among sexually reproducing species, there are many different **mating systems**, including monogamy, polyandry, polygyny, and promiscuity.
- In many species, different levels of **parental investment** favor different reproductive strategies in **females** (**egg** producers) and in **males** (**sperm** producers).
- All behavioral characteristics that have been closely studied are influenced by both genetic and environmental influences to various degrees.
- Behaviors that can be performed without the opportunity for prior learning are considered **innate**, and innate behaviors that are complex are called **instincts**.
- In animal species, behaviors related to mating and courtship are more often **instincts**, while **learning** has a stronger influence on most locomotor behaviors.
- Learned behavior is highly important among primates, especially among humans.

CONNECTIONS TO OTHER CHAPTERS

Chapter 1	Sociobiology is a good example of a paradigm.
Chapter 2	Social behavior can differ among different genotypes.
Chapter 5	Social behavior can greatly affect the fitness of each genotype and can thus alter allele frequencies. Social behavior also evolves, and the evolution of behavior is of prime interest to sociobiologists.
Chapter 9	Mating is one of the most important kinds of social behavior. Population growth is a result of mating behavior on a large scale.
Chapter 10	Access to good nutrition is one important motivating force in social behavior.
Chapter 13	Social behavior in animals happens as the result of brain activity.
Chapter 14	Drugs can alter social behavior.
Chapter 15	Social support can promote healing; stress can interfere with healing.
Chapter 16	AIDS is spread by certain social behaviors.

PRACTICE QUESTIONS

1. For each of the following human behaviors, state at least one piece of evidence pointing to an important learned component for the behavior:

   a. eating with utensils

   b. speaking English

   c. hunting

2. For each of the following behaviors, present an argument for an important innate component of the behavior:

   a. tail wagging in dogs

   b. mooing in cows

   c. smiling in humans

3. Present at least one argument supporting each of the following assertions:

   a. that piano playing ability has important learned components

   b. that piano playing ability has important innate components

4. State at least six research methods used in sociobiology.

5. Which of the following behaviors is most likely to have strong instinctive components in a wide variety of species?

   a. attracting a mate

   b. climbing a tree

   c. finding and capturing food

   d. moving about one's habitat

   e. none of the above

6. Natural selection favors the instinctive control of behavior in all of the following situations *except*:

   a. in species with short life spans

   b. in outsmarting prey

   c. in courtship displays or mating calls

   d. in escaping from sudden danger

   e. in building a nest or weaving a web

7. Which of the following does NOT fit the definition of an altruistic act?

   a. a millionaire leaves money to charity in her will

   b. a taxi driver runs through red lights to get a pregnant woman to the hospital in time to deliver her baby

   c. a man runs in front of oncoming traffic to save a small child

   d. a firefighter runs into a burning building to rescue people who may be trapped inside

8. Which of the following belongs in a different group from the rest?

   a. ants

   b. bees

   c. termites

   d. wasps

9. Which of the following situations favors sexual reproduction?

   a. microorganisms reproducing inside a human host

   b. fungi growing in a fallen tree as it decays

   c. insects or worms exploiting a large and dependable food supply

   d. insects colonizing new food supplies by laying eggs in them

10. What are the three conditions that define eusociality?

11. How is kin selection defined?