

51

Animal Behavior



▲ **Figure 51.1** What prompts a fiddler crab to wave its giant claw?

KEY CONCEPTS

- 51.1 Discrete sensory inputs can stimulate both simple and complex behaviors
- 51.2 Learning establishes specific links between experience and behavior
- 51.3 Selection for individual survival and reproductive success can explain most behaviors
- 51.4 Inclusive fitness can account for the evolution of behavior, including altruism

OVERVIEW

The How and Why of Animal Activity

Unlike most animals, male fiddler crabs (*genus Uca*) are highly asymmetrical: One claw grows to giant proportions, half the mass of the entire body (Figure 51.1). The name *fiddler* comes from the crab's appearance as it feeds on algae from the mudflats where it lives: The smaller front claw moves to and from the mouth in front of the enlarged claw.

Sometimes, however, the male waves his large claw in the air. What triggers this behavior? What purpose does it serve?

Claw waving by a male fiddler crab has two functions. Waving the claw, which can be used as a weapon, helps the crab *repel* other males wandering too close to his burrow. Vigorous claw waving also helps him *attract* females, who wander through the crab colony in search of a mate. After the male fiddler crab lures a female to his burrow, he seals her in with mud or sand in preparation for mating.

Animal behavior, be it solitary or social, fixed or variable, is based on physiological systems and processes. An individual **behavior** is an action carried out by muscles under control of the nervous system in response to a stimulus. Examples include an animal using its chest and throat muscles to produce a song, releasing a scent to mark its territory, or simply waving a claw. Behavior is an essential part of acquiring nutrients for digestion and finding a partner for sexual reproduction. Behavior also contributes to homeostasis, as in honeybees huddling to conserve heat (see Chapter 40). In short, all of animal physiology contributes to behavior, and animal behavior influences all of physiology.

Being essential for survival and reproduction, behavior is subject to substantial natural selection over time. This evolutionary process of selection also affects anatomy because the recognition and communication that underlie many behaviors depend on body form and appearance. Thus, the enlarged claw of the male fiddler crab is an adaptation that enables the display essential for recognition by other members of the species. Similarly, the positioning of the eyes on stalks held well above the crab's head enables him to see intruders from far off.

In this chapter, we'll examine how behavior is controlled, how it develops during an animal's life, and how it is influenced by genes and the environment. We'll also explore the ways in which behavior evolves over many generations. In moving from our study of an animal's inner workings to its interactions with the outside world, we will also provide a transition to ecology, the focus of Unit Eight.

CONCEPT 51.1

Discrete sensory inputs can stimulate both simple and complex behaviors

What approach do biologists use to determine how behaviors arise and what functions they serve? The Dutch scientist Niko Tinbergen, a pioneer in the study of animal behavior, suggested that understanding any behavior requires answering four questions, which can be summarized as follows:

1. What stimulus elicits the behavior, and what physiological mechanisms mediate the response?
2. How does the animal's experience during growth and development influence the response?

- How does the behavior aid survival and reproduction?
- What is the behavior's evolutionary history?

Tinbergen's first two questions ask about *proximate causation*: "how" a behavior occurs or is modified. The last two questions ask about *ultimate causation*: "why" a behavior occurs in the context of natural selection.

Today, Tinbergen's questions and the associated ideas of causation underlie **behavioral ecology**, the study of the ecological and evolutionary basis for animal behavior. As we explore this vibrant area of modern biological research, we will also review studies by Tinbergen and two other early researchers—Karl von Frisch and Konrad Lorenz—that earned the three scientists a Nobel Prize in 1973.

In addressing Tinbergen's first question, the nature of the stimuli that trigger behavior, we'll begin with behavioral responses to well-defined stimuli, starting with an example from Tinbergen's own experiments.

Fixed Action Patterns

As part of his research, Tinbergen kept fish tanks containing three-spined sticklebacks (*Gasterosteus aculeatus*). Male sticklebacks, which have red bellies, attack other males that invade their nesting territories. Tinbergen noticed that his male sticklebacks also behaved aggressively when a red truck passed in front of their tank. Inspired by this chance observation, he carried out experiments showing that the red color of an intruder's underside is what provokes the attack behavior. A male stickleback will not attack a fish lacking red coloration (note that female sticklebacks never have red bellies), but will attack even unrealistic models if they contain areas of red color (Figure 51.2).

The territorial response of male sticklebacks is an example of a **fixed action pattern**, a sequence of unlearned acts directly linked to a simple stimulus. Fixed action patterns are essentially unchangeable and, once initiated, usually carried to completion. The trigger for the behavior is an external cue called a **sign stimulus**, such as a red object prompting the male stickleback's aggressive behavior.

Migration

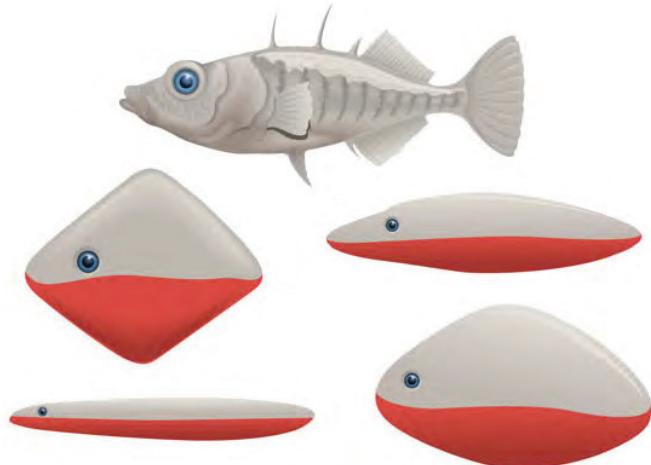
Environmental stimuli not only trigger behaviors but also provide cues that animals use to carry out those behaviors. For example, a wide variety of birds, fishes, and other animals use environmental cues to guide **migration**—a regular, long-distance change in location (Figure 51.3).

Many migrating animals pass through environments they have not previously encountered. How, then, do they find their way in these foreign settings?

Some migrating animals track their position relative to the sun, even though the sun's position relative to Earth changes throughout the day. Animals can adjust for these changes by means of a *circadian clock*, an internal mechanism that maintains a 24-hour activity rhythm or cycle (see Chapter 49). For



(a) A male stickleback fish attacks other male sticklebacks that invade its nesting territory. The red belly of the intruding male (left) acts as the sign stimulus that releases the aggressive behavior.



(b) The realistic model at the top, without a red underside, produces no aggressive response in a male three-spined stickleback. The other models, with red undersides, produce strong responses.

▲ **Figure 51.2 Sign stimuli in a classic fixed action pattern.**

? Suggest an explanation for why this behavior evolved (its ultimate causation).



▲ **Figure 51.3 Migration.** Each spring, snow geese (*Chen caerulescens*) migrate from their wintering grounds, which may be as far south as Mexico, to their breeding grounds in Greenland, Canada, and Alaska. In the autumn, they return to their wintering grounds.

example, experiments have shown that migrating birds orient differently relative to the sun at distinct times of the day. Nocturnal animals can instead use the North Star, which has a constant position in the night sky.

Although the sun and stars can provide useful clues for navigation, these landmarks can be obscured by clouds. How do migrating animals overcome this problem? A simple experiment with homing pigeons provides one answer. On an overcast day, placing a small magnet on the head of a homing pigeon prevents it from returning efficiently to its roost. Researchers concluded that pigeons can sense their position relative to Earth's magnetic field and thereby navigate without solar or celestial cues.

The way in which animals detect Earth's magnetic field remains a matter of debate. It is known that the heads of migrating fishes and birds contain bits of magnetite, a magnetic iron mineral. This fact leads some scientists to hypothesize that Earth's pull on magnetite-containing structures triggers transmission of nerve impulses to the brain. Others propose that migrating animals are guided by the effects of Earth's magnetic field on photoreceptors in the eye. The idea that animals "see" the magnetic field is supported by experiments showing that light of particular wavelengths must be present for birds to orient in a magnetic field during the day or night.

Behavioral Rhythms

Although the circadian clock plays a small but significant role in navigation by some migrating species, it has a major role in the daily activity of all animals. As discussed in Chapters 40 and 49, the output of the clock is a circadian rhythm, a daily cycle of rest and activity with far-reaching effects on behavioral physiology. The clock is normally synchronized with the light and dark cycles of the environment but can maintain rhythmic activity under constant environmental conditions, such as during hibernation.

Some behaviors, such as migration and reproduction, reflect biological rhythms with a longer cycle, or period, than the circadian rhythm. Behavioral rhythms linked to the yearly cycle of seasons are called *circannual rhythms*. Although migration and reproduction typically correlate with food availability, these behaviors are not a direct response to changes in food intake. Instead, circannual rhythms, like circadian rhythms, are influenced by the periods of daylight and darkness in the environment. For example, studies with several bird species have shown that an artificial environment with extended daylight can induce out-of-season migratory behavior.

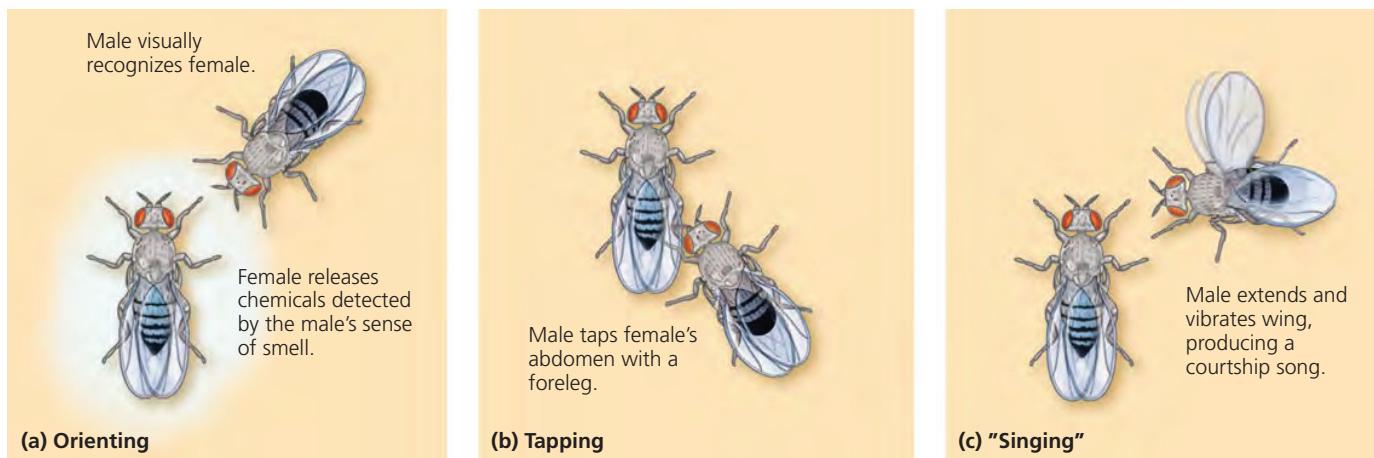
Not all biological rhythms are linked to the light and dark cycles in the environment. Consider, for instance, the fiddler crab shown in Figure 51.1. The male's claw-waving courtship behavior is linked not to day length but to the timing of the new and full moon. Why? Fiddler crabs begin their lives as plankton, settling in the mudflats after several larval stages. By courting at the time of the new or full moon, crabs link their reproduction to the times of greatest tidal movement. The tides disperse larvae to deeper waters, where they complete early development in relative safety before returning to the tidal flats.

Animal Signals and Communication

Claw waving by fiddler crabs during courtship is an example of one animal (the male crab) generating the stimulus that guides the behavior of another animal (the female crab). A stimulus transmitted from one animal to another is called a **signal**. The transmission and reception of signals constitute animal **communication**, an essential element of interactions between individuals.

Forms of Animal Communication

Let's consider the courtship behavior of *Drosophila melanogaster*, the fruit fly (Figure 51.4), as an introduction to the four



▲ **Figure 51.4** Courtship behavior of the fruit fly. Fruit fly courtship involves a fixed set of behaviors that follow one another in a fixed order.

common modes of animal communication: visual, chemical, tactile, and auditory.

Fruit fly courtship constitutes a *stimulus-response chain*, in which the response to each stimulus is itself the stimulus for the next behavior. In the first step, a male identifies a female of the same species and then orients his body toward hers. When the male sees and turns toward the female, he relies on *visual communication*. In addition, the male's sense of smell, or olfactory system, detects chemicals released into the air by the female. This is an example of *chemical communication*, the transmission and reception of signals in the form of specific molecules. Having recognized the female, the male approaches and taps the female with a foreleg. This touching, or *tactile communication*, alerts the female to the male's presence. In the process, chemicals on her abdomen are transferred to the male, providing further chemical confirmation of her species identity. In the third stage of courtship, the male extends and vibrates his wing, producing a specific courtship song. This singing, an example of *auditory communication*, informs the female that the male is of the same species. Only if all of these forms of communication are successful will a female allow the male to attempt copulation.

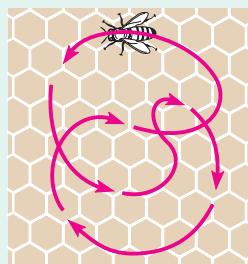
The information content of animal communication varies considerably. One of the most remarkable examples is the symbolic language of the European honeybee (*Apis mellifera*), discovered in the early 1900s by Austrian researcher Karl von Frisch. Using glass-walled observation hives, he and his students spent several decades observing these bees. Methodical recordings of bee movements enabled von Frisch to decipher a "dance language" that returning foragers use to inform other bees about the distance and direction of travel to food sources.

As illustrated in **Figure 51.5**, a returning bee quickly becomes the center of attention for other bees, called followers. If the food source is close to the hive (less than 50 m away), the returning bee moves in tight circles while wagging its abdomen from side to side. This behavior, called the "round dance," motivates the follower bees to leave the hive and search for nearby food.

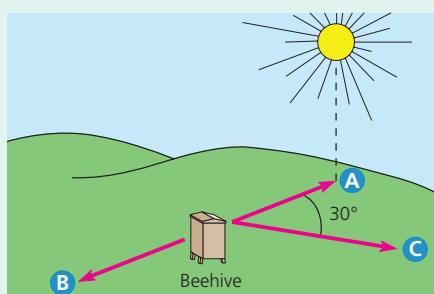
When the food source is farther from the nest, the returning bee instead performs a "waggle dance." This dance, consisting of a half-circle swing in one direction, a straight run during which the bee waggles its abdomen, and a half-circle swing in the other direction, communicates to the follower bees both the direction and distance of the food source in relation to the hive. The angle of the straight run relative to the hive's vertical surface is the same as the horizontal angle of the food in relation to the sun. For example, if the returning bee runs at a 30° angle to the right of vertical, the follower bees leaving the hive fly 30° to the right of the horizontal direction of the sun. A dance with a longer straight run, and



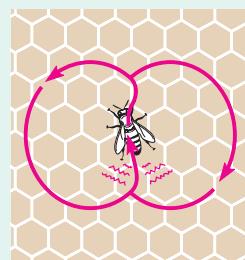
(a) Worker bees cluster around a bee that recently returned from a foraging trip.



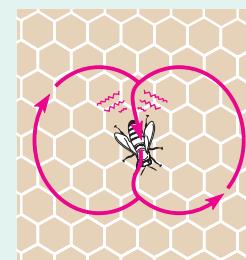
(b) The round dance indicates that food is near.



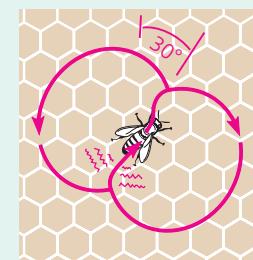
(c) The waggle dance, performed when food is distant, resembles a figure eight (below). Distance is indicated by the number of abdominal waggles performed in the straight-run part of the dance. Direction is indicated by the angle (in relation to the vertical surface of the hive) of the straight run.



Location **A**: Food source is in same direction as sun.



Location **B**: Food source is in direction opposite sun.



Location **C**: Food source is 30° to right of sun.

▲ Figure 51.5 Honeybee dance language. Honeybees returning to the hive communicate the location of food sources through the symbolic language of a dance.

therefore more abdominal waggles per run, indicates a greater distance to the food source. As follower bees exit the hive, they fly almost directly to the area indicated by the waggle dance. By using flower odor and other clues, they locate the food source within this area.

Pheromones

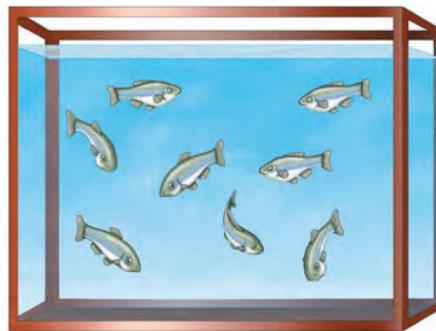
Animals that communicate through odors or tastes emit chemical substances called **pheromones**. Pheromones are especially common among mammals and insects and often relate to reproductive behavior. For example, pheromones are the basis for the chemical communication in fruit fly courtship (see Figure 51.4). Pheromones are not limited to short-distance signaling, however. Male silkworm moths have receptors that can detect the pheromone from a female moth from several kilometers away (see Figure 50.6). After the moths are together, pheromones also trigger specific courtship behaviors.

In a honeybee colony, pheromones produced by the queen and her daughters, the workers, maintain the hive's complex social order. One pheromone (once called the queen substance) has a particularly wide range of effects. It attracts workers to the queen, inhibits development of ovaries in workers, and attracts males (drones) to the queen during her mating flights out of the hive.

Pheromones can also serve as alarm signals. For example, when a minnow or catfish is injured, a substance released from the fish's skin disperses in the water, inducing a fright response in other fish. These nearby fish become more vigilant and often form tightly packed schools near the river or lake bottom, where they are safer from attack (**Figure 51.6**). Pheromones can be very effective at remarkably low concentrations. For instance, just 1 cm² of skin from a fathead minnow contains sufficient alarm substance to induce a reaction in 58,000 L of water.

As we have seen, the forms of animal communication used to convey information are quite diverse. In general, the form of communication that evolves is closely related to an animal's lifestyle and environment. For example, most terrestrial mammals are nocturnal, which makes visual displays relatively ineffective. Instead, these species use olfactory and auditory signals, which work as well in the dark as in the light. In contrast, most birds are diurnal (active mainly in daytime) and communicate primarily by visual and auditory signals. Humans are also diurnal and, like birds, use primarily visual and auditory communication. We can thus detect and appreciate the songs and bright colors used by birds to communicate but miss many chemical cues on which other mammals base their behavior.

So far in this chapter, we have explored the types of stimuli that elicit behaviors—the first part of Tinbergen's first question. The second part of that question—the physiological mechanisms that mediate responses—was the focus of



(a) Minnows are widely dispersed in an aquarium before an alarm substance is introduced.



(b) Within seconds of the alarm substance being introduced, minnows aggregate near the bottom of the aquarium and reduce their movement.

▲ **Figure 51.6** Minnows responding to the presence of an alarm substance.

Chapters 49 and 50. Stimuli activate sensory systems, are processed in the central nervous system, and result in motor outputs that constitute behavior. You may want to review those two chapters before proceeding to the next concept, which focuses on Tinbergen's second question—how experience influences behavior.

CONCEPT CHECK 51.1

- If an egg rolls out of the nest, a mother graylag goose will retrieve it by nudging it with her beak and head. If researchers remove the egg or substitute a ball during this process, the goose continues to bob her beak and head while she moves back to the nest. Explain how and why this behavior occurs.
- MAKE CONNECTIONS** How is the seasonal timing of plant flowering similar in mechanism and function to the lunar-linked rhythm of fiddler crab courtship? (See pp. 839–841 of Concept 39.3.)
- WHAT IF?** Suppose you exposed various fish species to the alarm substance from minnows. Based on what you know about natural selection, suggest why some species might respond like minnows, some might increase activity, and some might show no change.

For suggested answers, see Appendix A.

CONCEPT 51.2

Learning establishes specific links between experience and behavior

For many behaviors—such as a fixed action pattern, a courtship stimulus-response chain, and pheromone signaling—nearly all individuals in a population exhibit virtually the same behavior, despite internal and environmental differences during development and throughout life. Behavior that is developmentally fixed in this way is known as **innate behavior**. In other cases, behavior is variable, depending on experience.

Experience and Behavior

Tinbergen's second question asks how an animal's experiences during growth and development influence the response to stimuli. How do researchers answer this question? One informative approach is a **cross-fostering study**, in which the young of one species are placed in the care of adults from another species. The extent to which the offspring's behavior changes in such a situation provides one measure of how the social and physical environment influences behavior.

The males of certain mouse species have behavioral differences that are well suited for cross-fostering experiments. Males of the species *Peromyscus californicus*, commonly called California mice, are highly aggressive toward other mice and provide extensive parental care. In contrast, male white-footed mice (*Peromyscus leucopus*) are less aggressive and engage in little parental care. When the pups of each species were placed in the nests of the other species, the cross-fostering altered some behaviors of both species (Table 51.1). For instance, male California mice raised by white-footed mice were less aggressive toward intruders. Thus, experience during development can strongly influence aggressive behavior in these rodents.

One of the most important findings of the cross-fostering experiments with mice was that the influence of experience on behavior can be passed on to progeny: When the cross-fostered California mice became parents, they spent less time retrieving offspring who wandered off than did California mice raised by their own species. Thus, experience during development can modify physiology in a way that alters parental behavior, extending the influence of environment to a subsequent generation.

For humans, the influence of genetics and environment on behavior can be explored by a **twin study**, in which researchers compare the behavior of identical twins raised apart with the behavior of those raised in the same household. Twin studies have been instrumental in studying human behavioral disorders, such as schizophrenia, anxiety disorders, and alcoholism. As discussed in Chapter 49, these investigations have revealed that both genetics and environment (nature *and* nurture) contribute significantly to the behaviors that characterize these disorders in humans.

Learning

One of the most powerful ways that environmental conditions can influence behavior is through **learning**, the modification of behavior based on specific experiences. We will now consider a number of different types of learning, beginning with a form of learning first explored by Austrian biologist Konrad Lorenz.

Imprinting

A type of behavior that includes both learned and innate components is **imprinting**, the formation at a specific stage in life of a long-lasting behavioral response to a particular individual or object. Imprinting is distinguished from other types of learning by having a **sensitive period**, also called a critical period, a limited developmental phase when this type of learning can occur. During the sensitive period, the young imprint on their parent and learn the basic behaviors of their species, while the parent learns to recognize its offspring. Among gulls, for instance, the sensitive period for a parent to bond with its young lasts one to two days. If bonding does not occur, the parent will not care for the infant, leading to death for the offspring and a decrease in reproductive success for the parent.

But how do the young know on whom—or what—to imprint? For example, how do young birds know that they should follow their mother? The tendency to respond is innate in the birds; the outside world provides the *imprinting stimulus*, something to which the response will be directed. Experiments with many species of waterfowl indicate that they have no innate recognition of "mother." Rather, they identify with the first object they encounter that has certain

Table 51.1 Influence of Cross-Fostering on Male Mice *

Species	Aggression Toward an Intruder	Aggression in Neutral Situation	Paternal Behavior
California mice fostered by white-footed mice	Reduced	No difference	Reduced
White-footed mice fostered by California mice	No difference	Increased	No difference

*Comparisons are with mice raised by parents of their own species.

key characteristics. In classic experiments done in the 1930s, Lorenz showed that the principal imprinting stimulus in graylag geese (*Anser anser*) is a nearby object that is moving away from the young. When incubator-hatched goslings spent their first few hours with Lorenz rather than with a goose, they imprinted on him and steadfastly followed him from then on (**Figure 51.7a**). Furthermore, they showed no



(a) These young greylag geese imprinted on ethologist Konrad Lorenz.



(b) A pilot wearing a crane suit and flying an ultralight plane acts as a surrogate parent to direct the migration of whooping cranes.

▲ Figure 51.7 Imprinting. Imprinting can be altered to (a) investigate animal behavior or (b) direct animal behavior.

WHAT IF? Suppose the geese following Lorenz were bred to each other. How might their imprinting on Lorenz affect their offspring? Explain.

recognition of their biological mother or other adults of their own species.

Imprinting has become an important component of efforts to save endangered species, such as the whooping crane (*Grus americana*). Scientists tried raising whooping cranes in captivity by using sandhill cranes (*Grus canadensis*) as foster parents. However, because the whooping cranes imprinted on their foster parents, none formed a *pair-bond* (strong attachment) with a whooping crane mate. To avoid such problems, captive breeding programs now isolate young cranes, exposing them to the sights and sounds of members of their own species.

Scientists have made further use of imprinting to teach cranes born in captivity to migrate along safe routes. Young whooping cranes are imprinted on humans in “crane suits” and then allowed to follow these “parents” as they fly ultralight aircraft along selected migration routes (**Figure 51.7b**). Importantly, these cranes still form mating pair-bonds with other whooping cranes, indicating that the crane costumes have the features required to direct “normal” imprinting.

Spatial Learning and Cognitive Maps

Every natural environment has spatial variation, as in locations of nest sites, hazards, food, and prospective mates. Therefore, an organism’s fitness may be enhanced by the capacity for **spatial learning**, the establishment of a memory that reflects the environment’s spatial structure.

The idea of spatial learning intrigued Tinbergen while he was a graduate student in the Netherlands. At that time, he was studying the female digger wasp (*Philanthus triangulum*), which nests in small burrows dug into sand dunes. Tinbergen noticed that when a wasp left her nest to go hunting, she hid the entrance from potential intruders by covering it with sand. Upon her return, she flew directly to her hidden nest, despite the presence of hundreds of other burrows in the area. Tinbergen hypothesized that a wasp locates her nest by learning its position relative to visible landmarks, or location indicators. To test this hypothesis, he carried out an experiment in the wasps’ natural habitat (**Figure 51.8**). By manipulating objects around nest entrances, he demonstrated that digger wasps engage in spatial learning. This experiment was so simple and informative that it could be summarized very concisely. In fact, at 32 pages, Tinbergen’s Ph.D. thesis from 1932 is still the shortest ever approved at Leiden University.

In many animal species, spatial learning can be quite sophisticated. Some animals guide their activity by a **cognitive map**, a representation in the nervous system of the spatial relationships between objects in an animal’s surroundings. Rather than relying solely on moving from landmark to landmark, animals using cognitive maps can navigate more flexibly and efficiently by relating landmark positions to one another.

One striking example of cognitive mapping is found in the Clark’s nutcracker (*Nucifraga columbiana*). Nutcrackers are

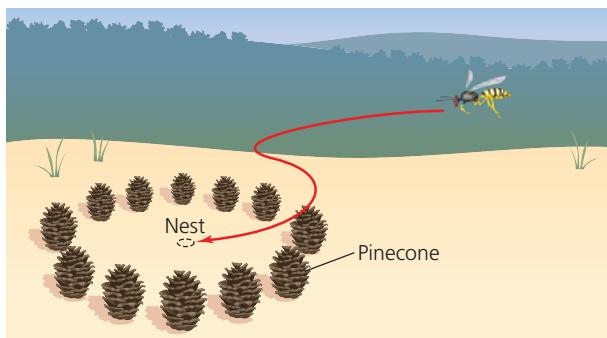
corvids, the bird family that also includes ravens, crows, and jays. In the fall, a single nutcracker stores as many as 30,000 pine seeds in thousands of hiding places called caches, distributed over an area as large as 35 km². During the winter,

▼ Figure 51.8

INQUIRY

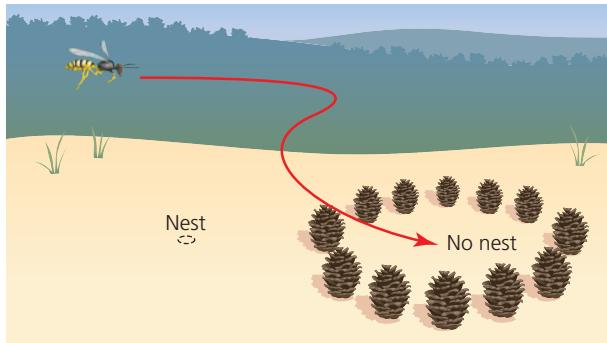
Does a digger wasp use landmarks to find her nest?

EXPERIMENT A female digger wasp covers the entrance to her nest while foraging for food, but finds the correct wasp nest reliably upon her return 30 minutes or more later. Niko Tinbergen wanted to test the hypothesis that a wasp learns visual landmarks that mark her nest before she leaves on hunting trips. First, he marked one nest with a ring of pinecones while the wasp was in the burrow. After leaving the nest to forage, the wasp returned to the nest successfully.



Two days later, after the wasp had again left, Tinbergen shifted the ring of pinecones away from the nest. Then he waited to observe the wasp's behavior.

RESULTS When the wasp returned, she flew to the center of the pinecone circle instead of to the nearby nest. Repeating the experiment with many wasps, Tinbergen obtained the same results.



CONCLUSION The experiment supported the hypothesis that digger wasps use visual landmarks to keep track of their nests.

SOURCE N. Tinbergen, *The Study of Instinct*, Clarendon Press, Oxford (1951).

WHAT IF? Suppose the digger wasp had returned to her original nest site, despite the pinecones having been moved. What alternative hypotheses might you propose regarding how the wasp finds her nest and why the pinecones didn't misdirect the wasp?

the birds relocate many of their caches. By experimentally varying the distance between landmarks, researchers demonstrated that birds could identify the halfway point between landmarks. This behavior suggests that nutcrackers employ an abstract geometric rule, which we can approximate as "Seed caches are found halfway between particular landmarks." Such rules, a fundamental property of cognitive maps, reduce the amount of detail required to remember an object's location. As we discussed in Chapter 49, corvids also display other forms of higher nervous system function.

Associative Learning

Learning often involves making associations between experiences. Consider, for example, a blue jay (*Cyanocitta cristata*) that ingests a brightly colored monarch butterfly (*Danaus plexippus*). Substances that the monarch accumulates from milkweed plants cause the blue jay to vomit almost immediately (Figure 51.9). Following such experiences, blue jays avoid attacking monarchs and similar-looking butterflies. The ability to associate one environmental feature (such as a color) with another (such as a foul taste) is called **associative learning**.

Among animal behaviors, associative learning is particularly suited to laboratory studies because they typically involve either classical conditioning or operant conditioning. In *classical conditioning*, an arbitrary stimulus becomes associated with a particular outcome. Russian physiologist Ivan Pavlov carried out early experiments in classical conditioning, demonstrating that if he always rang a bell just before feeding a dog, the dog would eventually salivate when the bell sounded, anticipating food. In *operant conditioning*, also called trial-and-error learning, an animal first learns to associate one of its behaviors with a reward or punishment and then tends to repeat or avoid that behavior (see Figure 51.9). B. F. Skinner, an American pioneer in the study of operant conditioning, explored this process in the laboratory by, for example, having a rat learn through trial-and-error to obtain food by pressing a lever.



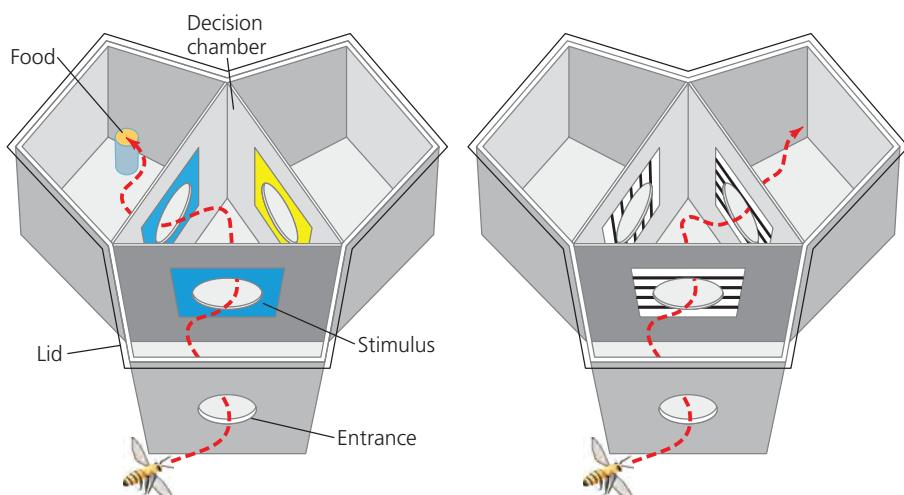
▲ **Figure 51.9** **Associative learning.** Having ingested and vomited a monarch butterfly, a blue jay has probably learned to avoid this species.

Studies reveal that animals can learn to link many pairs of features of their environment, but not all. For example, pigeons can learn to associate danger with a sound but not with a color. However, they can learn to associate a color with food. What does this mean? The development and organization of the pigeon's nervous system apparently restrict the associations that can be formed. Moreover, such restrictions are not limited to birds. Rats, for example, can learn to avoid illness-inducing foods on the basis of smells, but not on the basis of sights or sounds.

If we take into account the evolution of behavior, the fact that some animals can't learn to make particular associations appears logical. The associations an animal can readily form typically reflect relationships likely to occur in nature. Conversely, associations that can't be formed are those unlikely to be of selective advantage in a native environment. In the case of a rat's diet in the wild, for example, a harmful food is far more likely to have a certain odor than to be associated with a particular sound.

Cognition and Problem Solving

The most complex forms of learning involve **cognition**—the process of knowing that involves awareness, reasoning, recollection, and judgment. Although it was once argued that only primates and certain marine mammals have high-level thought processes, many other groups of animals, including insects, appear to exhibit cognition in controlled laboratory studies. For example, an experiment using Y-shaped mazes tested whether honeybees can distinguish between "same" and "different." One maze had different colors, and one had different black-and-white striped patterns, either vertical or horizontal bars. Two groups of honeybees were trained in the color maze.



(a) Bees were trained in a color maze. As shown here, one group were rewarded for choosing the same color as the stimulus.

(b) Bees were tested in a pattern maze. If previously rewarded for choosing the same color, bees most often chose lines oriented the same way as the stimulus.

▲ Figure 51.10 A maze test of abstract thinking by honeybees. These mazes are designed to test whether honeybees can distinguish "same" from "different."

Upon entering, a bee would see a sample color and could then choose between an arm of the maze with the same color or an arm with a different color. Only one arm contained a food reward. The first group of bees were rewarded for flying into the arm with the *same* color as the sample (**Figure 51.10a**); the second group were rewarded for choosing the arm with the *different* color. Next, they were tested in the bar maze, which had no food reward. After encountering a sample black-and-white pattern of bars, a bee could choose between an arm with the same pattern or an arm with a different pattern. The bees in the first group most often chose the arm with the same pattern (**Figure 51.10b**), whereas those in the second group typically chose the arm with the different pattern.

The maze experiments provide strong experimental support for the hypothesis that honeybees can distinguish on the basis of "same" and "different." Remarkably, research published in 2010 indicates that honeybees can also learn to distinguish between human faces.

The information-processing ability of a nervous system can also be revealed in **problem solving**, the cognitive activity of devising a method to proceed from one state to another in the face of real or apparent obstacles. For example, if a chimpanzee is placed in a room with several boxes on the floor and a banana hung high out of reach, the chimp can assess the situation and stack the boxes, enabling it to reach the food. Such problem-solving behavior is highly developed in some mammals, especially primates and dolphins. Notable examples have also been observed in some bird species, especially corvids. In one study, ravens were confronted with food hanging from a branch by a string. After failing to grab the food in flight, one raven flew to the branch and alternately pulled up and stepped on the string until the food was within reach. A number of other ravens eventually arrived at similar solutions. Nevertheless, some ravens failed to solve the problem, indicating that problem-solving success in this species, as in others, varies with individual experience and abilities.

Development of Learned Behaviors

Most of the learned behaviors we have discussed develop over a relatively short time. Some behaviors develop more gradually. For example, some bird species learn songs in stages.

In the case of the white-crowned sparrow (*Zonotrichia leucophrys*), the first stage of song learning takes place early in life, when the fledgling sparrow first hears the song. If a fledgling is prevented from hearing real sparrows or recordings of sparrow songs during the first 50 days of its life, it fails to

develop the adult song of its species. Although the young bird does not sing during the sensitive period, it memorizes the song of its species by listening to other white-crowned sparrows sing. During the sensitive period, fledglings chirp more in response to songs of their own species than to songs of other species. Thus, although young white-crowned sparrows learn the songs they will sing as adults, learning appears to be bounded by genetically controlled preferences.

The sensitive period when a white-crowned sparrow memorizes its species' song is followed by a second learning phase when the juvenile bird sings tentative notes called a subsong. The juvenile bird hears its own singing and compares it with the song memorized during the sensitive period. Once a sparrow's own song matches the one it memorized, the song "crystallizes" as the final song, and the bird sings only this adult song for the rest of its life.

The song-learning process is quite different for canaries than for white-crowned sparrows. Canaries, for example, do not have a single sensitive period for song learning. A young canary begins with a subsong, but the full song does not crystallize in the same way as in white-crowned sparrows. Between breeding seasons, the song becomes flexible again, and an adult male may learn new song "syllables" each year, adding to the song it already sings.

Song learning is one of many examples of how animals learn from other members of their species. In finishing our exploration of learning, we'll look at several more examples that reflect the more general phenomenon of social learning.

Social Learning

Many animals learn to solve problems by observing the behavior of other individuals. Young wild chimpanzees, for example, learn how to crack open oil palm nuts with two stones by copying experienced chimpanzees (**Figure 51.11**). This type of learning through observing others is called **social learning**.



▲ **Figure 51.11** A young chimpanzee learning to crack oil palm nuts by observing an experienced elder.

Another example of how social learning can modify behavior comes from studies of the vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya. Vervet monkeys, which are about the size of a domestic cat, produce a complex set of alarm calls. Amboseli vervets give distinct alarm calls for leopards, eagles, or snakes, all of which prey on vervets. When a vervet sees a leopard, it gives a loud barking sound; when it sees an eagle, it gives a short double-syllable cough; and the snake alarm call is a "chutter." Upon hearing a particular alarm call, other vervets in the group behave in an appropriate way: They run up a tree on hearing the alarm for a leopard (ververts are nimbler than leopards in the trees); look up on hearing the alarm for an eagle; and look down on hearing the alarm for a snake (**Figure 51.12**).

Infant vervet monkeys give alarm calls, but in a relatively undiscriminating way. For example, they give the "eagle" alarm on seeing any bird, including harmless birds such as bee-eaters. With age, the monkeys improve their accuracy. In fact, adult vervet monkeys give the eagle alarm only on seeing an eagle belonging to either of the two species that eat vervets. Infants probably learn how to give the right call by observing other members of the group and receiving social confirmation. For instance, if the infant gives the call on the right occasion—say, an eagle alarm when there is an eagle overhead—another member of the group will also give the eagle call. But if the infant gives the call when a bee-eater flies by, the adults in the group are silent. Thus, vervet monkeys have an initial, unlearned tendency to give calls upon seeing potentially threatening objects in the environment. Learning fine-tunes the call so that adult vervets give calls only in response to genuine danger and can fine-tune the alarm calls of the next generation.



▲ **Figure 51.12** Vervet monkeys learning correct use of alarm calls. On seeing a python (foreground), vervet monkeys give a distinct "snake" alarm call (inset), and the members of the group stand upright and look down.

Social learning forms the roots of **culture**, which can be defined as a system of information transfer through social learning or teaching that influences the behavior of individuals in a population. Cultural transfer of information can alter behavioral phenotypes and thereby influence the fitness of individuals.

Changes in behavior that result from natural selection occur on a much longer time scale than does learning. In Concept 51.3, we'll examine the relationship between particular behaviors and the processes of selection related to survival and reproduction.

CONCEPT CHECK 51.2

- How might associative learning explain why different species of distasteful or stinging insects have similar colors?
- WHAT IF?** How might you position and manipulate a few objects in a lab to test whether an animal can use a cognitive map to remember the location of a food source?
- MAKE CONNECTIONS** How can a learned behavior contribute to speciation? (See Concept 24.1, pp. 488–492.)

For suggested answers, see Appendix A.

that the enzyme encoded by the *forager* locus is more active in *for^R* larvae than in *for^s* larvae and has properties typical of an enzyme in a signal transduction pathway (see Chapter 45).

Both the *for^R* and *for^s* alleles are present in natural populations. What circumstances might favor one or the other allele? The answer became apparent in experiments when flies were kept for many generations at either low or high population densities. The larvae from the two samples clearly diverged in behavior, as measured by differences in average length of their foraging paths (**Figure 51.13**). Larvae maintained for many generations at a low density foraged over shorter distances than those kept at high density. Furthermore, genetic tests indicated that the *for^s* allele had increased in frequency in the low-density populations, whereas the *for^R* allele had increased in frequency in the high-density group. These changes make sense. At low population density, short-distance foraging yields sufficient food, while long-distance foraging would result in unnecessary energy expenditure. Under crowded conditions, however, long-distance foraging could enable larvae to move beyond areas of food depletion. In summary, there was an observable and interpretable evolutionary change in behavior in the laboratory populations.

Optimal Foraging Model

To study the proximate and ultimate causation of diverse foraging strategies, biologists sometimes apply a type of cost-benefit analysis used in economics. This idea proposes that foraging behavior is a compromise between the benefits of nutrition and the costs of obtaining food. These costs might include the energy expenditure of foraging as well as the risk of being eaten while foraging. According to this **optimal foraging model**, natural selection should favor a foraging behavior that minimizes the costs of foraging and maximizes the benefits.

CONCEPT 51.3

Selection for individual survival and reproductive success can explain most behaviors

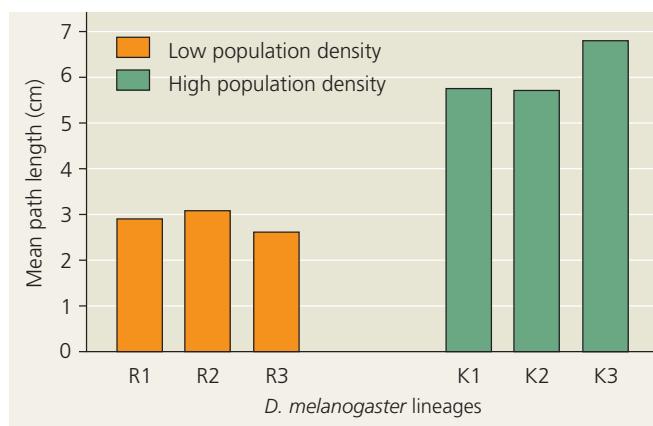
We turn now from the physiology of behavior (how animals behave) to the benefits to a species from a particular behavior (why animals behave the way they do). In particular, we will address Tinbergen's third question—how behavior enhances survival and reproductive success in a population. We'll begin with an activity essential for both types of success: gathering food.

Foraging Behavior

Because adequate nutrition is essential to an animal's survival and reproductive success, we should expect natural selection to refine behaviors that enhance the efficiency of feeding. Food-obtaining behavior, or **foraging**, includes not only eating but also any activities an animal uses to search for, recognize, and capture food items.

Evolution of Foraging Behavior

The fruit fly (*Drosophila melanogaster*) has provided an opportunity to examine how foraging behavior might have evolved. Variation in a gene called *forager* (*for*) dictates the food-search behavior of fruit fly larvae. On average, larvae carrying the *for^R* ("Rover") allele travel nearly twice as far while feeding as do larvae with the *for^s* ("sitter") allele. Experiments have shown



▲ **Figure 51.13 Evolution of foraging behavior by laboratory populations of *Drosophila melanogaster*.** After 74 generations of living at low population density, *D. melanogaster* larvae (populations R1–R3) followed foraging paths significantly shorter than those of *D. melanogaster* larvae that had lived at high density (populations K1–K3).

As an example of how the optimal foraging model can be applied, let's consider the feeding behavior of the Northwestern crow (*Corvus caurinus*). On islands off British Columbia, these crows search rocky tide pools for sea snails called whelks. After spotting a whelk, the crow picks the whelk up in its beak, flies upward, and drops the whelk onto the rocks. If the drop is successful, the shell breaks and the crow can dine on the whelk's soft parts. If not, the crow flies up and drops the whelk again and again until the shell breaks. What determines how high the crow flies? The higher the crow flies, the greater the force with which the whelk strikes the rocks, increasing the chance the shell will break. Flying higher, however, means consuming more energy.

If energetic considerations dominated selection for the crow's foraging behavior, the average drop height might reflect a trade-off between the cost of flying higher and the benefit of more frequent success. To test this idea, researchers dropped whelks from different heights and noted the number of drops required to break a shell. For each height, they calculated the average number of drops and the average *total flight height*, the drop height times the average number of drops (Figure 51.14). A drop height of about 5 m turned out to be optimal, breaking the shells with the lowest total flight height—in other words, with the least work. The actual average flight height for crows in their whelk-eating behavior is 5.23 m, very close to the prediction based on an optimal trade-off between energy gained (food) and energy expended.

The close agreement between the predicted and actual flight heights suggests that the optimal foraging model reflects the selective forces shaping the evolution of this behavior. However, other models could explain the findings equally well. For example, the average flight height could minimize the average *time* necessary to break open a whelk. Further experiments are needed to evaluate these possibilities.

Balancing Risk and Reward

One of the most significant potential costs to a forager is risk of predation. Maximizing energy gain and minimizing energy costs are of little benefit if the behavior makes the forager a likely meal for a predator. It seems logical, therefore, that predation risk would influence foraging behavior. Such appears to be the case for the mule deer (*Odocoileus hemionus*), which lives in the mountains of western North America. Researchers found that the food available for mule deer was fairly uniform across the potential foraging areas, although somewhat lower in open, nonforested areas. In contrast, the risk of predation differed greatly; mountain lions (*Puma concolor*), the major predator, killed large numbers of mule deer at forest edges and only a small number in open areas and forest interiors.

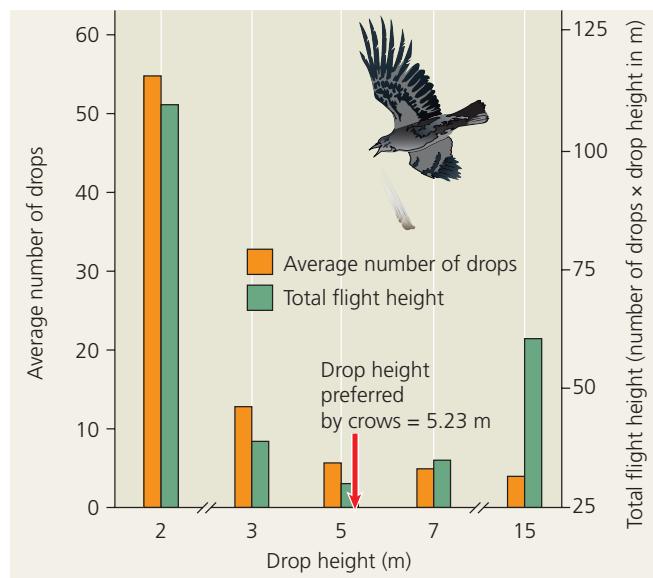
How does mule deer foraging behavior reflect the differences in predation risk in particular areas? Mule deer feed predominantly in open areas. Thus, it appears that mule deer foraging behavior reflects the large variation in predation risk and not the smaller variation in food availability. This result underscores the point that behavior typically reflects a compromise between competing selective pressures.

Mating Behavior and Mate Choice

Just as foraging is crucial for individual survival, mating behavior and mate choice play a major role in determining reproductive success. These behaviors include seeking or attracting mates, choosing among potential mates, competing for mates, and caring for offspring. Although we tend to think of mating simply as the union of a male and female, the mating relationship between males and females varies greatly from species to species, defining a number of distinct mating systems.

Mating Systems and Sexual Dimorphism

Mating systems vary with regard to both the length and number of relationships. In many animal species, mating is **promiscuous**, with no strong pair-bonds. In species in which the mates remain together for a longer period, the relationship may be **monogamous** (one male mating with one female) or **polygamous** (an individual of one sex mating with several of the other). Polygamous relationships most often involve a single male and many females, a system called *polygyny*, though some species exhibit *polyandry*, in which a single female mates with several males.



▲ Figure 51.14 Energy costs and benefits in foraging behavior.

Experimental results indicate that dropping shells from a height of 5 m results in breakage with the least amount of work. The actual drop height preferred by crows corresponds almost exactly to the height that minimizes total flight height.

The extent to which males and females differ in appearance, a characteristic known as *sexual dimorphism*, typically varies with the type of mating system (**Figure 51.15**). Among monogamous species, males and females are often so much alike morphologically that they may be difficult or impossible to distinguish based on external characteristics. In contrast, polygynous species are generally dimorphic, with males being showier and often larger than females. Polyandrous species are also dimorphic, but the females are generally more ornamented and larger than the males.

Mating Systems and Parental Care

The needs of the young are an important factor constraining the evolution of mating systems. Most newly hatched birds, for instance, cannot care for themselves. Rather, they require a large, continuous food supply, a need that is difficult for a single parent to meet. In such cases, a male that stays with and helps a single mate may ultimately have more viable offspring than it would by going off to seek additional mates. This may explain why most birds are monogamous. In contrast, for birds with young that can feed and care for themselves almost immediately after hatching, the males derive less benefit from staying with their partner. Males of these species, such as pheasants and quail, can maximize their reproductive success by seeking other mates, and polygyny is relatively common in such birds. In the case of mammals, the lactating female is often the only food source for the young; males usually play no role in raising the young. In mammalian species where males protect the females and young, such as lions, a male or small group of males typically takes care of a harem of many females at the same time.

Another factor influencing mating behavior and parental care is *certainty of paternity*. Young born to or eggs laid by a female definitely contain that female's genes. However, even within a normally monogamous relationship, a male other than the female's usual mate may have fathered that female's offspring. The certainty of paternity is relatively low in most species with internal fertilization because the acts of mating and birth (or mating and egg laying) are separated over time. This could explain why exclusively male parental care is rare in bird and mammal species. However, the males of many species with internal fertilization engage in behaviors that appear to increase their certainty of paternity. These behaviors include guarding females, removing any sperm from the female reproductive tract before copulation, and introducing large quantities of sperm that displace the sperm of other males.

Certainty of paternity is high when egg laying and mating occur together, as in external fertilization. This may explain why parental care in aquatic invertebrates, fishes, and amphibians, when it occurs at all, is at least as likely to be by males as

▼ **Figure 51.15 Relationship between mating system and male and female forms.**



(a) In monogamous species, such as these western gulls, males and females are difficult to distinguish using external characteristics only.



(b) Among polygynous species, such as elk, the male (right) is often highly ornamented.



(c) In polyandrous species, such as these Wilson's phalaropes, females (top) are generally more ornamented than males.



▲ **Figure 51.16 Paternal care by a male jawfish.** The male jawfish, which lives in tropical marine environments, holds the eggs it has fertilized in its mouth, keeping them aerated and protecting them from egg predators until the young hatch.

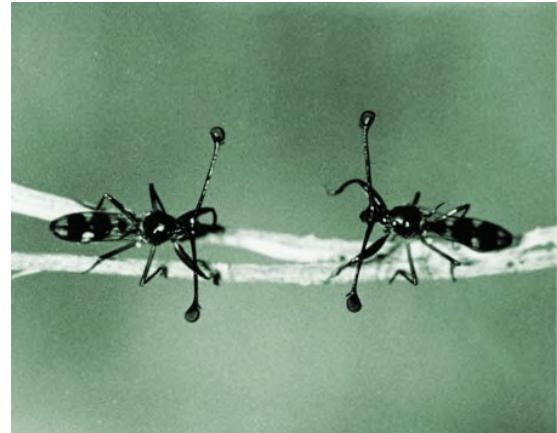
by females (**Figure 51.16**; see also Figure 46.7). Among fishes and amphibians, parental care occurs in only 7% of species with internal fertilization but in 69% of species with external fertilization.

It is important to point out that certainty of paternity does not mean that animals are aware of those factors when they behave a certain way. Parental behavior correlated with certainty of paternity exists because it has been reinforced over generations by natural selection. Nevertheless, the relationship between certainty of paternity and male parental care remains an area of active research, enlivened by controversy.

Sexual Selection and Mate Choice

As you read in Chapter 23, the degree of sexual dimorphism within a species results from sexual selection, a form of natural selection in which differences in reproductive success among individuals are a consequence of differences in mating success. Recall from that chapter that sexual selection can take the form of *intersexual selection*, in which members of one sex choose mates on the basis of characteristics of the other sex, such as courtship songs, or *intrasexual selection*, which involves competition between members of one sex for mates. Let's look at some experimental evidence for sexual selection.

Mate Choice by Females Mate preferences of females may play a central role in the evolution of male behavior and anatomy through intersexual selection. As an example, let's consider the courtship behavior of stalk-eyed flies. The eyes of these insects are at the tips of stalks, which are longer in males than in females (**Figure 51.17**). During courtship, a male approaches the female headfirst. Researchers have shown that females are more likely to mate with males that have relatively long eyestalks. Why would females favor this seemingly arbitrary trait? As discussed in Chapter 23, ornaments such as long



▲ **Figure 51.17 Male stalk-eyed flies.** Male eye span plays a role in mate selection by females and, as shown here, in ritualized contests between males. In such contests, two males face off, with the male whose eye span is smaller very often retreating without any combat taking place.

eyestalks in these flies and bright coloration in male birds correlate in general with the male's health and vitality. A female whose mate choice is a healthy male is likely to produce more offspring that survive to reproduce.

Mate choice can also be influenced by imprinting, as revealed by experiments carried out with zebra finches. Both male and female zebra finches normally lack any feather crest on their head (**Figure 51.18**). To explore whether parental appearance affects mate preference in offspring independent of any genetic influence, researchers provided zebra finches with artificial ornamentation. A 2.5-cm-long red feather was taped to the forehead feathers of either or both zebra finch parents when their chicks were 8 days old, approximately 2 days before they opened their eyes. A control group of zebra finches were raised by unadorned parents. When the chicks matured,



▲ **Figure 51.18 Appearance of zebra finches in nature.** The male zebra finch (left) is more patterned and colorful than the female zebra finch.

they were presented with prospective mates that were either artificially ornamented with a red feather or non-ornamented (**Figure 51.19**). Males showed no preference. Females also showed no preference if they were raised by a male parent that was not ornamented. However, females raised by an ornamented male parent preferred ornamented males as their own mates. Thus, female finches apparently take cues from their fathers in choosing mates.

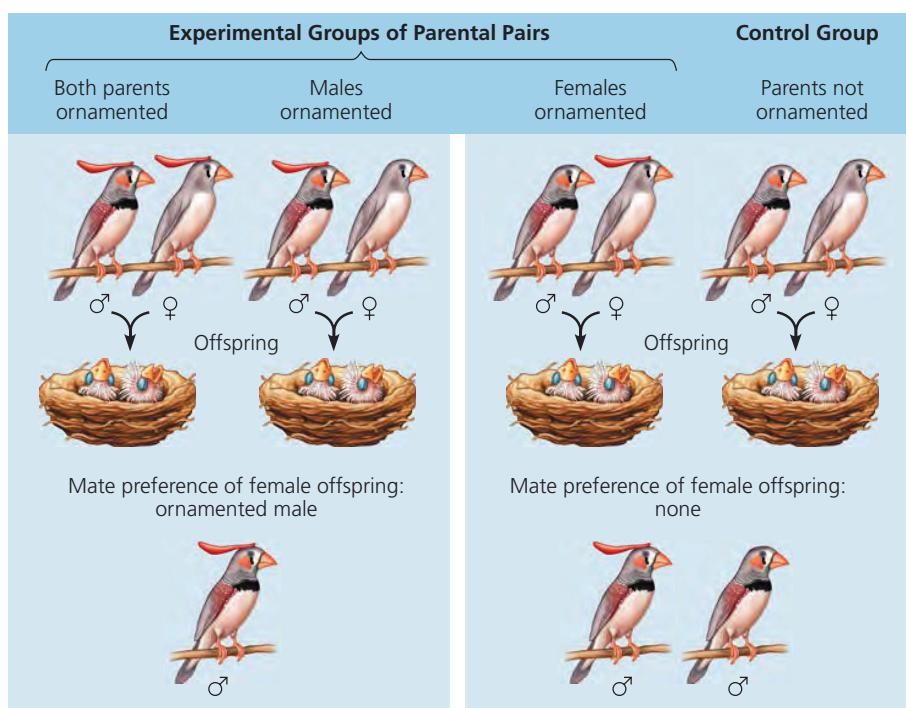
Mate-choice copying, a behavior in which individuals in a population copy the mate choice of others, has been studied in the guppy *Poecilia reticulata*. When a female guppy chooses between males with no other females present, the female almost always chooses the male with more orange coloration. To explore if the behavior of other females could influence this preference, an experiment was set up using both living females and artificial model females (**Figure 51.20**). If a female guppy observed the model “courting” a male with less extensive orange markings, she often copied the

preference of the model female. That is, the female chose the male that had been presented in association with a model female rather than a more orange alternative. The exceptions were also informative. Mate-choice behavior typically did not change when the difference in coloration was particularly large. Mate-choice copying can thus mask genetically controlled female preference below a certain threshold of difference, in this case for male color.

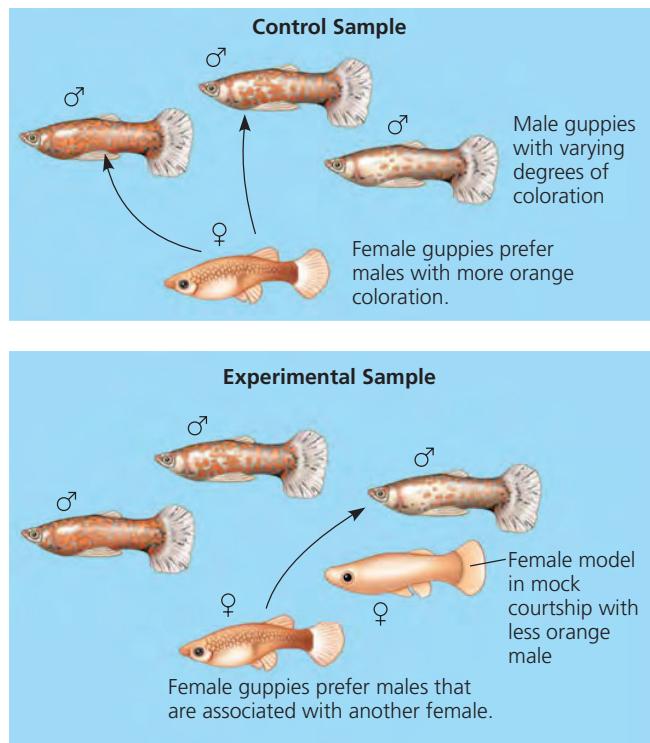
Mate-choice copying, a form of social learning, has also been observed in several other fish and bird species. What is the selective pressure for such a mechanism? One possibility is that a female that mates with males that are attractive to other females increases the probability that her male offspring will also be attractive and have high reproductive success.

Male Competition for Mates The previous examples show how female choice can select for one best type of male in a given situation, resulting in low variation among males. Male competition for mates also can reduce variation among males.

► Figure 51.20 Mate choice copying by female guppies (*Poecilia reticulata*). Female guppies generally choose the males with more orange coloration. But when males were matched for orange or differed in the amount of orange by 12% or 24%, the females in the experimental group chose the *less* orange male that was presented with a model female. Females ignored the apparent choice of the model female only where the alternative male had 40% more orange coloration.



▲ Figure 51.19 Sexual selection influenced by imprinting. Experiments demonstrated that female zebra finch chicks that had imprinted on artificially ornamented fathers preferred ornamented males as adult mates. For all experimental groups, male offspring showed no preference for either ornamented or non-ornamented female mates.



Such competition may involve *agonistic behavior*, an often-ritualized contest that determines which competitor gains access to a resource, such as food or mates (Figure 51.21). The outcomes of such contests are often determined by strength or size, but the consequences may nevertheless be psychological rather than physical (see Figure 51.17).

Despite the potential for male competition to select for reduced variation, behavioral and morphological variation in males is extremely high in some vertebrate species, including species of fish and deer, as well as in a wide variety of invertebrates. In some species, sexual selection has led to the evolution of alternative male mating behavior and morphology. How do scientists analyze situations where more than one mating behavior can result in successful reproduction? One approach relies on the rules that govern games.

Applying Game Theory

Often, the fitness of a particular behavioral phenotype is influenced by other behavioral phenotypes in the population. In studying such situations, behavioral ecologists use a range of tools, including game theory. Developed by American mathematician John Nash and others to model human economic behavior, **game theory** evaluates alternative strategies in situations where the outcome depends on the strategies of all the individuals involved.



▲ **Figure 51.21 Agonistic interaction.** Male eastern grey kangaroos (*Macropus giganteus*) often “box” in contests that determine which male is most likely to mate with an available female. Typically, one male snorts loudly before striking the other around the head and throat with his forelimbs. Further snorting and cuffing, as well as grappling, often follow. If the male under attack does not retreat, the fight may escalate, with each male balancing on his tail while attempting to kick his rival with the sharp toenails of a hind leg.



▲ **Figure 51.22 Male polymorphism in the side-blotched lizard (*Uta stansburiana*).** An orange-throat male, left; a blue-throat male, center; a yellow-throat male, right.

As an example of applying game theory to mating behavior, let's consider the side-blotched lizard (*Uta stansburiana*) of California. Males can have orange, blue, or yellow throats (Figure 51.22). Each throat color is associated with a different pattern of behavior. Orange-throat males are the most aggressive and defend large territories that contain many females. Blue-throat males are also territorial but defend smaller territories and fewer females. Yellow-throats are nonterritorial males that mimic females and use “sneaky” tactics to gain the chance to mate.

Evidence indicates that the mating success of each male lizard type is influenced by the relative abundance of the other types, an example of frequency-dependent selection. In one study population, the most frequent throat coloration changed over a period of several years from blue to orange to yellow and back to blue.

By comparing the competition between side-blotched lizard males to the children’s game of rock-paper-scissors, scientists devised an explanation for the cycles of variation in the lizard population. In the game, paper defeats rock, rock defeats scissors, and scissors defeats paper. Each hand symbol thus wins one matchup but loses the other. Similarly, each type of male lizard has an advantage over one of the other two types. When blue-throats are abundant, they can defend the few females in their territories from the advances of the sneaky yellow-throat males. However, blue-throats cannot defend their territories against the hyperaggressive orange-throats. Once the orange-throats become the most abundant, the larger number of females in each territory provides the opportunity for the yellow-throats to have greater mating success. The yellow-throats become more frequent, but then give way to the blue-throats, whose tactic of guarding small territories once again allows them the most success.

Game theory provides a way to think about complex evolutionary problems in which relative performance (reproductive success relative to other phenotypes), not absolute performance, is the key to understanding the evolution of behavior. This makes game theory an important tool because the relative performance of one phenotype compared with others is a measure of Darwinian fitness.

CONCEPT CHECK 51.3

- Why does the mode of fertilization correlate with the presence or absence of male parental care?
- MAKE CONNECTIONS** Balancing selection can maintain variation at a locus (see Concept 23.4, pp. 483–484). Based on the foraging experiments described in this chapter, devise a simple hypothesis to explain the presence of both *for^R* and *for^S* alleles in natural fly populations.
- WHAT IF?** Suppose an infection in a side-blotted lizard population killed many more males than females. What would be the immediate effect on male competition for reproductive success?

For suggested answers, see Appendix A.

CONCEPT 51.4

Inclusive fitness can account for the evolution of behavior, including altruism

EVOLUTION We'll now explore issues related to the focus of Tinbergen's fourth question—the evolutionary history of behaviors. We will first look at examples that reveal the genetic underpinnings of behavior. Next, we will examine the genetic variation underlying the evolution of particular behaviors. Finally, we will see how expanding the definition of fitness beyond individual survival can help explain “selfless” behavior.

Genetic Basis of Behavior

In exploring the behavioral basis of behavior, we'll begin with the courtship behavior of the male fruit fly, diagrammed in Figure 51.4. During courtship, the male fly carries out a complex series of actions in response to multiple sensory stimuli. Genetic studies have revealed that a single gene called *fru* controls this entire courtship ritual. If the *fru* gene is mutated to an inactive form, males do not court or mate with females. (The name *fru* is short for *fruitless*, reflecting the absence of offspring from the mutant males.) Normal male and female flies express distinct forms of the *fru* gene. When females are genetically manipulated to express the male form of *fru*, they court other females, performing the role normally played by the male. How can a single gene control so many behaviors and actions? Experiments carried out cooperatively in several laboratories demonstrated that *fru* is a master regulatory gene that directs the expression and activity of many genes with narrower functions. Together, genes that are controlled by the *fru* gene bring about sex-specific development of the fly nervous system. In effect, *fru* programs the fly for male courtship behavior by overseeing a male-specific wiring of the central nervous system.

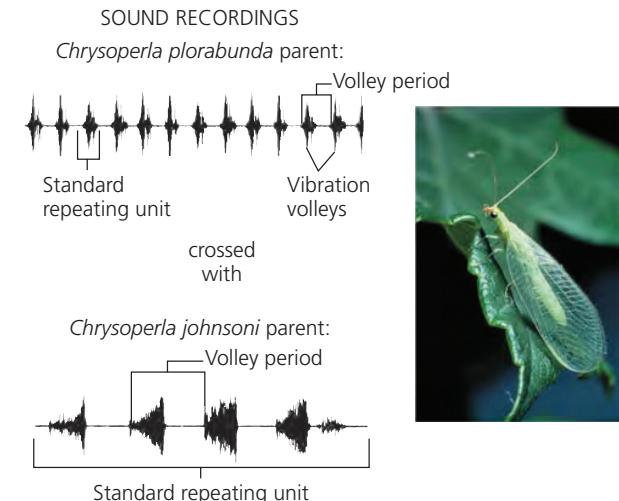
Researchers have also used insect courtship to explore genetic variation underlying differences in behavior. One well-studied example involves the courtship song of the green lacewing (**Figure 51.23**). Found throughout central to northern Eurasia and North America, these insects include at least

▼ Figure 51.23

INQUIRY

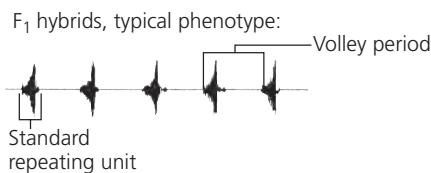
Are the songs of green lacewing species under the control of multiple genes?

EXPERIMENT Charles Henry, Lucía Martínez, and Kent Holsinger crossed males and females of *Chrysoperla plorabunda* and *Chrysoperla johnsoni*, two morphologically identical species of lacewings that sing different courtship songs.



The researchers compared the songs of the male and female parents with those of the hybrid offspring that had been raised in isolation from other lacewings.

RESULTS The F₁ hybrid offspring sang a song in which the length of the standard repeating unit was similar to that sung by the *Chrysoperla plorabunda* parent, but the volley period—the interval between vibration volleys—was more similar to that of the *Chrysoperla johnsoni* parent.



CONCLUSION Since the song of the hybrid offspring has features of the songs of both parents, the results indicate that the songs sung by *Chrysoperla plorabunda* and *Chrysoperla johnsoni* are under the control of more than one gene.

SOURCE C. S. Henry et al., The inheritance of mating songs in two cryptic, sibling lacewing species, *Genetica* 116:269–289 (2002).

WHAT IF? Suppose the hybrids generated in this experiment were fertile. Would the appearance of the hybrid song shown in the figure be likely to lead to the formation of a new species? Explain your answer.

15 species, identical in appearance but having different courtship songs. When researchers at the University of Connecticut reared lacewings in isolation in the laboratory, they found that the lacewings performed the song specific to their species. Thus, they concluded, the courtship song must be genetically controlled. They then crossed different green lacewing species in the laboratory and analyzed the songs produced by the hybrid offspring. These experiments demonstrated that a different gene governs each component or property of the courtship song. Furthermore, the distinct courtship song of each green lacewing species reflects genetic differences at multiple, independent loci.

Whereas variation in multiple genes can bring about distinct behaviors, as is true for the lacewing courtship song, variation in a single locus is sometimes sufficient to bring about dramatic differences in behavior. One striking example is the behavior of two closely related species of voles, which are small, mouse-like rodents. Male meadow voles (*Microtus pennsylvanicus*) are solitary and do not form lasting relationships with mates. Following mating, they pay little attention to their pups. In contrast, male prairie voles (*Microtus ochrogaster*) form a pair-bond with a single female after they mate (Figure 51.24). Male prairie voles hover over their young pups, licking them and carrying them, while acting aggressively toward intruders.

Research suggested that a neurotransmitter released during mating is critical for the partnering and parental behavior of male voles. Known as ADH or vasopressin (see Chapter 44), this peptide binds to a specific receptor in the central nervous system. When male prairie voles are treated with a drug that



▲ **Figure 51.24**
A pair of prairie voles (*Microtus ochrogaster*) huddling. Male North American prairie voles associate closely with their mates, as shown here, and contribute substantially to the care of young.

inhibits the brain receptor for vasopressin, they fail to form pair-bonds after mating. Scientists have also observed that the vasopressin receptor gene of prairie voles is highly expressed in the brain, whereas that of meadow voles is not.

To test whether the amount of the vasopressin receptor present in the brain regulates the postmating behavior of voles, researchers inserted the vasopressin receptor gene from prairie voles into male meadow voles. The meadow voles carrying this gene not only developed brains with higher levels of the vasopressin receptor but also showed many of the same mating behaviors as male prairie voles, such as pair-bonding. Thus, although many genes influence pair-bond formation and parenting among voles, the level of the vasopressin receptor alone determines which behavioral pattern develops.

Genetic Variation and the Evolution of Behavior

Behavioral differences between closely related species, such as meadow and prairie voles, are common. Significant differences in behavior can also be found *within* a species but are often less obvious. When behavioral variation between populations of a species corresponds to variation in environmental conditions, it may be evidence of past evolution.

Case Study: Variation in Prey Selection

An example of genetically based behavioral variation within a species involves prey selection by the western garter snake (*Thamnophis elegans*). The natural diet of this species differs widely across its range in California. Coastal populations feed predominantly on banana slugs (*Ariolimax californicus*) (Figure 51.25). Inland populations feed on frogs, leeches, and fish, but not on banana slugs. In fact, banana slugs are rare or absent in the inland habitats.



▲ **Figure 51.25** **Western garter snake from a coastal habitat eating a banana slug.** Experiments indicate that the preference of these snakes for banana slugs may be influenced mainly by genetics rather than by environment.

When researchers offered banana slugs to snakes from each wild population, most coastal snakes readily ate them, whereas inland snakes tended to refuse. To what extent does genetic variation contribute to a snake's fondness for banana slugs? To answer this question, researchers collected pregnant snakes from each wild population and housed them in separate cages in the laboratory. While still very young, the offspring were offered a small piece of banana slug on each of ten days. More than 60% of the young snakes from coastal mothers ate banana slugs on eight or more of the ten days. In contrast, fewer than 20% of the young snakes from inland mothers ate a piece of banana slug even once. Perhaps not surprisingly, banana slugs thus appear to be a genetically acquired taste.

How did a genetically determined difference in feeding preference come to match the snakes' habitats so well? It turns out that the coastal and inland populations also vary with respect to their ability to recognize and respond to odor molecules produced by banana slugs. Researchers hypothesize that when inland snakes colonized coastal habitats more than 10,000 years ago, some of them could recognize banana slugs by scent. Because these snakes took advantage of this food source, they had higher fitness than snakes in the population that ignored the slugs. Over hundreds or thousands of generations, the capacity to recognize the slugs as prey increased in frequency in the coastal population. The marked variation in behavior observed today between the coastal and inland populations may be evidence of this past evolutionary change.

Case Study: Variation in Migratory Patterns

Another species suited to the study of behavioral variation is the blackcap (*Sylvia atricapilla*), a small migratory warbler. Blackcaps that breed in Germany generally migrate southwest to Spain and then south to Africa for the winter. In the 1950s, a few blackcaps began to spend their winters in Britain, and over time the population of blackcaps wintering in Britain grew to many thousands. Leg bands showed that some of these birds had migrated westward from central Germany. Why were there now two patterns of migration from Germany? To answer this question, researchers at the Max Planck Research Center in Radolfzell, Germany, devised a strategy to study migratory orientation in the laboratory (**Figure 51.26**). The results demonstrated that the two patterns of migration reflect genetic differences between the two populations.

The study of western European blackcaps indicated that the change in their migratory behavior occurred both recently and rapidly. Before the year 1950, there were no known westward-migrating blackcaps in Germany. By the 1990s, westward migrants made up 7–11% of the blackcap populations of Germany. Once westward migration began, it persisted and increased in frequency, perhaps due to the widespread use of winter bird feeders in Britain, as well as shorter migration distances.

▼ Figure 51.26

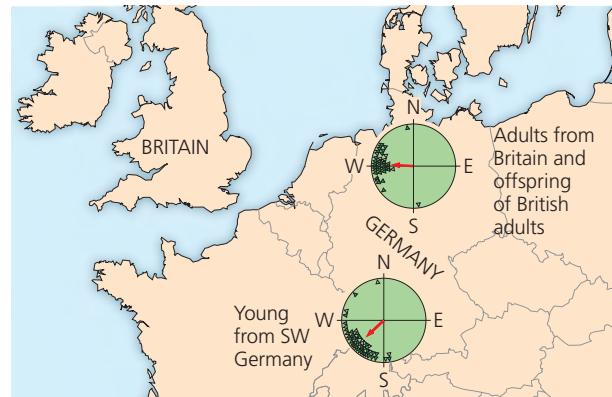
INQUIRY

Are differences in migratory orientation within a species genetically determined?

EXPERIMENT Peter Berthold and colleagues in southern Germany raised two sets of young birds for their study. One group consisted of the offspring of blackcaps captured while wintering in Britain and then bred in Germany in an outdoor cage. The other group consisted of young birds collected from nests near the laboratory and then raised in cages. In the autumn, Berthold's team placed the blackcaps captured in Britain and the young birds raised in cages in large, glass-covered funnel cages lined with carbon-coated paper for 1.5–2 hours. When the funnels were placed outside at night, the birds moved around, making marks on the paper that indicated the direction in which they were trying to "migrate."



RESULTS The wintering adult birds captured in Britain and their laboratory-raised offspring both attempted to migrate to the west. In contrast, the young birds collected from nests in southern Germany attempted to migrate to the southwest.



CONCLUSION The young of the British blackcaps and the young birds from Germany (the control group) were raised under similar conditions but showed very different migratory orientations, indicating that migratory orientation has a genetic basis.

SOURCE P. Berthold et al., Rapid microevolution of migratory behavior in a wild bird species, *Nature* 360:668–690 (1992).

WHAT IF? Suppose the birds had not shown a difference in orientation in these experiments. Could you conclude that the behavior was not genetically based? Explain.

Altruism

Reconstructing the evolutionary basis of a behavior requires an understanding of the behavior's genetic basis and of the selective advantage conferred by the behavior. Typically, we assume that behaviors are selfish; that is, they benefit the individual at the expense of others, especially competitors. For example, superior foraging ability by one individual may leave less food for others. The problem comes, however, with "unselfish" behaviors. How can such behaviors arise through natural selection? To answer this question, let's look more closely at some examples of unselfish behavior and then consider how such behaviors might arise.

In discussing selflessness, we will use the term **altruism** to describe a behavior that reduces an animal's individual fitness but increases the fitness of other individuals in the population. Consider the Belding's ground squirrel, which lives in some mountainous regions of the western United States and is vulnerable to predators such as coyotes and hawks. A squirrel that sees a predator approach often gives a high-pitched alarm call that alerts unaware individuals to retreat to their burrows. Note that for the squirrel that warns others, the conspicuous alarm behavior increases the risk of being killed because it brings attention to the caller's location.

Another example of altruistic behavior occurs in honeybee societies, in which the workers are sterile. The workers themselves never reproduce, but they labor on behalf of a single fertile queen. Furthermore, the workers sting intruders, a behavior that helps defend the hive but results in the death of those workers.

Altruism is also observed in naked mole rats (*Heterocephalus glaber*), highly social rodents that live in underground chambers and tunnels in southern and northeastern Africa. The naked mole rat, which is almost hairless and nearly blind, lives in colonies of 75 to 250 or more individuals (Figure 51.27). Each colony has only one reproducing female, the queen, who mates with one to three males, called kings. The rest of the colony consists of nonreproductive females and males who

forage for underground roots and tubers and care for the queen, the kings, and new offspring. The nonreproductive individuals may sacrifice their own lives in trying to protect the queen or kings from snakes or other predators that invade the colony.

Inclusive Fitness

How can a Belding's ground squirrel, a worker honeybee, or a naked mole rat enhance its fitness by aiding members of the population that may be its closest competitors? How can altruistic behavior be maintained by evolution if it does not enhance the survival and reproductive success of the self-sacrificing individuals?

The selection for altruistic behavior is most readily apparent in the case of parents sacrificing for their offspring. When parents sacrifice their own well-being to produce and aid offspring, this actually increases the fitness of the parents because it maximizes their genetic representation in the population. However, individuals sometimes help others who are not their offspring.

Biologist William Hamilton proposed that an animal could increase its genetic representation in the next generation by "altruistically" helping close relatives other than its own offspring. Like parents and offspring, full siblings have half their genes in common. Therefore, selection might also favor helping siblings or helping one's parents produce more siblings. This idea led to Hamilton's idea of **inclusive fitness**, the total effect an individual has on proliferating its genes by producing its own offspring *and* by providing aid that enables other close relatives, who share many of those genes, to produce offspring.

Hamilton's Rule and Kin Selection

According to Hamilton, the three key variables in an act of altruism are the benefit to the recipient, the cost to the altruist, and the coefficient of relatedness. The benefit, B , is the average number of *extra* offspring that the beneficiary of an altruistic act produces. The cost, C , is how many *fewer* offspring the altruist produces. The **coefficient of relatedness**, r , equals the fraction of genes that, on average, are shared. Natural selection favors altruism when the benefit to the recipient multiplied by the coefficient of relatedness exceeds the cost to the altruist—in other words, when $rB > C$. This statement is called **Hamilton's rule**.

To better understand Hamilton's rule, let's apply it to a human population in which the average individual has two children. We'll imagine that a young man is close to drowning in heavy surf, and his sister risks her life to swim out and pull her sibling to safety. If the young man had drowned, his reproductive output would have been zero; but now, if we use the average, he can father two children. The benefit to the brother is thus two offspring ($B = 2$). What about the risk taken by his sister? Let's say that the sister has a 25% chance of drowning in attempting to rescue her brother. We can

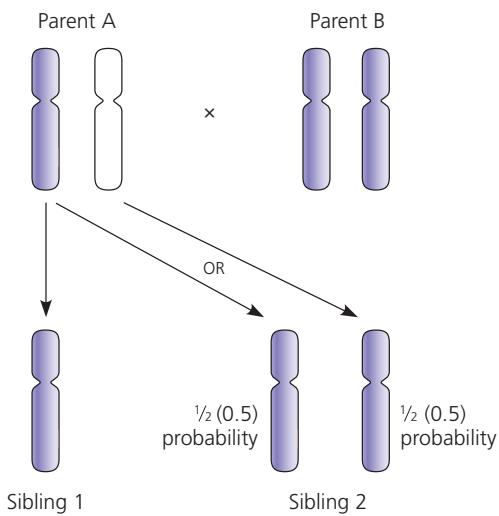


▲ **Figure 51.27** Naked mole rats, a species of colonial mammal that exhibits altruistic behavior. Pictured here is a queen nursing offspring while surrounded by other members of the colony.

then calculate the cost of the altruistic act to the sister as 0.25 times 2, the number of offspring she would be expected to have if she had stayed on shore ($C = 0.25 \times 2 = 0.5$). Finally, we note that a brother and sister share half their genes on average ($r = 0.5$). One way to see this is in terms of the segregation of homologous chromosomes that occurs during meiosis of gametes (Figure 51.28; see also Chapter 13).

We can now use our values of B , C , and r to evaluate whether natural selection would favor the altruistic act in our imaginary scenario. For the surf rescue, $rB = 0.5 \times 2 = 1$, whereas $C = 0.5$. Because rB is greater than C , Hamilton's rule is satisfied; thus, natural selection would favor this altruistic act of the sister attempting to save her brother. Averaging over many individuals and generations, any particular gene in a sister faced with this situation will be passed on to more offspring if she risks the rescue than if she does not. Furthermore, among genes propagated in this way may be some that contribute to altruistic behavior. The natural selection that favors altruistic behavior by enhancing reproductive success of relatives is called **kin selection**.

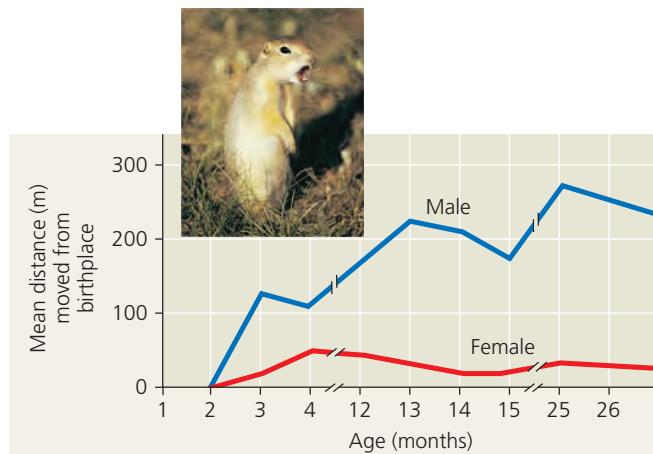
Kin selection weakens with hereditary distance. Siblings have an r of 0.5, but between an aunt and her niece, $r = 0.25$ ($\frac{1}{4}$), and between first cousins, $r = 0.125$ ($\frac{1}{8}$). Notice that as the degree of relatedness decreases, the rB term in the Hamilton inequality also decreases. Would natural selection favor rescuing a cousin? Not unless the surf were less treacherous. For the original conditions, $rB = 0.125 \times 2 = 0.25$, which is



▲ Figure 51.28 The coefficient of relatedness between siblings.

The red band indicates a particular allele (version of a gene) present on one chromosome, but not its homolog, in parent A. Sibling 1 has inherited the allele from parent A. There is a probability of $\frac{1}{2}$ that sibling 2 will also inherit this allele from parent A. Any allele present on one chromosome of either parent will behave similarly. The coefficient of relatedness between the two siblings is thus $\frac{1}{2}$, or 0.5.

WHAT IF? The coefficient of relatedness of an individual to a full (nontwin) sibling or to either parent is the same, 0.5. Does this value also hold true in the cases of polyandry and polygyny?



▲ Figure 51.29 Kin selection and altruism in Belding's ground squirrels. This graph helps explain the male-female difference in altruistic behavior of ground squirrels. Once weaned (pups are nursed for about one month), females are more likely than males to live near close relatives. Alarm calls that warn these relatives increase the inclusive fitness of the female altruist.

only half the value of C (0.5). British geneticist J. B. S. Haldane appears to have anticipated these ideas when he jokingly stated that he would not lay down his life for one brother, but would do so for two brothers or eight cousins.

If kin selection explains altruism, then the examples of unselfish behavior we observe among diverse animal species should involve close relatives. This is apparently the case, but often in complex ways. Like most mammals, female Belding's ground squirrels settle close to their site of birth, whereas males settle at distant sites (Figure 51.29). Since nearly all alarm calls are given by females, they are most likely aiding close relatives. In the case of worker bees, who are all sterile, anything they do to help the entire hive benefits the only permanent member who is reproductively active—the queen, who is their mother.

In the case of naked mole rats, DNA analyses have shown that all the individuals in a colony are closely related. Genetically, the queen appears to be a sibling, daughter, or mother of the kings, and the nonreproductive mole rats are the queen's direct descendants or her siblings. Therefore, when a nonreproductive individual enhances a queen's or king's chances of reproducing, the altruist increases the chance that some genes identical to its own will be passed to the next generation.

Reciprocal Altruism

Some animals occasionally behave altruistically toward others who are not relatives. A baboon may help an unrelated companion in a fight, or a wolf may offer food to another wolf even though they share no kinship. Such behavior can be adaptive if the aided individual returns the favor in the future. This sort of exchange of aid, called **reciprocal altruism**, is commonly invoked to explain altruism that occurs between

unrelated humans. Reciprocal altruism is rare in other animals; it is limited largely to species (such as chimpanzees) with social groups stable enough that individuals have many chances to exchange aid. It is generally thought to occur when individuals are likely to meet again and when there would be negative consequences associated with not returning favors to individuals who had been helpful in the past, a pattern of behavior that behavioral ecologists refer to as “cheating.”

Since cheating may benefit the cheater substantially, how could reciprocal altruism evolve? Game theory provides a possible answer in the form of a behavioral strategy called *tit for tat*. In the tit-for-tat strategy, an individual treats another in the same way it was treated the last time they met. Individuals adopting this behavior are always altruistic, or cooperative, on the first encounter with another individual and will remain so as long as their altruism is reciprocated. When their cooperation is not reciprocated, however, individuals employing tit for tat will retaliate immediately but return to cooperative behavior as soon as the other individual becomes cooperative. The tit-for-tat strategy has been used to explain the few apparently reciprocal altruistic interactions observed in animals—ranging from blood sharing between nonrelated vampire bats to social grooming in primates.

Evolution and Human Culture

Human culture is related to evolutionary theory in the discipline of **sociobiology**. The main premise of sociobiology is that certain behavioral characteristics exist because they are expressions of genes that have been perpetuated by natural selection. In his seminal 1975 book *Sociobiology: The New Synthesis*, E. O. Wilson speculated about the evolutionary basis of certain kinds of social behavior. By including a few examples from human culture, he sparked a debate that remains heated today.

The spectrum of human social behaviors may be influenced by our genetic makeup, but this is very different from saying that genes are rigid determinants of behavior. This distinction

is at the core of the debate about evolutionary perspectives on human behavior. Skeptics fear that evolutionary interpretations of human behavior could be used to justify the status quo in human society, thus rationalizing current social injustices. Evolutionary biologists argue that this is a gross oversimplification and misunderstanding of what the data tell us about human biology. Evolutionary explanations of human behavior do not reduce us to robots stamped out of rigid genetic molds. Just as individuals vary extensively in anatomical features, we should expect inherent variations in behavior as well. Environment intervenes in the pathway from genotype to phenotype for physical traits and even more so for behavioral traits. And because of our capacity for learning and our versatility, human behavior is probably more plastic than that of any other animal. Over our recent evolutionary history, we have built up a diversity of structured societies with governments, laws, cultural values, and religions that define what is acceptable behavior and what is not, even when unacceptable behavior might enhance an individual's Darwinian fitness. Perhaps it is our social and cultural institutions that make us distinct and that provide those qualities in which there is the least continuum between humans and other animals.

CONCEPT CHECK 51.4

- Explain why geographic variation in garter snake prey choice might indicate that the behavior evolved by natural selection.
- WHAT IF?** If an animal were unable to distinguish close from distant relatives, would the concept of inclusive fitness still be applicable? Explain.
- WHAT IF?** Suppose you applied Hamilton's logic to a situation in which one individual is past reproductive age. Could there still be a selection for an altruistic act?

For suggested answers, see Appendix A.

51 CHAPTER REVIEW

SUMMARY OF KEY CONCEPTS

CONCEPT 51.1

Discrete sensory inputs can stimulate both simple and complex behaviors (pp. 1118–1122)

- **Behavior** is the sum of responses to external and internal stimuli and includes muscular as well as nonmuscular activity. Tinbergen developed a set of questions that highlight the complementary nature of two perspectives. Proximate, or “how,” questions focus

on the environmental stimuli, if any, that trigger a behavior, as well as the genetic, physiological, and anatomical mechanisms underlying a behavioral act. Ultimate, or “why,” questions address the evolutionary significance of a behavior.

- A **fixed action pattern** is a largely invariant behavior triggered by a simple cue known as a **sign stimulus**. Migratory movements involve navigation, which can be based on orientation relative to the sun, the stars, or Earth's magnetic field. Animal behavior is sometimes synchronized to the daily, or circadian, cycle of light and dark in the environment or to environmental cues that cycle over the seasons.

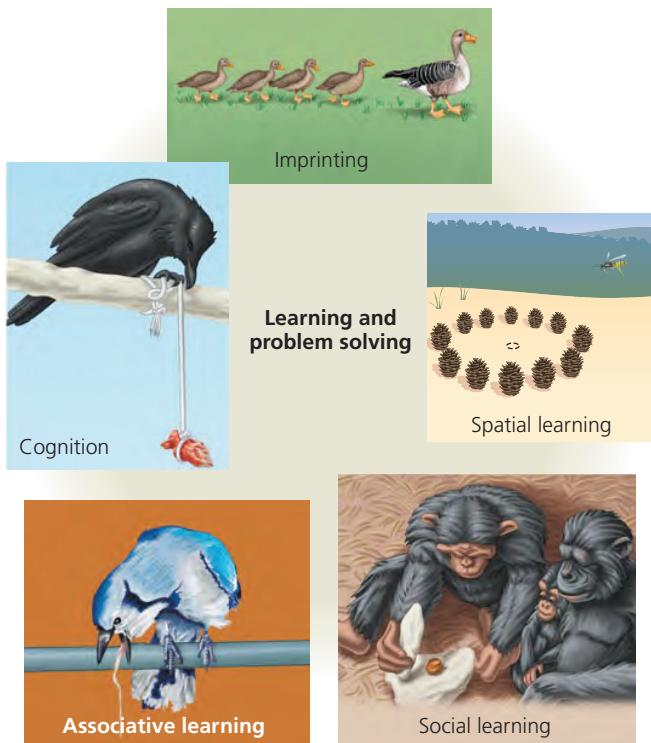
- The transmission and reception of signals constitute animal **communication**. Animals use visual, auditory, chemical (usually olfactory), and tactile signals, sometimes as part of a stimulus-response chain that governs a complex behavior. Chemical substances called pheromones transmit species-specific information through the environment in behaviors ranging from foraging to courtship.

? How is migration based on circannual rhythms poorly suited for adaptation to global climate change?

CONCEPT 51.2

Learning establishes specific links between experience and behavior (pp. 1123–1128)

- Cross-fostering studies can be used to measure the influence of social environment and experience on behavior.
- Learning**, the modification of behavior based on experience, can take many forms:



? How do imprinting in geese and song development in sparrows differ with regard to the resulting behavior?

CONCEPT 51.3

Selection for individual survival and reproductive success can explain most behaviors (pp. 1128–1134)

- An **optimal foraging model** is based on the idea that natural selection should favor foraging behavior that minimizes the costs of foraging and maximizes the benefits.
- Sexual dimorphism correlates with the type of mating relationship between males and females. These include **monogamous** and **polygamous** mating systems. Variation in mating system and variation in the mode of fertilization affect certainty of paternity, which in turn has a significant influence on mating behavior and parental care.

- Game theory provides a way of thinking about evolution in situations where the fitness of a particular behavioral phenotype is influenced by other behavioral phenotypes in the population.

? In some spider species, the female eats the male immediately after copulation. How might you explain this behavior from an evolutionary perspective?

CONCEPT 51.4

Inclusive fitness can account for the evolution of behavior, including altruism (pp. 1134–1139)

- Genetic studies in insects have revealed the existence of master regulatory genes that control complex behaviors. Within the underlying hierarchy, multiple genes influence specific behaviors, such as a courtship song. Research with two species of voles has revealed that variation in a single gene can determine differences in complex behaviors involved in both mating and parenting.
- When behavioral variation within a species corresponds to variation in environmental conditions, it may be evidence of past evolution. Field and laboratory studies have documented the genetic basis for a change in migratory behavior of certain birds and revealed behavioral differences in snakes that correlate with geographic variation in prey availability.
- On occasion, animals exhibit **altruism**. This behavior can be explained by the concept of **inclusive fitness**, the total effect an individual has on proliferating its genes by producing its own offspring *and* by providing aid that enables close relatives to produce offspring. **The coefficient of relatedness** and **Hamilton's rule** provide a way of measuring the strength of the selective forces favoring altruism against the potential cost of the “selfless” behavior. Kin selection favors altruistic behavior by enhancing the reproductive success of relatives. Altruistic behavior toward unrelated individuals can be adaptive if the aided individual returns the favor in the future, an exchange of aid called reciprocal altruism.

? Suppose you studied the genetics of the lacewing courtship song, but not the effects of courtship mutations in flies or of variation in the vasopressin receptor gene of voles. What insight about the genetic basis of behavior would you likely have missed?

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

- Which of the following is true of innate behaviors?
 - Their expression is only weakly influenced by genes.
 - They occur with or without environmental stimuli.
 - They are limited to invertebrate animals.
 - They are expressed in most individuals in a population.
 - They occur in invertebrates and some vertebrates but not mammals.
- According to Hamilton's rule,
 - natural selection does not favor altruistic behavior that causes the death of the altruist.
 - natural selection favors altruistic acts when the resulting benefit to the beneficiary, corrected for relatedness, exceeds the cost to the altruist.
 - natural selection is more likely to favor altruistic behavior that benefits an offspring than altruistic behavior that benefits a sibling.
 - the effects of kin selection are larger than the effects of direct natural selection on individuals.
 - altruism is always reciprocal.

3. Female spotted sandpipers aggressively court males and, after mating, leave the clutch of young for the male to incubate. This sequence may be repeated several times with different males until no available males remain, forcing the female to incubate her last clutch. Which of the following terms best describes this behavior?
- monogamy
 - polygyny
 - polyandry
 - promiscuity
 - certainty of paternity

LEVEL 2: APPLICATION/ANALYSIS

4. A region of the canary forebrain shrinks during the nonbreeding season and enlarges when breeding season begins. This change is probably associated with the annual
- addition of new syllables to a canary's song repertoire.
 - crystallization of subsong into adult songs.
 - sensitive period in which canary parents imprint on new offspring.
 - renewal of mating and nest-building behaviors.
 - elimination of the memorized template for songs sung the previous year.
5. Although many chimpanzees live in environments containing oil palm nuts, members of only a few populations use stones to crack open the nuts. The likely explanation is that
- the behavioral difference is caused by genetic differences between populations.
 - members of different populations have different nutritional requirements.
 - the cultural tradition of using stones to crack nuts has arisen in only some populations.
 - members of different populations differ in learning ability.
 - members of different populations differ in manual dexterity.
6. Which of the following is *not* required for a behavioral trait to evolve by natural selection?
- In each individual, the form of the behavior is determined entirely by genes.
 - The behavior varies among individuals.
 - An individual's reproductive success depends in part on how the behavior is performed.
 - Some component of the behavior is genetically inherited.
 - An individual's genotype influences its behavioral phenotype.

LEVEL 3: SYNTHESIS/EVALUATION

7. **DRAW IT** You are considering two optimal foraging models for the behavior of a mussel-feeding shorebird, the oystercatcher. In model A, the energetic reward increases solely with mussel size. In model B, you take into consideration that larger mussels are more difficult to open. Draw a graph of reward (energy benefit on a scale of 0–10) versus mussel length (scale of 0–70 mm) for each model. Assume that mussels under 10 mm provide no benefit and are ignored by the birds. Also assume that mussels start becoming difficult to open

when they reach 40 mm in length and impossible to open when 70 mm long. Considering the graphs you have drawn, how could you distinguish between the models by observation and measurement in the oystercatcher's habitat?

8. EVOLUTION CONNECTION

We often explain our behavior in terms of subjective feelings, motives, or reasons, but evolutionary explanations are based on reproductive fitness. What is the relationship between the two kinds of explanation? For instance, is a human explanation for behavior, such as "falling in love," incompatible with an evolutionary explanation?

9. SCIENTIFIC INQUIRY

Scientists studying scrub jays found that "helpers" often assist mated pairs of birds in raising their young. The helpers lack territories and mates of their own. Instead, they help the territory owners gather food for their offspring. Propose a hypothesis to explain what advantage there might be for the helpers to engage in this behavior instead of seeking their own territories and mates. How would you test your hypothesis? If it is correct, what results would you expect your tests to yield?

10. SCIENCE, TECHNOLOGY, AND SOCIETY

Researchers are very interested in studying identical twins separated at birth and raised apart. So far, the data reveal that such twins frequently have similar personalities, mannerisms, habits, and interests. What general question do you think researchers hope to answer by studying such twins? Why do identical twins make good subjects for this research? What are the potential pitfalls of this research? What abuses might occur if the studies are not evaluated critically?

11. WRITE ABOUT A THEME

The Genetic Basis of Life Learning is defined as a change in behavior based on experience. In a short essay (100–150 words), describe the role of heritable information in the acquisition of learning, using some examples from imprinting and associative learning.

For selected answers, see Appendix A.

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