Part VIII Ecology and Behavior

52

Behavioral Biology

Chapter Outline

2.1 Many behavioral patterns are innate.

Approaches to the Study of Behavior. Field biologists focus on evolutionary aspects of behavior.

Behavioral Genetics. At least some behaviors are genetically determined.

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Nonassociative Learning and Conditioning. Conditioning requires association between two stimuli or between a stimulus and a response.

The Development of Behavior. Parent-offspring interactions influence behavioral development.

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Migratory Behavior. Animals use many cues from the environment to navigate during migrations.

.3 Communication is a key element of many animal behaviors.

Courtship. Animals use signals to court one another.

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Behavioral Ecology. Behavior is shaped by natural selection.

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Reproductive Competition and Sexual Selection. Mate choice affects reproductive success, and so is a target of natural selection.

Mating Systems. Mating systems are reproductive solutions to particular ecological challenges.

5 There is considerable controversy about the evolution of social behavior.

Altruism and Group Living. Many ideas have been put forward to explain the evolution of altruism.

Group Living and the Evolution of Social Systems. Social organisms exhibit cooperation and altruism.

FIGURE 52.1
Rearing offspring involves complex behavior. Living in groups called prides makes lions better mothers. Females share the responsibilities of nursing and protecting the pride's young, increasing the probability that the youngsters will survive into adulthood.

Organisms interact with their environment in many ways. To understand these interactions, we need to appreciate the internal factors that shape the way an animal behaves, as well as aspects of the external environment that affect individual organisms. In this chapter, we explore the mechanisms that determine an animal's behavior (figure 52.1) and examine the field of behavioral ecology, which investigates how natural selection has molded behavior through evolutionary time.

52.1 Many behavioral patterns are innate.

Approaches to the Study of Behavior

During the past two decades, the study of animal behavior has emerged as an important and diverse science that bridges several disciplines within biology. Evolution, ecology, physiology, genetics, and psychology all have natural and logical linkages with the study of behavior, each discipline adding a different perspective and addressing different questions.

Research in animal behavior has made major contributions to our understanding of nervous system organization, child development, and human communication, as well as the speciation process, community organization, and the mechanism of natural selection itself. The study of the behavior of nonhuman animals has led to the identification of general principles of behavior, which have been applied, often controversially, to humans. This has changed the way we think about the origins of human behavior and the way we perceive ourselves.

Behavior can be defined as the way an animal responds to stimuli in its environment. A stimulus might be as simple as the odor of food. In this sense, a bacterial cell "behaves" by moving toward higher concentrations of the sugar. This behavior is very simple and well suited to the life of bacteria, allowing these organisms to live and reproduce. As animals evolved, they occupied different environments and faced diverse problems that affected their survival and reproduction. Their nervous systems and behavior concomitantly became more complex. Nervous systems perceive and process information concerning environmental stimuli and trigger adaptive motor responses, which we see as patterns of behavior.

When we observe animal behavior, we can explain it in two different ways. First, we might ask *how* it all works—that is, how the animal's senses, nerve networks, or internal state provide a physiological basis for the behavior. In this way, we would be asking a question about *proximate causation.* To analyze the proximate cause of behavior, we might measure hormone levels or record the impulse activity of neurons in the animal. We could also ask *why* the behavior evolved—that is, what is its adaptive value? This is a question concerning *ultimate causation.* To study the ultimate cause of a behavior, we would attempt to determine how it influenced the animal's survival or reproductive success. Thus, a male songbird may sing during the breeding season because it has a level of the steroid sex hormone testosterone, which binds to hormone receptors in the brain and triggers the production of song; this would be the proximate cause of the male bird's song. But the male sings to defend a territory from other males and to attract a female with which to reproduce; this is the ultimate, or evolutionary, explanation for the male's vocalization.

The study of behavior has had a long history of controversy. One source of controversy has been the question of whether behavior is determined more by an individual's genes or by its learning and experience. In other words, is behavior the result of nature (instinct) or nurture (experience)? In the past, this question has been considered an either/or proposition, but we now know that instinct and experience both play significant roles, often interacting in complex ways to produce the final behavior. The scientific study of instinct and learning, as well as their interrelationship, has led to the growth of several scientific disciplines, including ethology (the study of behavior), behavioral genetics, behavioral neuroscience, and comparative psychology.

Innate Behavior

Early research in the field of animal behavior—most notably by Nobel Prize winners Karl von Frisch, Konrad Lorenz, and Niko Tinbergen (figure 52.2)—focused on behavioral patterns that appeared to be instinctive or innate. Because behavior is often *stereotyped* (appearing in the same way in different individuals of a species), these early researchers argued that it must be based on preset paths in the nervous system. In their view, these paths are structured from genetic blueprints and cause animals to show essentially the same behavior from the first time it is produced throughout their lives.

These researchers based their opinions on behaviors such as egg retrieval by geese. Geese incubate their eggs in a nest. If a goose notices that an egg has been knocked out of the nest, it will extend its neck toward the egg, get up, and roll the egg back into the nest with a side-to-side motion of its neck while the egg is tucked beneath its bill (figure 52.3). Even if the egg is removed during retrieval, the goose completes the behavior, as if driven by a program released by the initial sight of the egg outside the nest. According to ethologists, egg retrieval behavior is triggered by a **sign stimulus** (also called a **key stimulus**), the appearance of an egg out of the nest; a component of the goose's nervous system, the **innate releasing mechanism,** provides the neural instructions for the motor program, or **fixed action pattern.** More generally, the sign stimulus is a "signal" in the environment that triggers a behavior. The innate releasing mechanism is the sensory mechanism that detects the signal, and the fixed action pattern is the stereotyped act.

One interesting aspect of sign stimuli is that they are often not very specific; in some situations, a wide variety of objects will trigger a fixed action pattern. For example, geese will attempt to roll baseballs and even beer cans back into their nests. Moreover, once the objects are in the nest, the goose recognizes that they are not eggs and removes them! A simi-

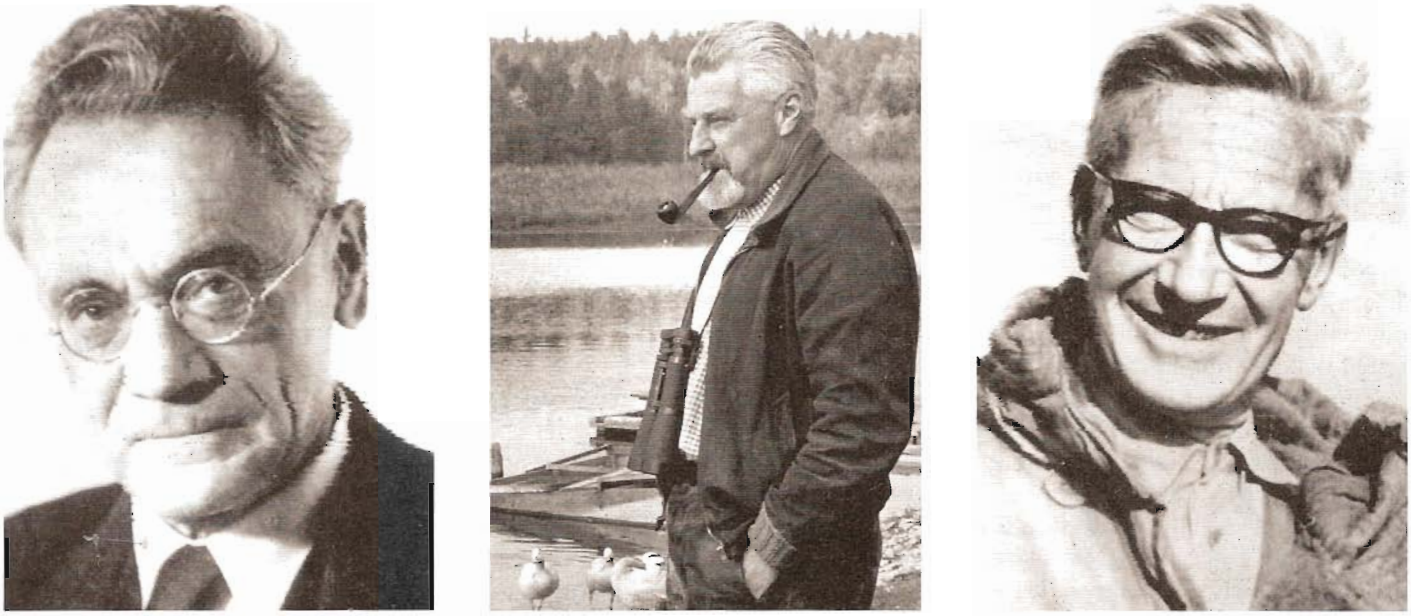


FIGURE 52.2
The founding fathers of ethology. Karl von Frisch, Konrad Lorenz, and Niko Tinbergen pioneered the study of behavioral science. In 1973, they received the Nobel Prize in physiology or medicine for their path-making contributions. Von Frisch led the study of honeybee communication and sensory biology. Lorenz focused on social development (imprinting) and the natural history of aggression. Tinbergen examined the functional significance of behavior and was the first behavioral ecologist.

lar example is provided by male stickleback fish. During the breeding season, males develop bright red coloration on their undersides. Territorial males react aggressively to the approach of other males, performing an aggressive display and even attacking. When Niko Tinbergen observed a male stickleback in a laboratory aquarium displaying aggressively when a red fire truck passed by the window, he realized that the red coloration was the sign stimulus. Subsequent experiments revealed that males would respond to many unfishlike models as long as the models had a red stripe.

This phenomenon is taken one step further by what are termed **supernormal stimuli.** Given a choice between two sign stimuli, one of normal size and the other much larger, many animals will respond to the larger of the two. Thus, geese given a choice of a normal goose egg and one the size of a volleyball will choose to roll the bigger one back to the nest. Why supernormal stimuli exist is not always clear. One aspect to keep in mind, however, is that in many cases, supernormal stimuli do not occur in nature. Thus, geese may prefer eggs the size of volleyballs, but they never encounter eggs of that size. It may be that geese have evolved to respond to the larger object so that they will attend to eggs, rather than smaller, circular rocks. As a result, natural selection may have favored the evolution of a preference for larger objects; this general response may lead to unexpected outcomes in experiments, but probably doesn't often lead to maladaptive behavior.

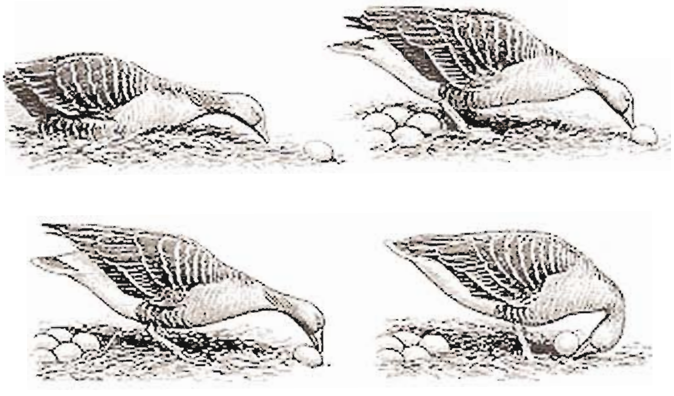


FIGURE 52.3
Innate egg-rolling response in geese. The series of movements used by a goose to retrieve an egg is a fixed action pattern. Once it detects the sign stimulus (in this case, an egg outside the nest), the goose goes through the entire set of movements: It will extend its neck toward the egg, get up, and roll the egg back into the nest with a side-to-side motion of its neck while the egg is tucked beneath its bill.

Early research in animal behavior emphasized innate behaviors that are the result of preset pathways in the nervous system and thus are likely to be genetically controlled.

Behavioral Genetics

In a famous experiment carried out in the 1940s, Robert Tryon studied the ability of rats to find their way through a maze with many blind alleys and only one exit, where a reward of food awaited. Some rats quickly learned to zip through the maze to the food, making few incorrect turns, while other rats took much longer to learn the correct path. Tryon bred the fast learners with one another to establish a "maze-bright" colony, and he bred the slow learners with one another to establish a "maze-dull" colony. He then tested the offspring in each colony to see how quickly they learned the maze. The offspring of maze-bright rats learned even more quickly than their parents had, while the offspring of maze-dull parents were even poorer at maze learning. After repeating this procedure over several generations, Tryon was able to produce two behaviorally distinct types of rat with very different maze-learning abilities (figure 52.4). Clearly, the ability to learn the maze was to some degree hereditary, governed by genes passed from parent to offspring. Furthermore, those genes appeared to be specific to this behavior, because the two groups of rats did not differ in their ability to perform other behavioral tasks, such as running a completely different kind of maze. Tryon's research demonstrates how a study can reveal that behavior has a heritable component.

Further support for the genetic basis of behavior has come from studies of hybrids. William Dilger of Cornell University examined two species of lovebird (genus *Agapornis*), which differ in the way they carry twigs, paper, and other materials used to build a nest. *Agapornis fischeri* holds nest material in its beak, while *A. roseicollis* carries material tucked under its flank feathers (figure 52.5). When Dilger crossed the two species to produce hybrids, he found that the hybrids carry nest material in a way that seems intermediate between that of the parents: They repeatedly shift material between the beak and the flank feathers. Other studies conducted on courtship songs in crickets and tree frogs also demonstrate the intermediate nature of hybrid behavior.

The role of genetics can also be seen in humans by comparing the behavior of identical twins. Identical twins are, as their name implies, genetically identical. However, most sets of identical twins are raised in the same environment, so it is not possible to determine whether similarities in behavior result from their genetic similarity or from experiences shared as they grew up (the classic nature-versus-nurture debate). However, in some cases, twins have been separated at birth. A recent study of 50 such sets of twins revealed many similarities in personality, temperament, and even leisure-time activities, even though the twins had often been raised in very different environments. These similarities indicate that genetics plays a role in determining behavior even in humans, although the relative importance of genetics versus environment is still hotly debated.

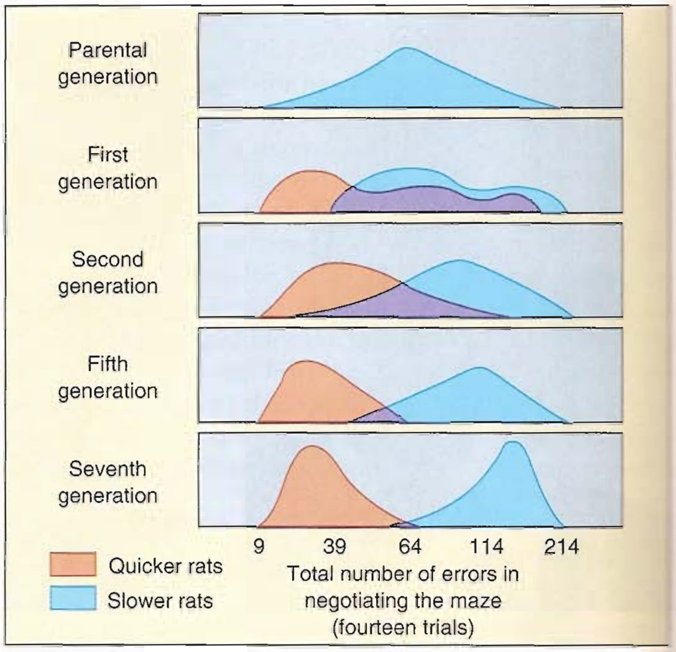


FIGURE 52.4
The genetics of learning. Selection experiments in the laboratory established a genetic basis for differences in the ability to learn to run through a maze.
What would happen if, after the seventh generation, rats were randomly assigned mates regardless of their ability to learn the maze?

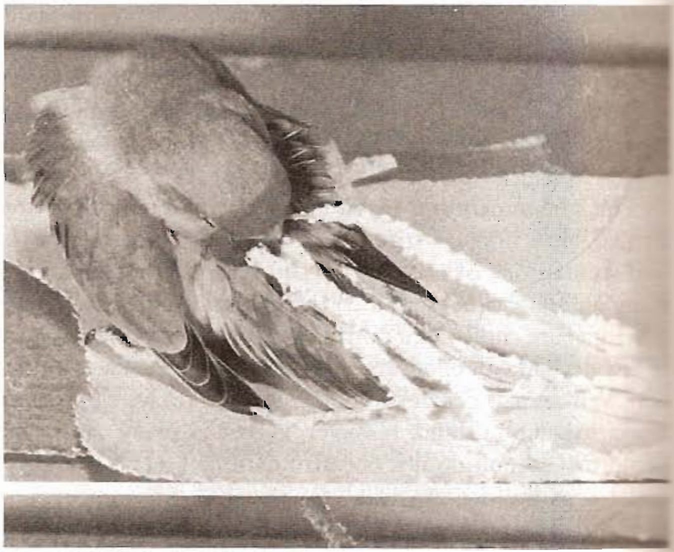


FIGURE 52.5
Genetics of lovebird behavior. Some species of lovebirds carry nest material, such as these paper strips, under their flank feathers. When mated with species that carry material in their beaks, the hybrids show intermediate behavior, attempting to carry the material in both ways.

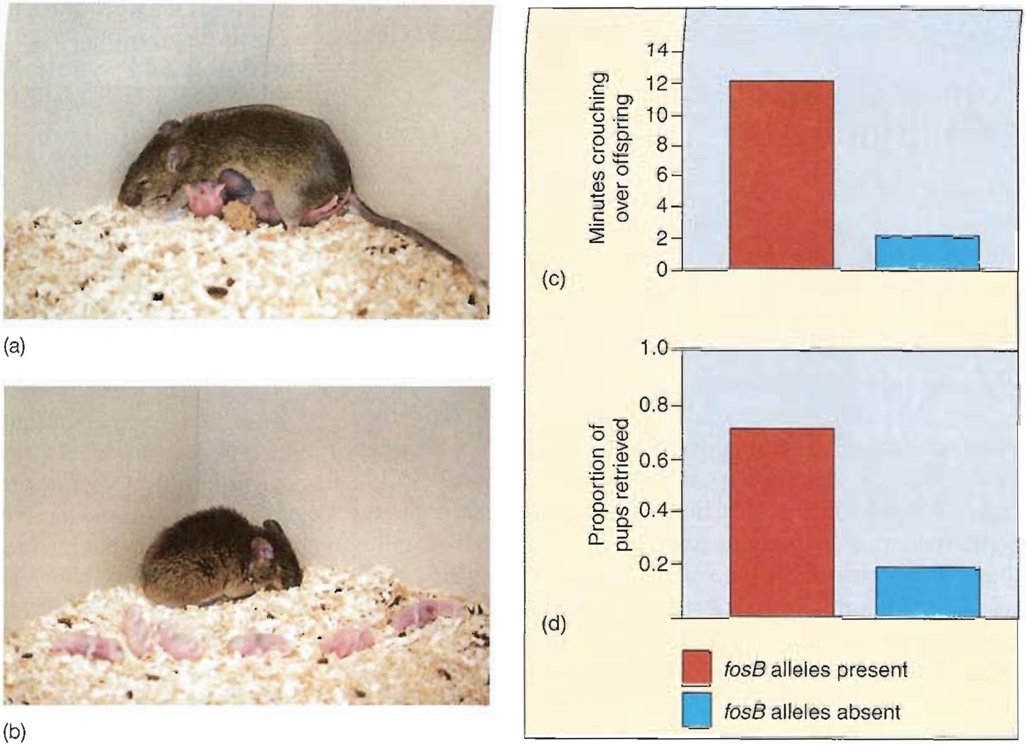


FIGURE 52.6
Genetically caused defect in maternal care. (*a*) In mice, normal mothers take very good care of their offspring, retrieving them if they move away and crouching over them. (*b*) Mothers with the mutant *fosB* allele perform neither of these behaviors, leaving their pups exposed. (*c*) Amount of time female mice were observed crouching in a nursing posture over offspring. (*d*) Proportion of pups retrieved when they were experimentally moved.
Why does the lack of *fosB* alleles lead to maternal inattentiveness?

Single Gene Effects on Behavior

The maze-learning, hybrid, and identical twins studies just described suggest that genes play a role in behavior, but recent research has provided much greater detail on the genetic basis of behavior. In both *Drosophila* and mice, many mutations have been associated with particular behavioral abnormalities.

In fruit flies, for example, individuals that possess alternative alleles for a single gene differ greatly in their feeding behavior as larvae; larvae with one particular allele move around a great deal as they eat, whereas individuals with the alternative allele move hardly at all. A wide variety of mutations at other genes are now known in *Drosophila* that affect almost every aspect of courtship behavior.

The ways in which genetic differences affect behavior have been worked out for several mouse genes. For example, some mice with one mutation have trouble remembering information learned two days earlier about where objects are located. This difference appears to result because the mutant mice do not produce the enzyme α-calcium-calmodulin-dependent kinase II, which plays an important role in the functioning of the hippocampus, a part of the brain important for spatial learning.

Modern molecular biology techniques allow the role of genetics in behavior to be investigated with ever greater precision. For example, male mice genetically engineered to lack the ability to synthesize nitric oxide, a brain neurotransmitter, show increased aggressive behavior.

A particularly fascinating breakthrough occurred in 1996, when scientists discovered a new gene, *fosB*, that seems to determine whether or not female mice will nurture their young. Females with both *fosB* alleles disabled will initially investigate their newborn babies, but then ignore them, in stark contrast to the caring and protective maternal behavior displayed by normal females (figure 52.6).

The cause of this inattentiveness appears to result from a chain reaction. When mothers of new babies initially inspect them, information from their auditory, olfactory, and tactile senses is transmitted to the hypothalamus, where *fosB* alleles are activated, producing a particular protein, which in turn activates other enzymes and genes that affect the neural circuitry within the hypothalamus. These modifications within the brain cause the female to react maternally toward her offspring. In contrast, in mothers lacking the *fosB* alleles, this reaction is stopped midway. No protein is activated, the brain's neural circuitry is not rewired, and maternal behavior does not result.

As these genetic techniques are becoming used more widely, the next few years should see similar dramatic advances in our knowledge of how genes affect various human behaviors.

The genetic basis of behavior is supported by artificial selection experiments, hybridization studies, and studies on the behavior of mutants. Research has also identified specific genes that control behavior.

52.2 Learning influences behavior.

Nonassociative Learning and Conditioning

Many of the behavioral patterns displayed by animals are not solely the result of instinct. In many cases, animals alter their behavior as a result of previous experiences, a process termed **learning.** The role of learning was first studied intensively in laboratory rodents, but now researchers have learned much about the learning processes and capabilities of a wide range of organisms.

The simplest type of learning, **nonassociative learning,** does not require an animal to form an association between two stimuli or between a stimulus and a response. One form of nonassociative learning is **habituation,** which can be defined as a decrease in response to a repeated stimulus that has no positive or negative consequences. In many cases, the stimulus evokes a strong response when it is first encountered, but the magnitude of the response gradually declines with repeated exposure. For example, young birds see many types of objects moving overhead. At first, they may respond by crouching down and remaining still. Some of the objects, such as falling leaves or members of their own species flying by, are seen very frequently and have no positive or negative consequence to the nestlings. Over time, the young birds may habituate to such stimuli and stop responding. Thus, habituation can be thought of as learning not to respond to a stimulus. Being able to ignore unimportant stimuli is critical for an animal confronting a barrage of stimuli in a complex environment; animals that could not do so would fail to focus their attention on important activities, such as finding food and avoiding predators, and probably would leave few offspring in the next generation.

A change in behavior that involves an association between two stimuli or between a stimulus and a response is termed **associative learning** (figure 52.7). The behavior is modified, or **conditioned,** through the association. This form of learning is more complex than habituation. The two major types of associative learning are **classical conditioning** and **operant conditioning;** they differ in the way the associations are established.

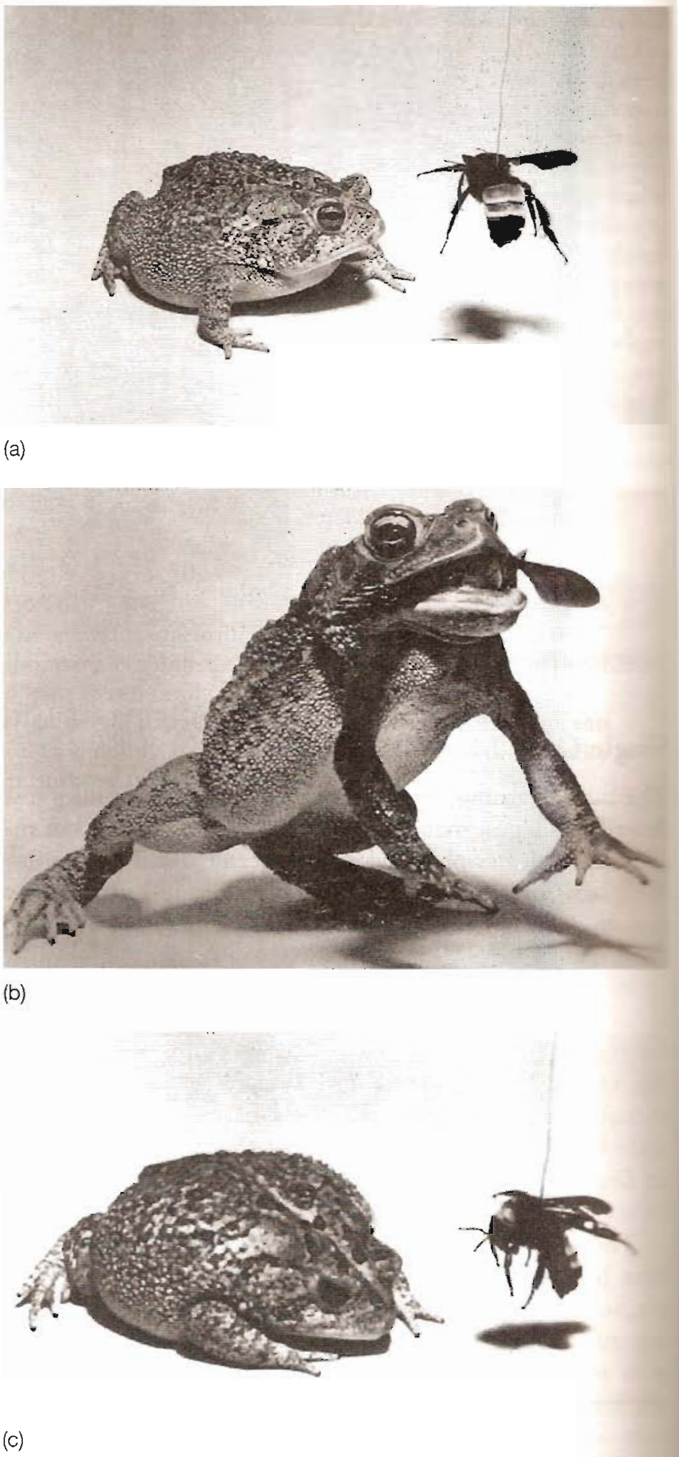


FIGURE 52.7
Learning what is edible. Associative learning is involved in predator-prey interactions. (*a*) A naive toad is offered a bumblebee as food. (*b*) The toad is stung, and (*c*) subsequently avoids feeding on bumblebees or any other insects having black-and-yellow coloration. The toad has associated the appearance of the insect with pain, and modifies its behavior.

Classical Conditioning

In classical conditioning, the paired presentation of two different kinds of stimuli causes the animal to form an association between the stimuli. Classical conditioning is also called **Pavlovian conditioning,** after Russian psychologist Ivan Pavlov, who first described it. Pavlov presented meat powder, an *unconditioned stimulus,* to a dog and noted that the dog responded by salivating, an *unconditioned response.* If an unrelated stimulus, such as the ring-

g of a bell, was presented at the same time as the meat
owder, over repeated trials the dog would salivate in re-
onse to the sound of the bell alone. The dog had
arned to associate the unrelated sound stimulus with the
eat powder stimulus. Its response to the sound stimulus
as, therefore, conditioned, and the sound of the bell is
ferred to as a *conditioned stimulus*.

perant Conditioning

operant conditioning, an animal learns to associate its
havioral response with a reward or punishment. Ameri-
n psychologist B. F. Skinner studied operant condition-
g in rats by placing them in an apparatus that came to be
lled a "Skinner box." As the rat explored the box, it
ould occasionally press a lever by accident, causing a pel-
t of food to appear. At first, the rat would ignore the
ver, eat the food pellet, and continue to move about.
oon, however, it learned to associate pressing the lever
he behavioral response) with obtaining food (the reward).
hen it was hungry, it would spend all its time pressing
e lever. This sort of trial-and-error learning is of major
nportance to most vertebrates.

Comparative psychologists used to believe that any two
imuli could be linked in classical conditioning and that
imals could be conditioned to perform any learnable be-
avior in response to any stimulus by operant conditioning.
s you will see in the following discussion, this view has
anged. Today, it is thought that instinct guides learning
y determining what type of information can be learned
rough conditioning.

nstinct and Learning

is now clear that some animals have innate predisposi-
ons toward forming certain associations. For example, if a
t is offered a food pellet at the same time it is exposed to
rays (which later produce nausea), the rat will remember
e taste of the food pellet but not its size. Similarly, pi-
eons can learn to associate *food* with colors but not with
ounds, while they can associate *danger* with sounds but not
ith colors.

These examples of *learning preparedness* demonstrate
at what an animal can learn is biologically influenced—
at is, learning is possible only within the boundaries set
y instinct. Innate programs have evolved because they
nderscore adaptive responses. In nature, food that is
xic to a rat is likely to have a particular taste; thus, it is
daptive to be able to associate a taste with a feeling of
ckness that may develop hours later. The seed a pigeon
ats may have a distinctive color that the pigeon can see,
ut it makes no sound the pigeon can hear. The study of
arning has expanded to include its ecological signifi-
ance, so that we are now able to consider the evolution
f learning.

FIGURE 52.8
The Clark's nutcracker has an extraordinary memory. A Clark's nutcracker can remember the locations of up to 2000 seed caches months after hiding them. After conducting experiments, scientists have concluded that the birds use features of the landscape and other surrounding objects as spatial references to memorize the locations of the caches.

An animal's ecology, of course, is key to understanding its mental capabilities. Some species of birds, such as Clark's nutcracker, feed on seeds. Birds store seeds in caches they bury when seeds are abundant so they will have food during the winter. Thousands of seed caches may be buried and then later recovered, sometimes as much as nine months later. One would expect the birds to have an extraordinary spatial memory, and this is indeed what has been found (figure 52.8). Clark's nutcracker, and other seed-hoarding birds, have an unusually large hippocampus, the center for memory storage in the brain (see chapter 45).

Habituation is a simple form of learning in which there is no association between stimuli and responses. In contrast, associative learning (classical and operant conditioning) involves the formation of an association between two stimuli or between a stimulus and a response.

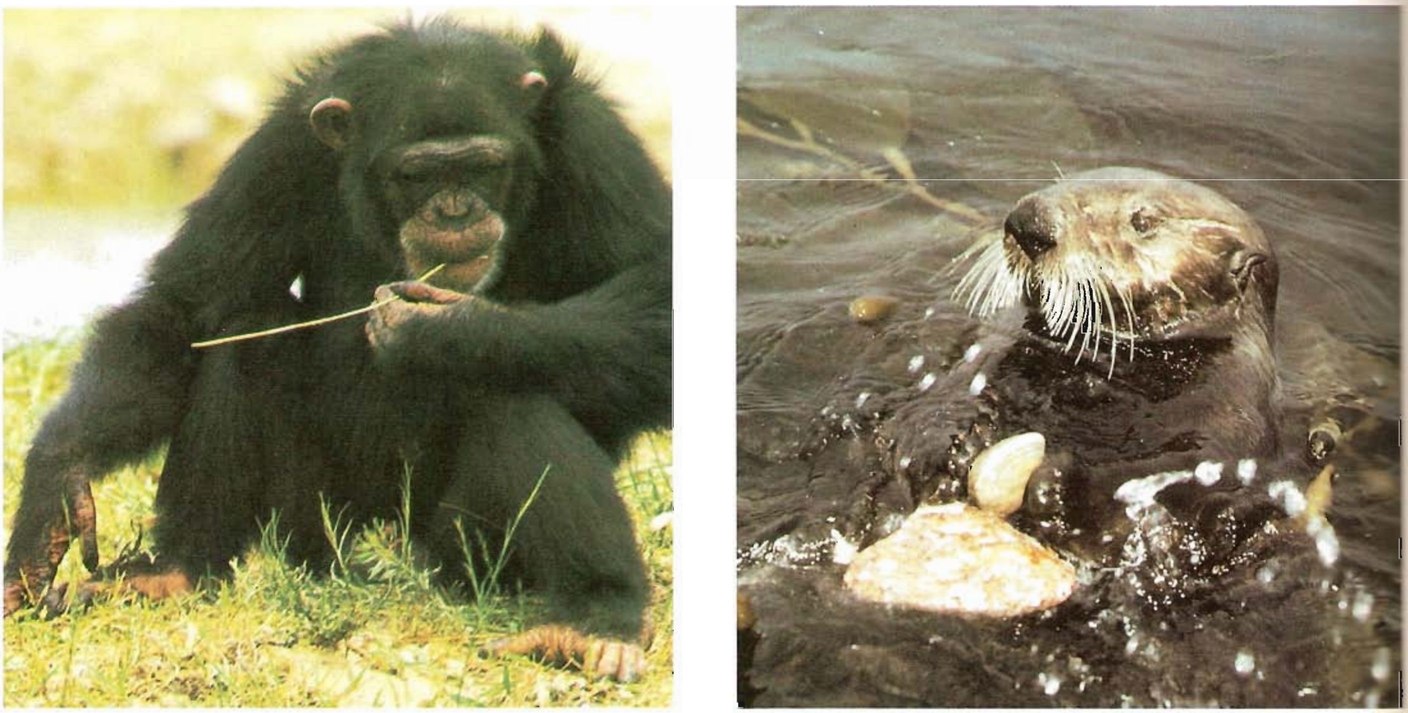
Animal Cognition

To what degree animals "think" is a subject of lively dispute. It is likely each of us could tell an anecdotal story about the behavior of a pet cat or dog that would suggest the animal had a degree of reasoning ability or was capable of thinking. For many decades, however, students of animal behavior flatly rejected the notion that nonhuman animals can think. In fact, behaviorist Lloyd Morgan stated that one should never assume a behavior represents conscious thought if there is any other explanation that precludes the assumption of consciousness. The prevailing approach was to treat animals as though they responded to the environment through instinctive behaviors and simple, innately programmed learning.

In recent years, serious attention has been given to the topic of animal awareness. The central question is whether animals show **cognitive behavior**—that is, do they process information and respond in a manner that suggests thinking (figure 52.13)? What kinds of behavior would demonstrate cognition? Some birds in urban areas remove the foil caps from nonhomogenized milk bottles to get at the cream beneath, and this behavior is known to have spread within a population to other birds. Japanese macaques learn to wash potatoes and float grain to separate it from sand. A chimpanzee pulls the leaves off a tree branch and uses the branch to probe the entrance to a termite nest and gather termites. Vervet monkeys have a vocabulary that identifies specific predators (see figure 52.24).

Only a few experiments have tested the thinking ability of nonhuman animals. Some of these studies suggest that animals may deliberately give false information (that is, they "lie"). Currently, researchers are trying to determine if some primates deceive others to manipulate the behavior of the other members of their troop. Many anecdotal accounts appear to support the idea that deception occurs in some nonhuman primate species, such as baboons and chimpanzees, but it has been difficult to devise field-based experiments to test this idea. Much of this type of research on animal cognition is in its infancy, but it is sure to grow and to raise controversy. In any case, there is nothing to be gained by dogmatically denying the possibility of animal consciousness.

Some examples, particularly those involving problem solving by animals, are hard to explain in any way other


(a)

(b)

FIGURE 52.13
Animal thinking? (*a*) This chimpanzee is stripping the leaves from a twig, which it will then use to probe a termite nest. This behavior strongly suggests that the chimpanzee is consciously planning ahead, with full knowledge of what it intends to do. (*b*) This sea otter is using a rock as an "anvil," against which it bashes a clam to break it open. A sea otter will often keep a favorite rock for a long time, as though it has a clear idea of its future use of the rock. Behaviors such as these suggest that animals have cognitive abilities.

FIGURE 52.14
Problem solving by a chimpanzee. Unable to get the bananas by jumping, the chimpanzee devises a solution.

han as a result of some sort of mental process. For example, in a series of classic experiments conducted in the 1920s, a chimpanzee was left in a room with a banana hanging from the ceiling out of reach. Also in the room were several boxes, each lying on the floor. After some unsuccessful attempts to jump up and grab the bananas, the chimpanzee suddenly looked at the boxes and then immediately proceeded to move them underneath the banana, stack one on top of another, and climb up to claim its prize (figure 52.14).

Perhaps it is not surprising to find obvious intelligence n animals as closely related to us as chimpanzees. But recent studies have found that other animals also show evidence of cognition. Ravens have always been considered among the most intelligent of birds. Bernd Heinrich of he University of Vermont recently conducted an experiment using a group of hand-reared ravens that lived in an outdoor aviary. Heinrich placed a piece of meat on the end of a string and hung it from a branch in the aviary. The birds liked to eat meat, but had never seen string before and were unable to get at the meat. After several hours, during which time the birds periodically looked at he meat but did nothing else, one bird flew to the branch, reached down, grabbed the string, pulled it up, and placed it under his foot. He then reached down and grabbed another piece of the string, repeating this action over and over, each time bringing the meat closer (figure 52.15). Eventually, he brought the meat within reach and grasped it. The raven, presented with a completely novel problem, had devised a solution. Eventually, three of the other five ravens also figured out how to get the meat. Heinrich has conducted other similarly creative experiments that leave little doubt that ravens have advanced cognitive abilities.

Research on the cognitive behavior of animals is in its infancy, but some examples are compelling.

FIGURE 52.15
Problem solving by a raven. Confronted with a problem it has never previously faced, the raven figures out how to get the meat at the end of the string by repeatedly pulling up a bit of string and stepping on it.

52.3 Communication is a key element of many animal behaviors.

Much of the research in animal behavior is devoted to analyzing the nature of communication signals, determining how they are perceived, and identifying their ecological roles and their evolutionary origins.

Courtship

During courtship, animals produce signals to communicate with potential mates and with other members of their own sex. A *stimulus-response chain* sometimes occurs, in which the behavior of one individual in turn releases a behavior by another individual (figure 52.19).

Courtship Signaling

A male stickleback fish will defend the nest it builds on the bottom of a pond or stream by attacking *conspecific* males (that is, males of the same species) that approach the nest. Niko Tinbergen studied the social releasers responsible for this behavior by making simple clay models. He found that a model's shape and degree of resemblance to a fish were unimportant; any model with a red underside (like the underside of a male stickleback) could release the attack behavior. Tinbergen also used a series of clay models to demonstrate that a male stickleback recognizes a female by her abdomen when it is swollen with eggs.

Courtship signals are often *species-specific*, limiting communication to members of the same species and thus playing a key role in reproductive isolation (see chapter 23). The flashes of fireflies (which are actually beetles) are such species-specific signals. Females recognize conspecific males by their flash pattern (figure 52.20), and males recognize conspecific females by their flash response. This series of reciprocal responses provides a continuous "check" on the species identity of potential mates.

Long-Distance Communication

Chemical signals also mediate interactions between males and females. **Pheromones,** chemical messengers used for communication between individuals of the same species, serve as sex attractants, among other functions, in many animals. Even the human egg produces a chemical attractant to communicate with sperm! Female silk moths (*Bombyx mori*) produce a sex pheromone called *bombykol* in a gland

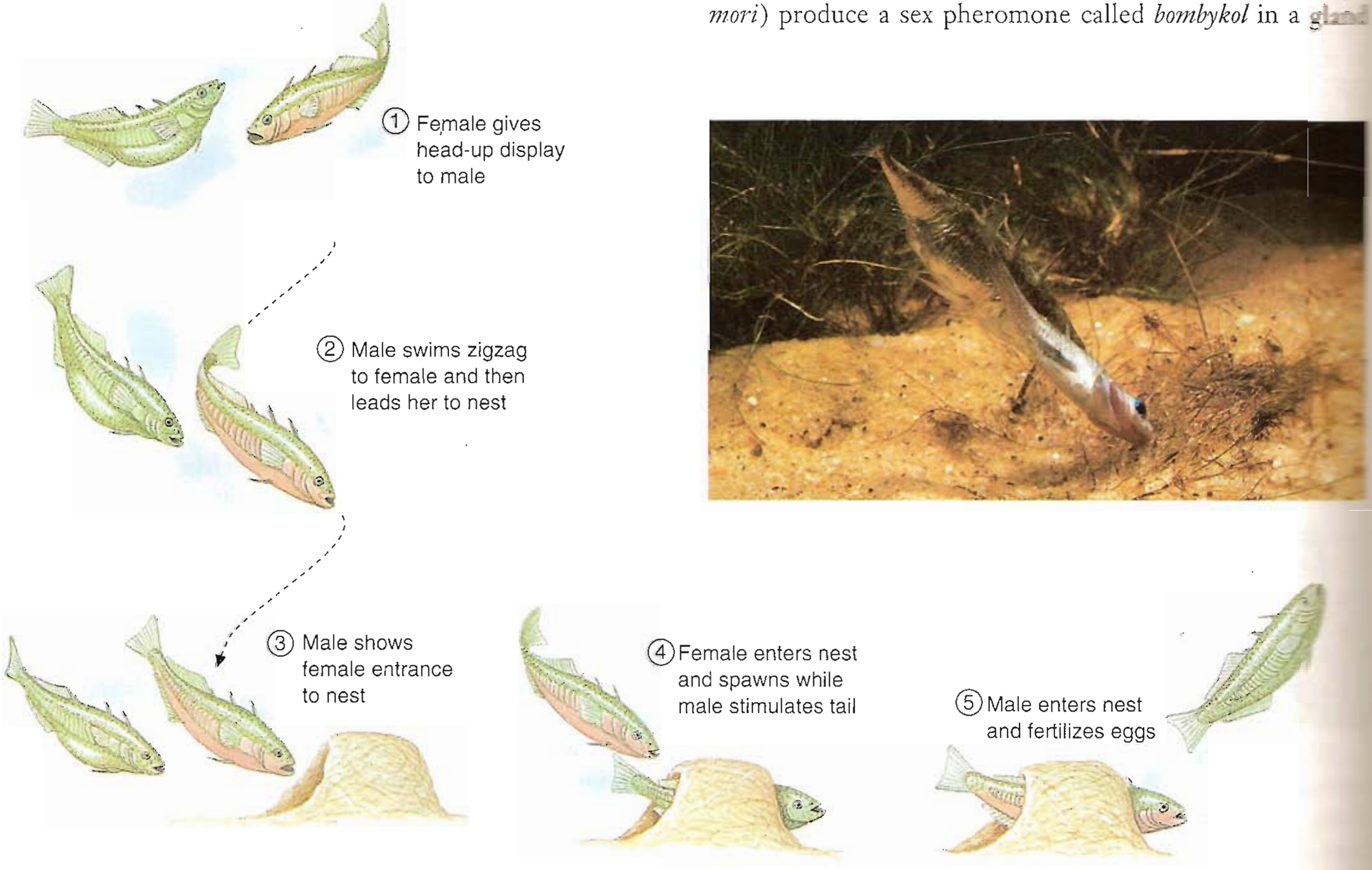


FIGURE 52.19
A stimulus-response chain. Stickleback courtship involves a sequence of behaviors leading to the fertilization of eggs.

associated with the reproductive system. Neurophysiological studies show that the male's antennae contain numerous sensory receptors specific for bombykol. These receptors are extraordinarily sensitive, enabling the male to respond behaviorally to concentrations of bombykol as low as one molecule in 1017 molecules of oxygen in the air.

Many insects, amphibians, and birds produce species-specific acoustic signals to attract mates. Bullfrog males call by inflating and discharging air from their vocal sacs, located beneath the lower jaw. Females can distinguish a conspecific male's call from the call of other frogs that may be in the same habitat and calling at the same time. As mentioned in section 52.2, male birds produce songs, complex sounds composed of notes and phrases, to advertise their presence and to attract females. In many species, variations in the males' songs identify *particular* males in a population. In these species, the song is individually specific as well as species-specific.

Level of Specificity

Different signals provide different levels of information about the sender. The **level of specificity** relates to the function of the signal. Many courtship signals are species-specific to help animals avoid making errors in mating that would produce inviable hybrids or otherwise waste reproductive effort. A male bird's song is individually specific because it allows his presence (as opposed to simply the presence of an unidentifiable member of the species) to be recognized by neighboring birds. When territories are being established, males may sing and aggressively confront neighboring conspecifics to defend their space. Aggression carries the risk of injury, and singing is energetically costly. After territorial borders have been established, intrusions by neighbors are few because the outcomes of the contests have already been determined. Each male then "knows" his neighbor by the song he sings, and also "knows" that male does not constitute a threat because they have already settled their territorial contests. So, all birds in the population can lower their energy costs by identifying their neighbors through their individual songs. Similarly, mammals mark their territories with pheromones that signal individual identity, encoded as a blend of a number of chemicals. Other signals, such as the mobbing and alarm calls of birds, are anonymous, conveying no information about the identity of the sender. These signals may permit communication about the presence of a predator common to several bird species.

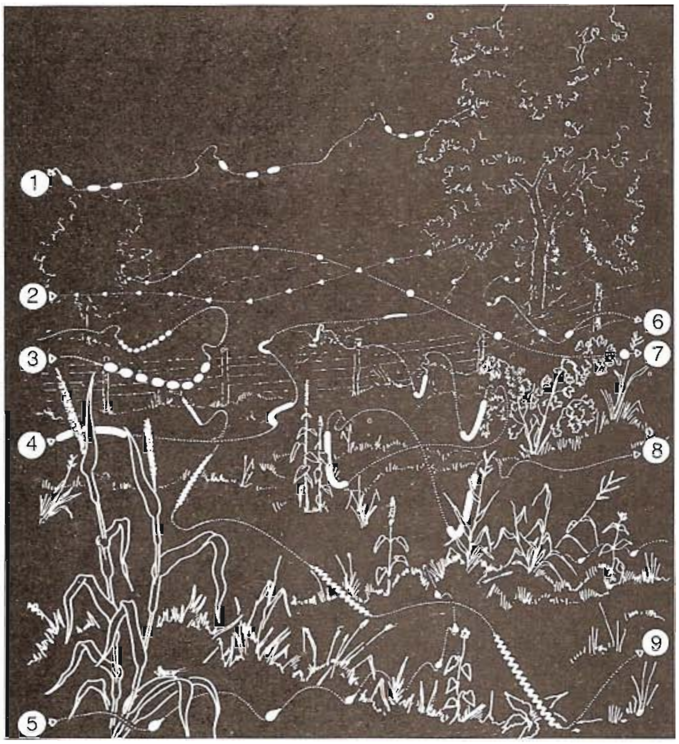


FIGURE 52.20
Firefly fireworks. The bioluminescent displays of these lampyrid beetles are species-specific and serve as behavioral mechanisms of reproductive isolation. Each number represents the flash pattern of a male of a different species.

FIGURE 52.21
Cleaner fish. This grouper has entered the cleaner fish's "station" and adopted a posture that allows the cleaner fish to enter the mouth and gills and feed on attached parasites.

Although in most cases signals are used for communication between members of the same species, sometimes two different species are involved. For example, fish with parasites adopt a specific posture in the presence of cleaner fish that signals to the cleaner fish that they are ready to be cleaned (figure 52.21). In a similar vein, some animals send signals to predators. White-tailed deer, for example, raise their tails to display their prominent white undersides while running away from a predator. These *pursuit deterrent* signals are presumed to indicate to the predator that it has already been seen and thus should not waste its time trying to catch the deer.

Animal communications serve many purposes and are transmitted in many ways.

Communication in Social Groups

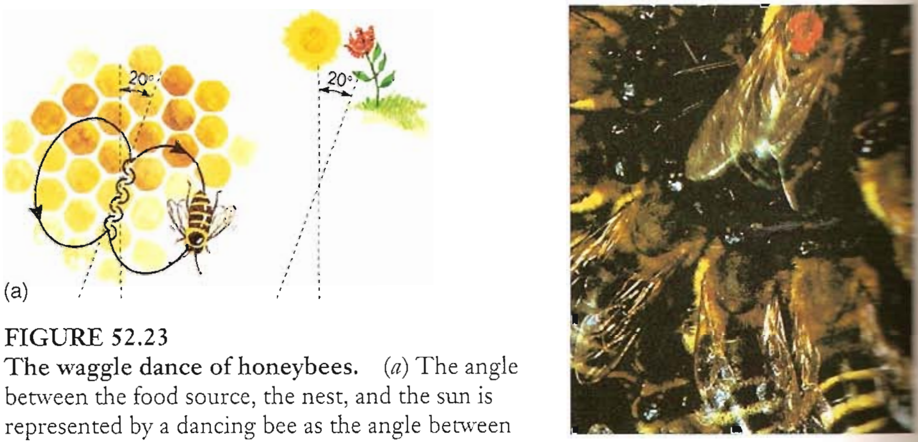
Many insects, fish, birds, and mammals live in social groups in which information is communicated between group members. For example, some individuals in mammalian societies serve as "guards." When a predator appears, the guards give an *alarm call*, and group members respond by seeking shelter. Social insects, such as ants and honeybees, produce *alarm pheromones* that trigger attack behavior. Ants also deposit *trail pheromones* between the nest and a food source to lead other colony members to food (figure 52.22). Honeybees have an extremely complex *dance language* that directs hivemates to rich nectar sources.


(a)
(b)

FIGURE 52.22
The chemical control of fire ant foraging. Trail pheromones, produced in an accessory gland near the fire ant's sting, organize cooperative foraging. The trails taken by the first ants to travel to a food source (*a*) are soon followed by most of the other ants (*b*).

The Dance Language of the Honeybee

The European honeybee, *Apis mellifera*, lives in hives consisting of 30,000 to 40,000 individuals whose behaviors are integrated into a complex colony. Worker bees may forage for miles from the hive, collecting nectar and pollen from a variety of plants and switching between plant species and populations on the basis of how energetically rewarding their food is. The food sources used by bees tend to occur in patches, and each patch offers much more food than a single bee can transport to the hive. A colony is able to exploit the resources of a patch because of the behavior of scout bees, which locate patches and communicate their location to hivemates through a dance language. Over many years, Nobel laureate Karl von Frisch was able to unravel the details of this communication system.



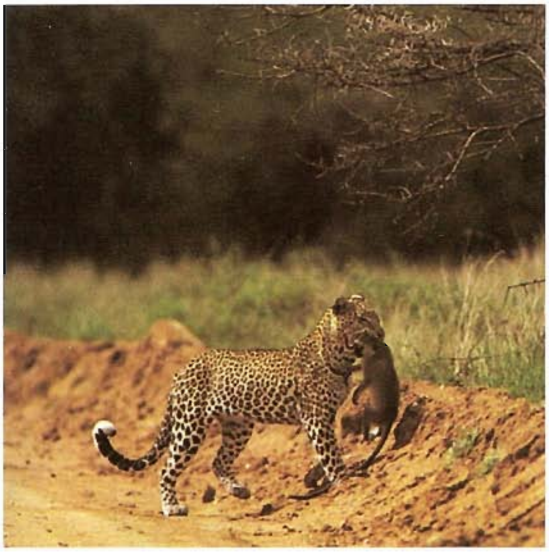
(a)
(b)

FIGURE 52.23
The waggle dance of honeybees. (*a*) The angle between the food source, the nest, and the sun is represented by a dancing bee as the angle between the straight part of the dance and vertical. The food is 20° to the right of the sun, and the straight part of the bee's dance on the hive is 20° to the right of vertical. (*b*) A scout bee dances on a comb in the hive.

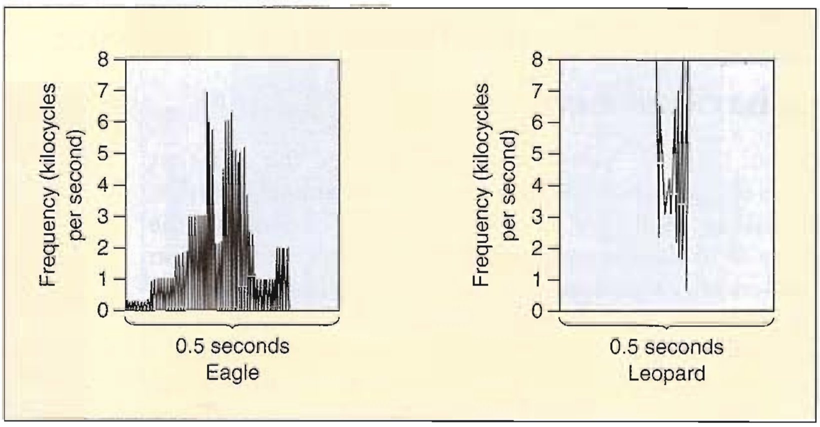
After a successful scout bee returns to the hive, she performs a remarkable behavior pattern called a *waggle dance* on a vertical comb (figure 52.23). The path of the bee during the dance resembles a figure-eight. on the straight part of the path, the bee vibrates or waggles her abdomen while producing bursts of sound. She may stop periodically to give her hivemates a sample of the nectar she has carried back to the hive in her crop. As she dances, she is followed closely by other bees, which soon appear as foragers at the new food source.

Von Frisch and his colleagues claimed that the other bees use information in the waggle dance to locate the food source. According to their explanation, the scout bee indicates the *direction* of the food source by representing the angle between the food source, the hive, and the sun as the deviation from vertical of the straight part of the dance performed on the hive wall (that is, if the bee moved straight, then the food source would be in the direction of the sun, but if the food were at a 30° angle relative to the sun's position, then the bee would move upward at a 30° angle from vertical). The *distance* to the food source is indicated by the tempo, or degree of vigor, of the dance.

Adrian Wenner, a scientist at the University of California, did not believe that the dance language communicated anything about the location of food, and he challenged von Frisch's explanation. Wenner maintained that flower odor was the most important cue leading bees to arrive at a new food source. A heated controversy ensued as the two groups of researchers published articles supporting their positions.



(a)



(b)

FIGURE 52.24
Primate semantics. (*a*) Predators, such as this leopard, attack and feed on vervet monkeys. (*b*) The monkeys give different alarm calls when troupe members sight an eagle, leopard, or snake. Each distinctive call elicits a different and adaptive escape behavior.

Such controversies can be very beneficial, because they often generate innovative experiments. In this case, the "dance language controversy" was resolved (in the minds of most scientists) in the mid-1970s by the creative research of James L. Gould. Gould devised an experiment in which hive members were tricked into misinterpreting the directions given by the scout bee's dance. As a result, Gould was able to manipulate where the hive members would go if they were using visual signals. If odor were the cue they were using, hive members would have appeared at the food source, but instead they appeared exactly where Gould had predicted. This confirmed von Frisch's ideas.

Recently, researchers have extended the study of the honeybee dance language by building robot bees whose dances can be completely controlled. Their dances are programmed by a computer and perfectly reproduce the natural honeybee dance; the robots even stop to give food samples! The use of robot bees has allowed scientists to determine precisely which cues direct hivemates to food sources.

Primate Language

Some primates have a "vocabulary" that allows individuals to communicate the identity of specific predators. The vocalizations of African vervet monkeys, for example, distinguish among eagles, leopards, and snakes (figure 52.24). Chimpanzees and gorillas can learn to recognize a large number of symbols and use them to communicate abstract concepts. The complexity of human language would at first appear to defy biological explanation, but closer examination suggests that the differences are in fact superficial—all languages share many basic structural similarities. All of the roughly 3000 languages draw from the same set of 40 consonant sounds (English uses two dozen of them), and any human can learn them. Researchers believe these similarities reflect the way our brains handle abstract information, a genetically determined characteristic of all humans.

Language develops at an early age in humans. Human infants are capable of recognizing the 40 consonant sounds characteristic of speech, including those not present in the particular language they will learn, while ignoring other sounds. In contrast, individuals who have not heard certain consonant sounds as infants can only rarely distinguish or produce them as adults. That is why English speakers have difficulty mastering the throaty French "r," French speakers typically replace the English "th" with "z," and native Japanese often substitute "r" for the unfamiliar English "l." Children go through a "babbling" phase, in which they learn by trial and error how to make the sounds of language. Even deaf children go through a babbling phase using sign language. Next, children quickly and easily learn a vocabulary of thousands of words. Like babbling, this phase of rapid learning seems to be genetically programmed. It is followed by a stage in which children form simple sentences that, though they may be grammatically incorrect, can convey information. Learning the rules of grammar constitutes the final step in language acquisition.

While language is the primary channel of human communication, odor and other nonverbal signals (such as "body language") may also convey information. However, it is difficult to determine the relative importance of these other communication channels in humans.

The study of animal communication involves analysis of the specificity of signals, their information content, and the methods used to produce and receive them.

52.4 Evolutionary forces shape behavior.

Behavioral Ecology

Nobel laureate Niko Tinbergen outlined the different types of questions biologists can ask about animal behavior. In essence, he divided the investigation of behavior into the study of its development, physiological basis, and function (evolutionary significance). One type of evolutionary analysis pioneered by Tinbergen himself was the study of the **survival value** of behavior. That is, how does an animal's behavior allow it to stay alive or keep its offspring alive? For example, Tinbergen observed that after gull nestlings hatch, the parents remove the eggshells from the nest. To understand why this behavior occurs, he camouflaged chicken eggs by painting them to resemble the natural background where they would lie and distributed them throughout the area in which the gulls were nesting (figure 52.25). He placed broken eggshells next to some of the eggs, and as a control, he left other camouflaged eggs alone without eggshells. He then noted which eggs were found more easily by crows. Because the crows could use the white interior of a broken eggshell as a cue, they ate more of the camouflaged eggs that were near eggshells. Thus, Tinbergen concluded that eggshell removal behavior is *adaptive:* It reduces predation and thus increases the offspring's chances of survival.

Tinbergen is credited with being one of the founders of **behavioral ecology,** the study of how natural selection shapes behavior. This branch of ecology examines the **adaptive significance** of behavior, or how behavior may increase survival and reproduction. Current research in behavioral ecology focuses on how behavior contributes to an animal's reproductive success, or **fitness.** As we saw in section 52.1, differences in behavior among individuals often result from genetic differences. Thus, natural selection operating on behavior has the potential to produce evolutionary change. To study the relation between behavior and fitness, then, is to study the process of adaptation itself.

Consequently, the field of behavioral ecology is concerned with two questions. First, is behavior adaptive? Although it is tempting to assume that the behavior produced by individuals must in some way represent an adaptive response to the environment, this need not be the case. As discussed in chapter 21, traits can evolve for many reasons other than natural selection, such as genetic drift, gene flow, or the correlated consequences of selection on other traits. Moreover, traits may be present in a population because they evolved as adaptations in the past, but are no longer useful. These possibilities hold true for behavioral traits as much as for any other kind of trait.

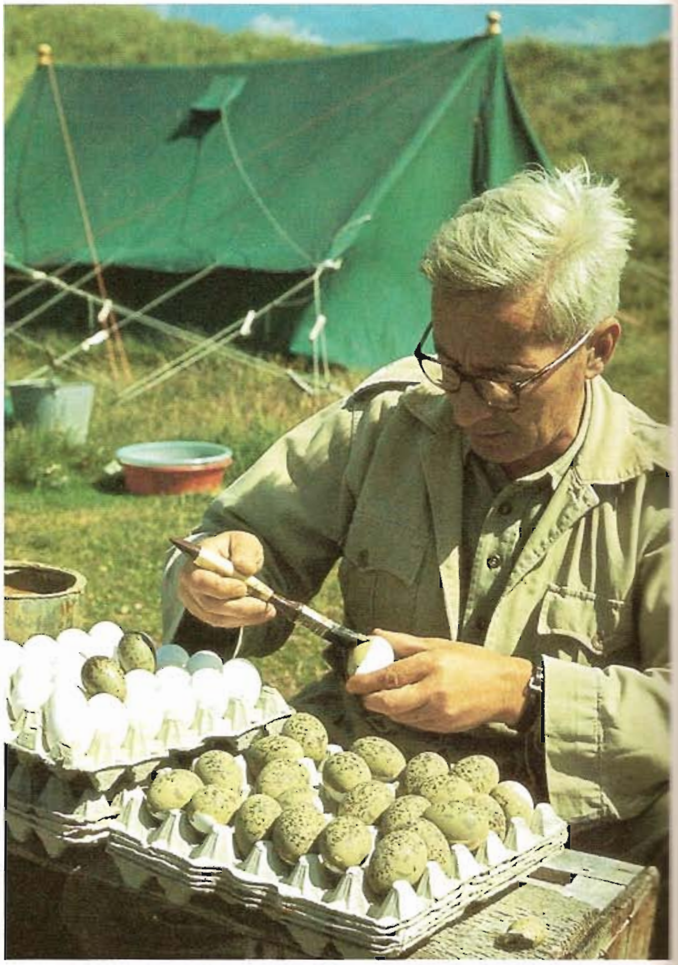


FIGURE 52.25

The adaptive value of egg coloration. Niko Tinbergen painted chicken eggs to resemble the mottled brown camouflage of gull eggs. The eggs were used to test the hypothesis that camouflaged eggs are more difficult for predators to find and thus increase the young's chances of survival.

If a trait is adaptive, the question then becomes: How is it adaptive? Although the ultimate criterion is reproductive success, behavioral ecologists are interested in *how* a trait can lead to greater reproductive success. By enhancing energy intake, thus increasing the number of offspring produced? By improving success in getting more matings? By decreasing the chance of predation? The job of a behavioral ecologist is to determine the effect of a behavioral trait on each of these activities and then to discover whether increases in, for example, foraging efficiency, translate into increased fitness.

Behavioral ecology is the study of how natural selection shapes behavior.

Foraging Behavior

The best way to introduce behavioral ecology is by examining one well-defined behavior in detail. While many behaviors might be chosen, we will focus on foraging behavior. For many animals, food comes in a variety of sizes. Larger foods may contain more energy but may be harder to capture and less abundant. In addition, some types of food may be farther away than other types. Hence, for these animals foraging involves a trade-off between a food's energy content and the cost of obtaining it. The *net energy* (in calories or Joules) gained by feeding on prey of each size is simply the energy content of the prey minus the energy costs of pursuing and handling it. According to **optimal foraging theory,** natural selection favors individuals whose foraging behavior is as energetically efficient as possible. In other words, animals tend to feed on prey that maximize their net energy intake per unit of foraging time.

A number of studies have demonstrated that foragers do preferentially utilize prey that maximize the energy return. Shore crabs, for example, tend to feed primarily on intermediate-sized mussels, which provide the greatest energetic return; larger mussels yield more energy, but also take considerably more energy to crack open (figure 52.26).

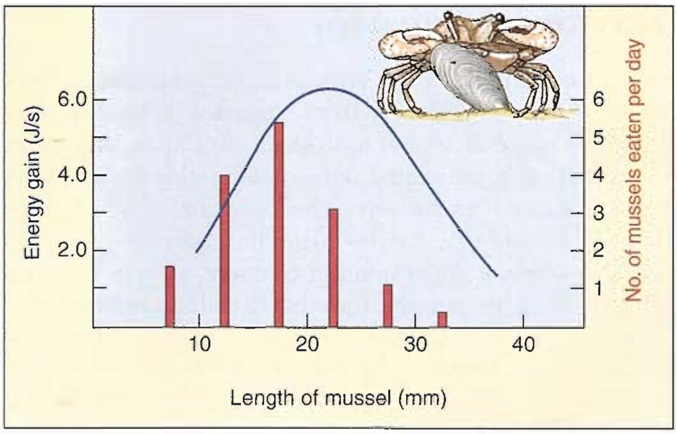


FIGURE 52.26
Optimal diet. The shore crab selects a diet of energetically profitable prey. The curve describes the net energy gain (equal to energy gained minus energy expended) derived from feeding on different sizes of mussels. The bar graph shows the numbers of mussels of each size in the diet. Shore crabs tend to feed on those mussels that provide the most energy.
What factors might be responsible for the slight difference in peak prey length relative to the length optimal for maximum energy gain?

This optimal foraging approach makes two assumptions. First, natural selection will only favor behavior that maximizes energy acquisition if increased energy reserves lead to increases in reproductive success. In some cases, this is true. For example, in both Columbian ground squirrels and captive zebra finches, a direct relationship exists between net energy intake and the number of offspring raised; similarly, the reproductive success of orb-weaving spiders is related to how much food they can capture.

However, animals have other needs besides energy, and sometimes these needs conflict. One obvious alternative is avoiding predators: Often, the behavior that maximizes energy intake is not the one that minimizes predation risk. Thus, the behavior that maximizes fitness often may reflect a trade-off between obtaining the most energy at the least risk of being eaten. Not surprisingly, many studies have shown that a wide variety of animal species alter their foraging behavior—becoming less active, spending more time watching for predators, or staying nearer to cover—when predators are present. Still another alternative is finding mates: Males of many species, for example, will greatly reduce their feeding rate to enhance their ability to attract and defend females. Even within foraging, trade-offs must be made, because maximizing energy is not the sole goal of foraging; particular nutrients are needed as well. Moose, for example, will feed on energy-poor aquatic vegetation to ensure that they get an adequate supply of calcium.

The second assumption of optimal foraging theory is that it has resulted from natural selection. As we have seen, natural selection can lead to evolutionary change only when differences among individuals have a genetic basis. Few studies have investigated whether differences among individuals in their ability to maximize energy intake are the result of genetic differences, but there are some exceptions. For example, one study found that female zebra finches that were particularly successful in maximizing net energy intake tended to have similarly successful offspring. Because birds were removed from their mothers before they left the nest, this similarity indicated that foraging behavior probably has a genetic basis rather than being a result of young birds learning to forage from their mothers.

Differences in foraging behavior among individuals may also be a function of age. Inexperienced yellow-eyed juncos (a small North American bird), for example, have not learned how to handle large prey items efficiently. As a result, the energetic costs of eating such prey are higher than the benefits, and these birds tend to focus on smaller prey. Only when the birds are older and more experienced do they learn to easily dispatch these prey, which are then included in the diet.

Natural selection may favor the evolution of foraging behaviors that maximize the amount of energy gained per unit time spent foraging. Animals that acquire energy efficiently during foraging may increase their fitness by having more energy available for reproduction, but other considerations, such as avoiding predators, are also important in determining reproductive success.

Territorial Behavior

Animals often move over a large area, or **home range,** during their daily course of activity. In many animal species, the home range of several individuals overlap in time or in space, but each individual defends a portion of its home range and uses it exclusively. This behavior, in which individual members of a species maintain exclusive use of an area that contains some limiting resource, such as foraging ground, food, or potential mates, is called **territoriality** (figure 52.27). The critical aspect of territorial behavior is *defense* against intrusion by other individuals. Territories are defended by displays advertising that the territories are occupied and by overt aggression. A bird sings from its perch within a territory to prevent takeover by a neighboring bird. If an intruder is not deterred by the song, the territory owner may attack and try to drive it away. However, territorial defense has its costs. Singing is energetically expensive, and attacks can lead to injury. In addition, advertisement through song or visual display can reveal one's position to a predator.

Why does an animal bear the costs of territorial defense? Over the past two decades, it has become increasingly clear that an economic approach can be useful in answering this question. Although there are costs to defending a territory, there are also benefits; these benefits may take the form of increased food intake, exclusive access to mates, or access to refuges from predators. Studies of nectar-feeding birds such as hummingbirds and sunbirds provide an example (figure 52.28). A bird benefits from having the exclusive use of a patch of flowers because it can efficiently harvest the nectar they produce. To maintain exclusive use, however, the bird must actively defend the flowers. The benefits of exclusive use outweigh the costs of defense only under certain conditions. Sunbirds, for example, expend 3000 calories per hour chasing intruders from a territory. Whether or not the benefit of defending a territory will exceed this cost depends upon the amount of nectar in the flowers and how efficiently the bird can collect it. For example, if flowers are very scarce or nectar levels are very low, a nectar-feeding bird may not gain enough energy to balance the energy used in defense. Under this circumstance, it is not advantageous to be territorial. Similarly, if flowers are very abundant, a bird can efficiently meet its daily energy requirements without behaving territorially and adding the costs of defense. From an energetic standpoint, defending abundant resources isn't worth the cost. Territoriality thus only occurs at intermediate levels of flower availability and nectar production, where the benefits of defense outweigh the costs.

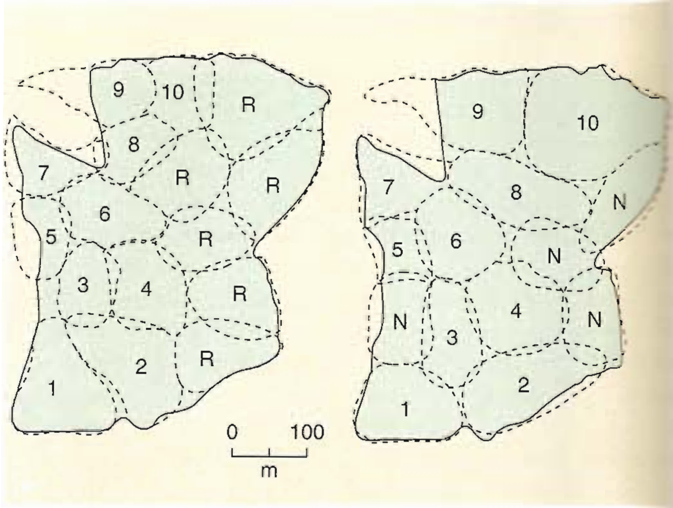


FIGURE 52.27
Competition for space. Territory size in birds is adjusted according to the number of competitors. When six pairs of great tits (*Parus major*) were removed from their territories (indicated by R in the left figure), their territories were taken over by other birds in the area and by four new pairs (indicated by N in the right figure). Numbers correspond to the birds present before and after.

FIGURE 52.28
The benefit of territoriality. Sunbirds, found in Africa and ecologically similar to New World hummingbirds, increase nectar availability by defending flowers.

In many species, exclusive access to females is a more important determinant of territory size for males than is food availability. In some lizards, for example, males maintain enormous territories during the breeding season. These territories, which encompass the territories of several females, are much larger than what would be required to supply enough food, and they are defended vigorously. In the nonbreeding season, by contrast, male territory size decreases dramatically, as does aggressive territorial behavior.

An economic approach can be used to explain the evolution and ecology of behaviors such as territoriality. This approach assumes that animals that gain more energy from a behavior than they expend will have an advantage in survival and reproduction over animals that behave in less efficient ways.

Reproductive Strategies

During the breeding season, animals make several important "decisions" concerning their choice of mates, how many mates to have, and how much time and energy to devote to rearing offspring. These decisions are all aspects of an animal's **reproductive strategy,** a set of behaviors that presumably have evolved to maximize reproductive success. Reproductive strategies have evolved partly in response to the energetic costs of reproduction and the way food resources, nest sites, and members of the opposite sex are spatially distributed in the environment.

Parental Investment and Mate Choice

Males and females usually differ in their reproductive strategies. Darwin was the first to observe that females often do not simply mate with the first male they encounter, but instead seem to evaluate a male's quality and then decide whether to mate. This behavior, called **mate choice,** has since been described in many invertebrate and vertebrate species.

By contrast, mate choice by males is much less common. Why should this be? Many of the differences in reproductive strategies between the sexes can be understood by comparing the parental investment made by males and females. **Parental investment** refers to the contributions each sex makes in producing and rearing offspring; it is, in effect, an estimate of the energy expended by males and females in each reproductive event.

Many studies have shown that parental investment is high in females. One reason is that eggs are much larger than sperm—195,000 times larger in humans! Eggs contain proteins and lipids in the yolk and other nutrients for the developing embryo, but sperm are little more than mobile DNA. Furthermore, in some groups of animals, females are responsible for gestation and lactation, costly reproductive functions only they can carry out.

The consequence of such great disparities in reproductive investment is that the sexes should face very different selective pressures. Because any single reproductive event is relatively cheap for males, they can best increase their fitness by mating with as many females as possible—male fitness is rarely limited by the amount of sperm they can produce. By contrast, each reproductive event for females is much more costly, and the number of eggs that can be produced often does limit reproductive success. For this reason, a female has an incentive to be choosy, trying to pick the male that can provide the greatest benefit to her offspring. As we shall see, this benefit can take a number of different forms.

These conclusions only hold when female reproductive investment is much greater than that of males. In species with biparental care, males may contribute equally to the cost of raising young; in this case, the degree of mate choice should be equal between the sexes.

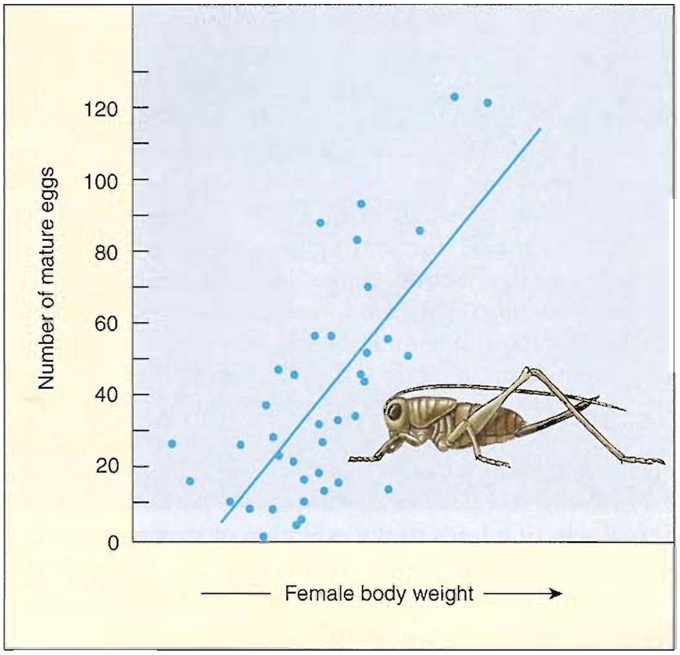


FIGURE 52.29
The advantage of male mate choice. Male mormon crickets choose heavier females as mates, and larger females have more eggs. Thus, male mate selection increases fitness.
Is there a benefit to females for mating with large males?

Furthermore, in some cases, male investment exceeds that of females. For example, male mormon crickets transfer a protein-containing spermatophore to females during mating. Almost 30% of a male's body weight is made up by the spermatophore, which provides nutrition for the female and helps her develop her eggs. As we might expect, in this case it is the females that compete with each other for access to males that are the choosy sex. Indeed, males are quite selective, favoring heavier females. The selective advantage of this strategy results because heavier females have more eggs; thus, males that choose larger females leave more offspring (figure 52.29).

Another example comes from species in which the males take care of the eggs and developing young. This reversal of the normal sex roles occurs in a wide variety of species, including seahorses and a number of bird and insect species. In such species, as with mormon crickets, males are often choosy, and females must compete for mates.

The relative reproductive investment of the sexes determines reproductive strategies.

Reproductive Competition and Sexual Selection

As discussed in chapter 21, the reproductive success of an individual is determined by a number of factors: how long the individual lives, how frequently it mates, and how many offspring it produces per mating. The second of these factors, competition for mating opportunities, has been termed **sexual selection.** Some people consider sexual selection to be distinctive from natural selection, but others see it as a subset of natural selection, just one of the many ways organisms can increase their fitness.

Sexual selection involves both *intrasexual selection*, or interactions between members of one sex ("the power to conquer other males in battle," as Darwin put it), and *intersexual selection*, essentially mate choice ("the power to charm"). Sexual selection leads to the evolution of structures used in combat with other males, such as a deer's antlers and a ram's horns, as well as ornaments used to "persuade" members of the opposite sex to mate, such as long tail feathers and bright plumage (figure 52.30*a*,*b*). These traits are called **secondary sexual characteristics.**

Intrasexual Selection

In many species, individuals of one sex—usually males—compete with each other for the opportunity to mate with individuals of the other sex. These competitions may take place over ownership of a territory in which females reside or direct control of the females themselves. The latter case is exemplified by many species, such as the impala, in which females travel in large groups with a single male that gets exclusive access to mate with the females and thus strives vigorously to defend this access against other males that would like to supplant him.

In mating systems such as these, a few males may get an inordinate number of matings, and most males do not mate at all. In elephant seals, males control territories on the breeding beaches, and a few dominant males do most of the breeding (see figure 52.32). On one beach, for example, eight males impregnated 348 females, while the remaining males mated rarely, if at all.

For this reason, selection strongly favors any trait that confers greater ability to outcompete other males. In many cases, larger males are able to dominate smaller ones. As a result, in many territorial species, males have evolved to be considerably larger than females, for the simple reason that the largest males are the ones that get to mate. Such differences between the sexes are referred to as **sexual dimorphism.** In other species, males have evolved structures used for fighting, such as horns, antlers, and large canine teeth. These traits are also often sexually dimorphic and may have evolved because of the advantage they give in intrasexual conflicts.

Sometimes competition is not between the males themselves, but between their sperm, a phenomenon called **sperm competition.** In species whose females mate with multiple males, many features have evolved to maximize success at sperm competition. For example, in such species, the testes are often large to produce many sperm per mating, and the sperm themselves are also often larger so that they swim more rapidly and thus enhance the likelihood of fertilizing an egg.

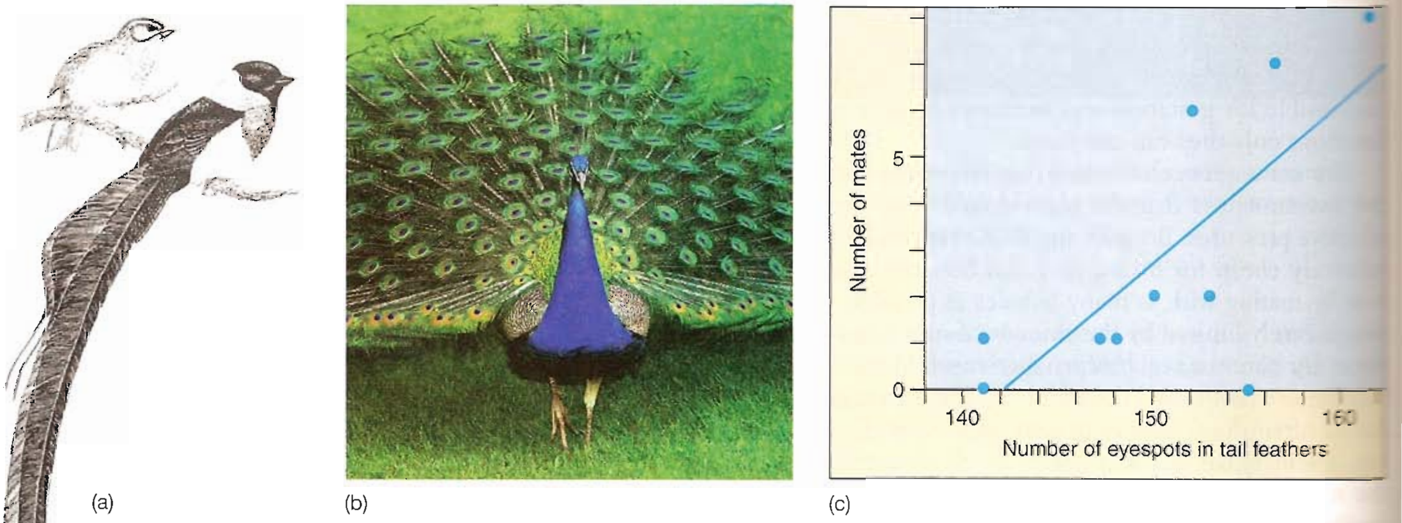


FIGURE 52.30
Products of sexual selection. Attracting mates with long feathers is common in bird species such as (*a*) the African paradise whydah and (*b*) the peacock, which show pronounced sexual dimorphism. (*c*) Female peahens prefer to mate with males having greater numbers of eyespots in their tail feathers.
Why do females prefer males with more spots?

Intersexual Selection

Peahens prefer to mate with peacocks that have more spots in their long tail feathers (figure 52.30*b,c*). Similarly, female frogs prefer to mate with males having more complex calls. Why did such mating preferences evolve?

Direct Benefits of Mate Choice. In some cases, the benefits of mate choice are obvious. In many species of birds and mammals and in some species of other types of animals, males help raise the offspring. In these cases, females would benefit by choosing the male that can provide the best care—the better the parent, the more offspring she is likely to rear.

In other species, males provide no care, but maintain territories that provide food, nesting sites, and predator refuges. In such species, females that choose males with the best territories will maximize their reproductive success.

Indirect Benefits. In other species, however, males provide no direct benefits of any kind to females. In such cases, it is not intuitively obvious what females have to gain by being choosy. Moreover, what could be the possible benefit of choosing a male with an extremely long tail or a complex song?

A number of theories have been proposed to explain the evolution of such preferences. One idea is that females choose the male that is the healthiest or oldest. Large males, for example, have probably been successful at living long, acquiring a lot of food, and resisting parasites and disease. Similarly, in guppies and some birds, the brightness of a male's color reflects the quality of his diet and overall health. Females may gain two benefits from mating with large or colorful males. First, to the extent that the males' success in living long and prospering is the result of genetic makeup, the female will be ensuring that her offspring receive good genes from their father. Indeed, according to several studies, males that are preferred by females produce offspring that are more vigorous and survive better than offspring of males that are not preferred. Second, healthy males are less likely to be carrying diseases, which might be transmitted to the female during mating.

A variant of this theory goes one step further. In some cases, females prefer mates with traits that are detrimental to survival (figure 52.30). The long tail of the peacock is a hindrance in flying and makes males more vulnerable to predators. Why should females prefer males with such traits? The **handicap hypothesis** states that only genetically superior mates can survive with such a handicap. By choosing a male with the largest handicap, the female is ensuring that her offspring will receive these quality genes. Of course, the male offspring will also inherit the genes for the handicap. For this reason, evolutionary biologists are still debating this hypothesis.

FIGURE 52.31
Male Túngara frog calling. Female frogs of the genus *Physalaemus* prefer males that include a "chuck" in their call. However, only males of the species *Physalaemus pustulosus* produce such calls.

Other courtship displays appear to have evolved from a predisposition in the female's sensory system toward a certain type of stimulus. For example, females may be better able to detect particular colors or sounds at a certain frequency. **Sensory exploitation** involves the evolution in males of an attractive signal that "exploits" these preexisting biases—for example, if females are particularly adept at detecting red objects, then males will often evolve red coloration. Consider the vocalizations of the Túngara frog (*Physalaemus pustulosus*) (figure 52.31). Unlike related species, males include a "chuck" in their calls. Recent research suggests that not only are females of this species particularly attracted to calls of this sort, but so are females of related species, even though males of these species do not produce "chucks." Why this preference evolved is unknown, but males of the Túngara frog have evolved to take advantage of it.

A great variety of other hypotheses have been proposed to explain the evolution of mating preferences. Many of these hypotheses may be correct in some circumstances, but none seems capable of explaining all of the variation in mating behavior in the animal world. This is an area of vibrant research, with new discoveries appearing regularly.

Natural selection has favored the evolution of behaviors that maximize the reproductive success of males and females. By evaluating and selecting mates with superior qualities, an animal can increase its reproductive success.

Mating Systems

The number of individuals with which an animal mates during the breeding season varies throughout the animal kingdom. Mating systems include monogamy (one male mates with one female), polygyny (one male mates with more than one female; figure 52.32), and polyandry (one female mates with more than one male). Like mate choice, mating systems have evolved to maximize reproductive fitness. Much research has shown that mating systems are strongly influenced by ecology. For instance, a male may defend a territory that holds nest sites or food sources necessary for a female to reproduce, and the territory may have resources sufficient for more than one female. If males differ in the quality of the territories they hold, a female's fitness is maximized if she mates with a male holding a high-quality territory. Such a male may already have a mate, but it is still more advantageous for the female to breed with that male than with an unmated male that defends a low-quality territory. In this case, natural selection would favor the evolution of polygyny.

Mating systems are also constrained by the needs of offspring. If the presence of both parents is necessary for young to be reared successfully, then monogamy may be favored. This is generally the case in birds, in which over 90% of all species are monogamous. A male may either remain with his mate and provide care for the offspring or desert that mate to search for others; both strategies may increase his fitness. The strategy that natural selection will favor depends upon the requirement for male assistance in feeding or defending the offspring. In some species, offspring are **altricial**—they require prolonged and extensive care. In these species, the need for care by two parents reduces the tendency for the male to desert his mate and seek other matings. In species where the young are **precocial** (requiring little parental care), males may be more likely to be polygynous.

Although polygyny is much more common, polyandrous systems—in which one female mates with several males—are known in a variety of animals. For example, in spotted sandpipers, males take care of all incubation and parenting, and females mate and leave eggs with two or more males.

In recent years, researchers have uncovered many unexpected aspects of animal mating. Some of these discoveries have resulted from the application of new technologies, whereas others have come from detailed and intensive field studies.

Extra-Pair Copulations

Chapter 16 describes how DNA fingerprinting can be used to identify blood samples. Another common use of this technology is to establish paternity. DNA fingerprints are so variable that each individual's pattern is unique. Thus, by comparing the DNA of a man and a child, experts can establish with a relatively high degree of confidence whether the man is the child's father.

FIGURE 52.32
Female defense polygyny in elephant seals. Male elephant seals fight with each other for possession of territories. Only the largest males can hold territories, which contain many females.

This approach is now commonly used in paternity lawsuits, but it has also become a standard weapon in the arsenal of behavioral ecologists. By establishing paternity, researchers can precisely quantify the reproductive success of individual males and thus assess how successful their particular reproductive strategies have been (figure 52.33*a*). In one classic study of red-winged blackbirds (figure 52.33*b*), researchers established that half of all nests contained at least one bird fertilized by a male other than the territory owner; overall, 20% of the offspring were the result of such **extra-pair copulations (EPCs).**

Studies such as this have established that EPCs—"cheating"—are much more pervasive in the bird world than originally suspected. Even in some species that were believed to be monogamous on the basis of behavioral observations, the incidence of offspring being fathered by a male other than the female's mate is sometimes surprisingly high.

Why do individuals have extra-pair copulations? For males, the answer is obvious: increased reproductive success. For females, it is less clear, because in most cases, it does not result in an increased number of offspring. One possibility is that females mate with genetically superior individuals, thus enhancing the genes passed on to their offspring. Another possibility is that females can increase the amount of help they get in raising their offspring. If a female mates with more than one male, each male may help raise the offspring. This is exactly what happens in a common English bird, the dunnock. Females mate not only with the territory owner, but also with subordinate males that hang around the edge of the territory. If these subordinates mate enough with a female, they will help raise her young, presumably because they may have fathered some of these young.

Alternative Mating Tactics

Natural selection has led to the evolution of a variety of other means of increasing reproductive success. For example, in many species of fish, there are two genetic classes of males. One group is large and defends territories to obtain matings. The other type of male is small and adopts a completely different strategy. They do not maintain territories, but loiter at the edge of the territories of large males. Just at the end of a male's courtship, when the female is laying her eggs and the territorial male is depositing sperm, the smaller male will dart in and release its own sperm into the water, thus fertilizing some of the eggs. If this strategy is successful, natural selection will favor the evolution of these two different male reproductive strategies.

Similar patterns are seen in other organisms. In some dung beetles, territorial males have large horns that they use to guard the chambers in which females reside, whereas genetically small males don't have horns; instead, they dig side tunnels and attempt to intercept the female inside her chamber. In isopods, there are three genetic size classes. The medium-sized males pass for females and enter a large male's territory in this way; the smallest class are so tiny, they are able to sneak in completely undetected.

This is just a glimpse of the rich diversity in mating systems that have evolved. The bottom line is: If there is a way of increasing reproductive success, natural selection will favor its evolution.

Mating systems represent reproductive adaptations to ecological conditions. The need for parental care and the ability of both sexes to provide it are important influences on the evolution of monogamy, polygyny, and polyandry. Detailed studies of animal mating systems, along with the use of modern molecular techniques, are revealing many surprises. This diversity is a testament to the power of natural selection to favor any trait that increases an animal's fitness.

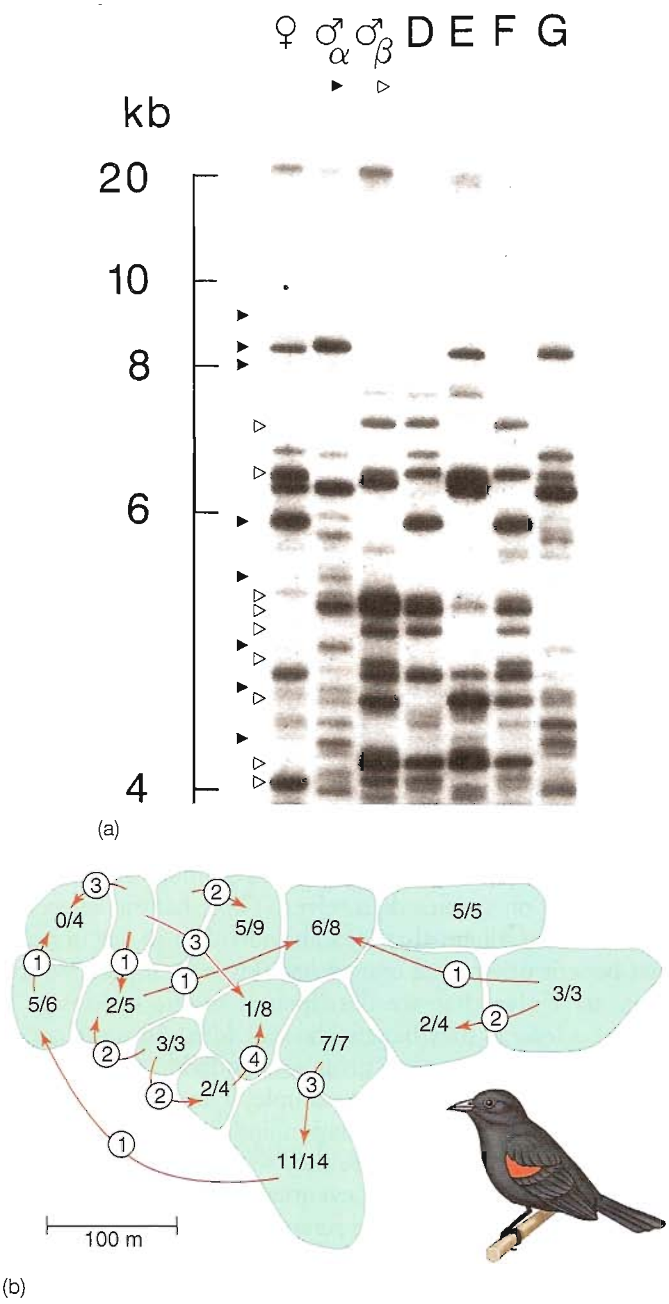


FIGURE 52.33
The study of paternity. (*a*) A DNA fingerprinting gel from the dunnock. The bands represent fragments of DNA of different lengths. The four nestlings (D–G) were in the nest of the female. By comparing the bands present in the two males, we can determine which male fathered which offspring. The triangles point to the bands that are diagnostic for one male and not the other. In this case, the β male fathered three (D, E, F, but not G) of the four offspring. (*b*) Results of a DNA fingerprinting study in red-winged blackbirds. Fractions indicate the proportion of offspring fathered by the male in whose territory the nest occurred. Arrows indicate how many offspring were fathered by particular males outside of each territory. Nests on some territories were not sampled.

52.5 There is considerable controversy about the evolution of social behavior.

Altruism and Group Living

Altruism—the performance of an action that benefits another individual at a cost to the actor—occurs in many guises in the animal world. In many bird species, for example, parents are assisted in raising their young by other birds, which are called *helpers at the nest.* In species of both mammals and birds, individuals that spy a predator will give an alarm call, alerting other members of their group, even though such an act would seem to call the predator's attention to the caller. Finally, lionesses with cubs will allow all cubs in the pride to nurse, including cubs of other females.

The existence of altruism has long perplexed evolutionary biologists. If altruism imposes a cost to an individual, how could an allele for altruism be favored by natural selection? One would expect such alleles to be at a disadvantage, and thus their frequency in the gene pool should decrease through time.

A number of explanations have been put forward to explain the evolution of altruism. One suggestion often heard on television documentaries is that such traits evolve for the good of the species. The problem with such explanations is that natural selection operates on individuals within species, not on species themselves. Thus, natural selection will not favor alleles that lead an individual to act in ways that benefit others at a cost to itself; it is even possible for traits to evolve that are detrimental to the species as a whole, as long as they benefit the individual. In some cases, selection can operate on groups of individuals, but such **group selection** is rare. For example, if an allele for cannibalism evolved within a population, individuals with that allele would be favored because they would have more to eat; however, the group might eventually eat itself to extinction, and the allele would be removed from the species. Although group selection can occur, the necessary conditions are rarely met in nature. In most cases, consequently, the "good of the species" cannot explain the evolution of altruistic traits.

Another possibility is that seemingly altruistic acts aren't altruistic after all. For example, helpers at the nest are often young and gain valuable parenting experience by assisting established breeders. Moreover, by hanging around an area, such individuals may inherit the territory when the established breeders die. Similarly, alarm callers may actually benefit by causing other animals to panic. In the ensuing confusion, the caller may be able to slip off undetected. Detailed field studies in recent years have demonstrated that some acts truly are altruistic, but others are not.

Reciprocity

Robert Trivers, now of Rutgers University, proposed that individuals may form "partnerships" in which mutual exchanges of altruistic acts occur because they benefit both participants. In the evolution of such **reciprocal altruism**, "cheaters" (nonreciprocators) are discriminated against and are cut off from receiving future aid. According to Trivers, if the altruistic act is relatively inexpensive, the small benefit a cheater receives by not reciprocating is far outweighed by the potential cost of not receiving future aid. Under these conditions, cheating should not occur.

Vampire bats roost in hollow trees in groups of 8 to 12 individuals. Because these bats have a high metabolic rate, individuals that have not fed recently may die. Bats that have found a host imbibe a great deal of blood, so giving up a small amount to keep a roostmate from starvation presents no great energy cost to the donor. Vampire bats tend to share blood with past reciprocators. If an individual fails to give blood to a bat from which it received blood in the past, it will be excluded from future bloodsharing.

Kin Selection

The most influential explanation for the origin of altruism was presented by William D. Hamilton in 1964. It is perhaps best introduced by quoting a passing remark made in a pub in 1932 by the great population geneticist J. B. S. Haldane. Haldane said that he would willingly lay down his life for *two brothers* or *eight first cousins.* Evolutionarily speaking, Haldane's statement makes sense, because for each allele Haldane received from his parents, his brothers each had a 50% chance of receiving the same allele (figure 52.34). Consequently, it is statistically expected that two of his brothers would pass on as many of Haldane's particular combination of alleles to the next generation as Haldane himself would. Similarly, Haldane and a first cousin would share an eighth of their alleles (see figure 52.34). Their parents, who are siblings, would each share half their alleles, and each of their children would receive half of these, of which half on the average would be in common: ½ × ½ × ½ = ⅛. Eight first cousins would therefore pass on as many of those alleles to the next generation as Haldane himself would. Hamilton saw Haldane's point clearly: Natural selection will favor any strategy that increases the net flow of an individual's alleles to the next generation.

Hamilton showed that by directing aid toward kin, or close genetic relatives, an altruist may increase the reproductive success of its relatives enough to compensate for the reduction in its own fitness. Because the altruist's

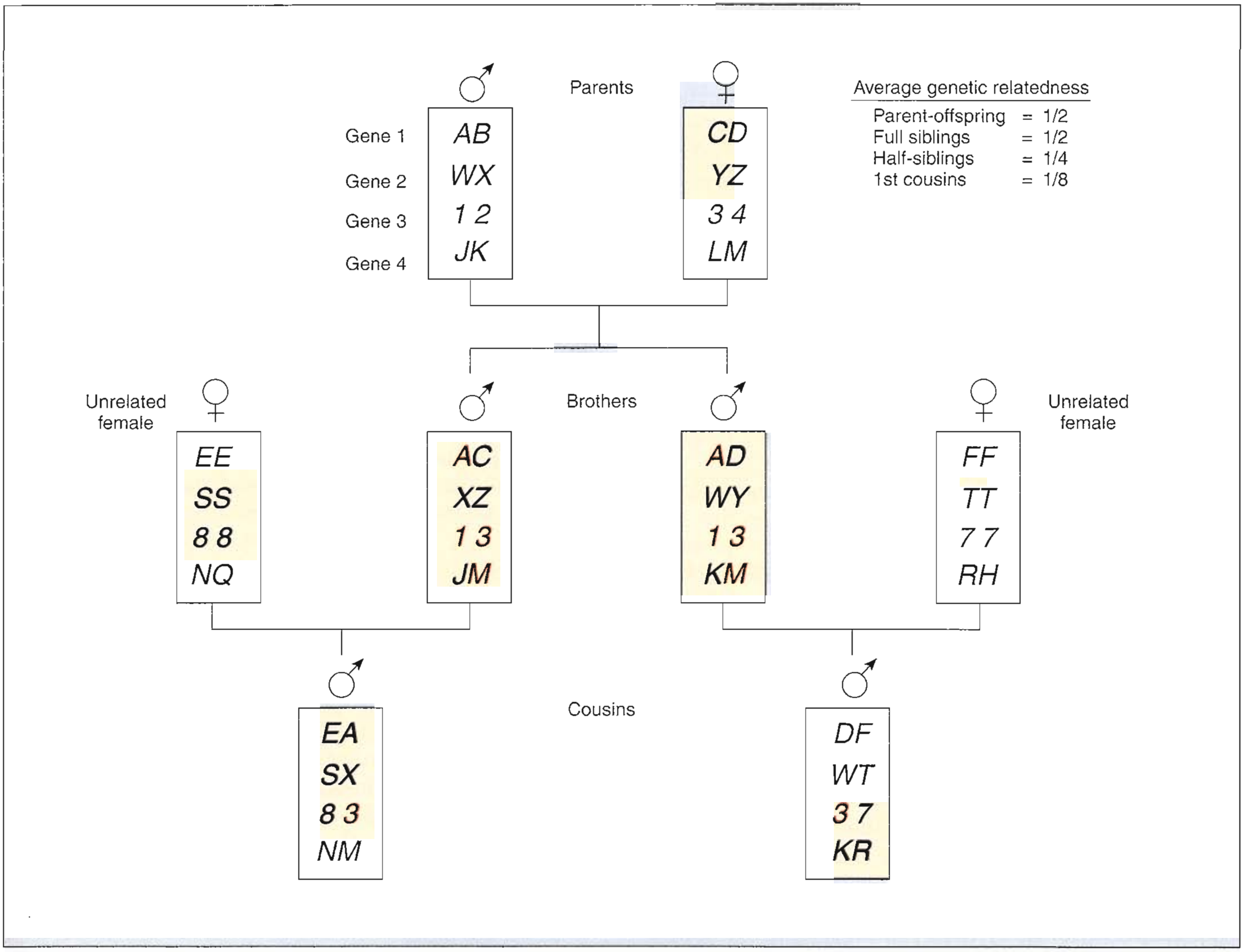


FIGURE 52.34

Hypothetical example of genetic relationships. On average, full siblings share half of their alleles. By contrast, cousins only share one-eighth of their alleles on average.

behavior increases the propagation of alleles in relatives, it will be favored by natural selection. Selection that favors altruism directed toward relatives is called **kin selection.** Although the behaviors being favored are cooperative, the genes are actually "behaving selfishly," because they encourage the organism to support copies of themselves in other individuals. In other words, if an individual has a dominant allele that causes altruism, any action that increases the frequency of this allele in future generations will be favored, even if that action is detrimental to the particular individual taking the action.

Hamilton's kin selection model predicts that altruism is likely to be directed toward close relatives. The more closely related two individuals are, the greater the potential genetic payoff. This relationship is described by **Hamilton's rule,** which states that altruistic acts are favored when $rb > c$. In this expression, b and c are the benefits and costs of the altruistic act, respectively, and r is the coefficient of relatedness, the proportion of alleles shared by two individuals through common descent. For example, an individual should be willing to have one less child ($c = 1$) if such actions allow a half-sibling, which shares one-quarter of its genes ($r = 0.25$), to have five or more additional offspring ($b = 5$).

Examples of Kin Selection

Many examples of kin selection are known from the animal world. For example, Belding's ground squirrels give alarm calls when they spot a predator such as a coyote or a badger. Such predators may attack a calling squirrel, so giving a signal places the caller at risk. The social unit of a ground squirrel colony consists of a female and her daughters, sisters, aunts, and nieces. When they mature, males disperse long distances from where they are born; thus, adult males in the colony are not genetically related to the females. By marking all squirrels in a colony with an individual dye pattern on their fur and by recording which individuals gave calls and the social circumstances of their calling, researchers found that females who have relatives living nearby are more likely to give alarm calls than females with no kin nearby. Males tend to call much less frequently, as would be expected because they are not related to most colony members.

Another example of kin selection comes from a bird called the white-fronted bee-eater that lives along rivers in Africa in colonies of 100 to 200 birds. In contrast to ground squirrels, it is the male bee-eaters that usually remain in the colony in which they were born, and the females that disperse to join new colonies. Many bee-eaters do not raise their own offspring, but rather help others. Many of these birds are relatively young, but helpers also include older birds whose nesting attempts have failed. The presence of a single helper, on average, doubles the number of offspring that survive. Two lines of evidence support the idea that kin selection is important in determining helping behavior in this species. First, helpers are normally males, which are usually related to other birds in the colony, and not females, which are not related. Second, when birds have the choice of helping different parents, they almost invariably choose the parents to which they are most closely related.

Haplodiploidy and Hymenopteran Social Evolution

Probably the most famous application of kin selection theory has been to social insects. A hive of honeybees consists of a single queen, who is the sole egg-layer, and up to 50,000 of her offspring, nearly all of whom are female workers with nonfunctional ovaries (figure 52.35). In addition to this reproductive division of labor, honeybees exhibit cooperative care of the brood and overlap of generations, such that queens live alongside their offspring. These are the hallmarks of a **eusocial** system.

The evolutionary origin of eusociality was long a mystery. How could natural selection favor the evolution of sterile workers that provided no offspring? Hamilton explained the origin of eusociality in hymenopterans (that is, bees, wasps, and ants) with his kin selection model. In these insects, males are haploid and females are diploid. This unusual system of sex determination, called *haplodiploidy*, leads to an unusual situation. If the queen is fertilized by a single male, then all female offspring will inherit exactly the same alleles from their father (because he is haploid and has only one copy of each allele). These female offspring will also share among themselves, on average, half of the alleles they get from the queen. Consequently, each female offspring will share, on average, 75% of her alleles with each sister (to verify this, rework figure 52.34, but allow the father to only have one allele for each gene). By contrast, should a female offspring have offspring of her own, she would only share half of her alleles with these offspring (the other half would come from their father). Thus, because of this close genetic relatedness, *workers propagate more of their own alleles by giving up their own reproduction to assist their mother in rearing their sisters, some of whom will be new queens and start new colonies and reproduce.* Thus, this unusual haplodiploid system may have set the stage for the evolution of eusociality in hymenopterans, and indeed, such systems have evolved as many as 12 or more times in the Hymenoptera.

One wrinkle in this theory, however, is that eusocial systems have evolved in several other groups, including thrips, termites, and naked mole rats. Although thrips are also haplodiploid, both termites and naked mole rats are not. Thus, although haplodiploidy may have facilitated the evolution of eusociality, it is not a necessary prerequisite.

FIGURE 52.35
Reproductive division of labor in honeybees. The queen (shown here with a red spot painted on her thorax) is the sole egg-layer. Her daughters are sterile workers.

Many factors could be responsible for the evolution of altruistic behaviors. Individuals may benefit directly if altruistic acts are reciprocated; kin selection explains how alleles for altruism can increase in frequency if altruistic acts are directed toward relatives. Kin selection is a potent force favoring, in some situations, the evolution of altruism and even complex social systems.

Group Living and the Evolution of Social Systems

Organisms as diverse as prokaryotes, cnidarians, insects, fish, birds, prairie dogs, lions, whales, and chimpanzees exist in social groups. To encompass the wide variety of social phenomena, we can broadly define a **society** as a group of organisms of the same species that are organized in a cooperative manner.

Why have individuals in some species given up a solitary existence to become members of a group? We have just seen that one explanation is kin selection: Groups may be composed of close relatives. In other cases, individuals may benefit directly from social living. For example, a bird that joins a flock may receive greater protection from predators. As flock size increases, the risk of predation decreases because there are more individuals to scan the environment for predators (figure 52.36). A member of a flock may also increase its feeding success if it can acquire information from other flock members about the location of new, rich food sources. In some predators, hunting in groups can increase success and allow the group to tackle prey too large for any one individual.

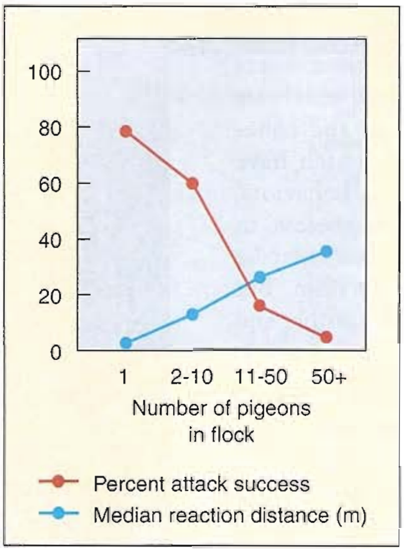


FIGURE 52.36
Flocking behavior decreases predation. As the size of a pigeon flock increases, hawks are less successful at capturing pigeons. Also, when more pigeons are present in the flock, they can detect hawks at greater distances, thus allowing more time for the pigeons to escape.
Would living in a flock affect the time available for foraging in pigeons?

Insect Societies

In insects, sociality has chiefly evolved in two orders, the Hymenoptera (ants, bees, and wasps) and the Isoptera (termites), although a few other insect groups include social species. As we have just discussed, a number of types of insects have evolved eusocial systems. These social insect colonies are composed of different **castes,** groups of individuals that differ in size and morphology and perform different tasks, such as workers and soldiers (figure 52.37).

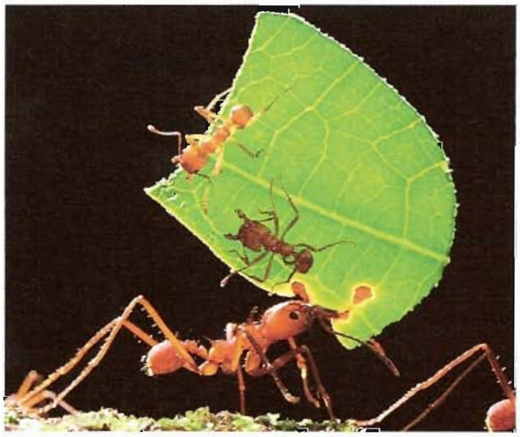


FIGURE 52.37
Castes of ants. These two leaf-cutter ants are members of different castes. The large ant is a worker carrying leaves to the nest, whereas the smaller ants are protecting the worker from attack.

In honeybees, the queen maintains her dominance in the hive by secreting a pheromone, called "queen substance," that suppresses development of the ovaries in other females, turning them into sterile workers. Drones (male bees) are produced only for purposes of mating. When the colony grows larger in the spring, some members do not receive a sufficient quantity of queen substance, and the colony begins preparations for swarming. Workers make several new queen chambers, in which new queens begin to develop. Scout workers look for a new nest site and communicate its location to the colony. The old queen and a swarm of female workers then move to the new site. Left behind, a new queen emerges, kills the other potential queens, flies out to mate, and returns to assume "rule" of the hive.

Leafcutter ants provide another fascinating example of the remarkable lifestyles of social insects. Leafcutters live in colonies of up to several million individuals, growing crops of fungi beneath the ground. Their moundlike nests are underground "cities" covering more than 100 square meters, with hundreds of entrances and chambers as deep as 5 meters beneath the ground. The division of labor among the worker ants is related to their size. Every day, workers travel along trails from the nest to a tree or a bush, cut its leaves into small pieces, and carry the pieces back to the nest (see figure 52.37). Smaller workers chew the leaf fragments into a mulch, which they spread like a carpet in the underground fungus chambers. Even smaller workers implant fungal hyphae in the mulch; recent molecular studies suggest that ants have been cultivating these fungi for more than 50 million years! Soon a luxuriant garden of fungi is growing. While other workers weed out undesirable kinds of fungi, nurse ants carry the larvae of the nest to choice spots in the garden, where the larvae graze. Some of these larvae grow into reproductive queens that will disperse from the parent nest and start new colonies, repeating the cycle.

Vertebrate Societies

In contrast to the highly structured and integrated insect societies and their remarkable forms of altruism, vertebrate social groups are usually less rigidly organized and cohesive. It seems paradoxical that vertebrates, which have larger brains and are capable of more complex behaviors, are generally less altruistic than insects. Nevertheless, in some complex vertebrate social systems, individuals may be exhibiting both reciprocity and kin-selected altruism. But vertebrate societies also generally display more conflict and aggression among group members than do insect societies. Conflict in vertebrate societies generally centers on access to food and mates.

Like insect societies, vertebrate societies have particular types of organization. Each social group of vertebrates has a certain size, stability of members, number of breeding males and females, and type of mating system. Behavioral ecologists have learned that the way a group is organized is influenced most often by ecological factors such as food type and predation. For example, meerkats take turns watching for predators while other group members forage for food (figure 52.38).

African weaver birds, which construct nests from vegetation, provide an excellent example of the relationship between ecology and social organization. Their roughly 90 species can be divided according to the type of social group they form. One set of species lives in the forest and builds camouflaged, solitary nests. Males and females are monogamous; they forage for insects to feed their young. The second group of species nests in colonies in trees on the savanna. They are polygynous and feed in flocks on seeds. The feeding and nesting habits of these two sets of species are correlated with their mating systems. In the forest, insects are hard to find, and both parents must cooperate in feeding the young. The camouflaged nests do not call the attention of predators to their brood. On the open savanna, building a hidden nest is not an option. Rather, savanna-dwelling weaver birds protect their young from predators by nesting in trees, which are not very abundant. This shortage of safe nest sites means that birds must nest together in colonies. Because seeds occur abundantly, a female can acquire all the food needed to rear young without a male's help. The male, free from the duties of parenting, spends his time courting many females—a polygynous mating system.

One exception to the general rule that vertebrate societies are not organized like those of insects is the naked mole rat, a small, hairless rodent that lives in and near East Africa. Unlike other kinds of mole rats, which live alone or in small family groups, naked mole rats form large underground colonies with a far-ranging system of tunnels and a central nesting area. It is not unusual for a colony to contain 80 individuals.

Naked mole rats feed on bulbs, roots, and tubers, which they locate by constant tunneling. As in insect societies, there is a division of labor among the colony members, with some mole rats working as tunnelers while others perform different tasks, depending upon the size of their bodies. Large mole rats defend the colony and dig tunnels.

Naked mole rat colonies have a reproductive division of labor similar to the one normally associated with the eusocial insects. All of the breeding is done by a single female or "queen," who has one or two male consorts. The workers, consisting of both sexes, keep the tunnels clear and forage for food.

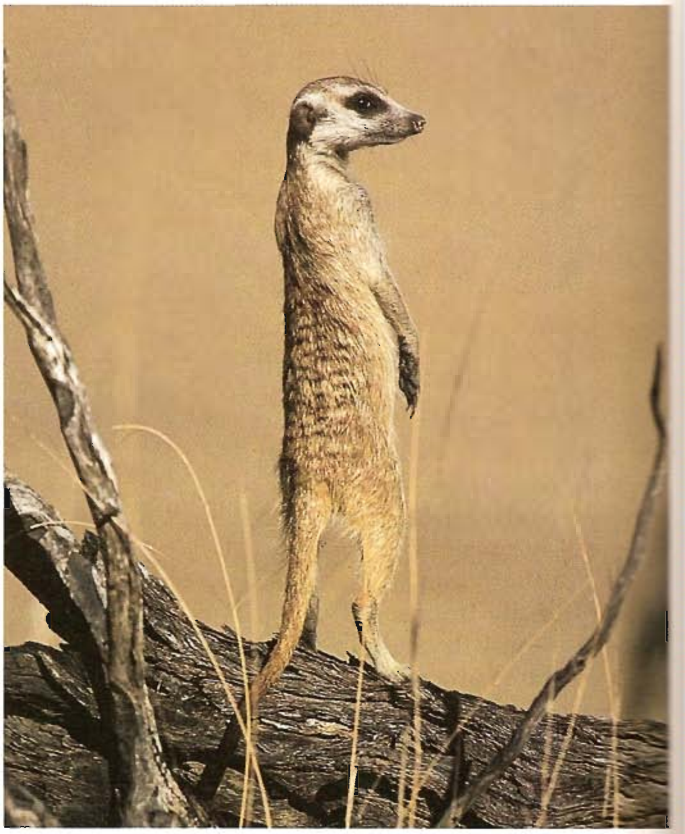


FIGURE 52.38
Foraging and predator avoidance. A meerkat sentinel on duty. Meerkats, *Suricata suricata*, are a species of highly social mongoose living in the semiarid sands of the Kalahari Desert in southern Africa. This meerkat is taking its turn to act as a lookout for predators. Under the security of its vigilance, the other group members can focus their attention on foraging.

Eusocial insects exhibit an advanced social structure that includes reproductive division of labor and workers with different tasks. Social behavior in vertebrates is often characterized by kin-selected altruism. Altruistic behavior is involved in cooperative breeding in birds and alarm-calling in mammals.