The How and Why of Animal Activity

Unlike most animals, male fiddler crabs (genus *Uca*) are highly asymmetrical: One claw grows to giant proportions, up to half the mass of the entire body (Figure 51.1). The name *fiddler* comes from the crab’s behavior as it feeds on algae from the mudflats where it lives: The smaller of the front claws moves to and from the mouth in front of the enlarged claw. At other times 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. Examples include an animal using its 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 and finding a partner for sexual reproduction. Behavior also contributes to homeostasis, as when honeybees huddle to conserve heat (see Concept 40.3). In short, all of animal physiology contributes to behavior, and 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. Shifting our focus from an animal’s inner workings to its interactions with the outside world will set the stage for exploring ecology, the subject 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?
3. How does the behavior aid survival and reproduction?
4. 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. Thus any given behavior has both proximate and ultimate causes.

Studies on proximate causation by Tinbergen and two other early researchers—Karl von Frisch and Konrad Lorenz—earned the three scientists a Nobel Prize in 1973. We’ll consider those experiments in the early part of the chapter. The concept of ultimate causation is central to behavioral ecology, the study of the ecological and evolutionary basis for animal behavior. We’ll explore this vibrant area of modern biological research in the rest of the chapter.

**Fixed Action Patterns**

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.

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 within view of their tank. Inspired by this chance observation, he carried out experiments showing that the red color of an intruder’s underside is the proximate cause of 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
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Animal Behavior

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A homing pigeon prevents it from returning efficiently to its roost. Researchers concluded that pigeons sense their position relative to Earth’s magnetic field and can thereby navigate without solar or celestial cues.

The way in which animals detect Earth’s magnetic field remains a matter of investigation. It is known that the heads of migrating birds (and fishes) contain bits of magnetite, a magnetic iron mineral. There is also evidence that cells in the pigeon’s brainstem encode information about magnetic field direction, intensity, and polarity. The search continues for magnetoreceptors, which in migrating birds appear to be located in the eye, beak, and perhaps inner ear.

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 clock is responsible for a circadian rhythm, a daily cycle of rest and activity. The clock is normally synchronized with the light and dark cycles of the environment but can maintain rhythmic activity even 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 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 organism to another is called a **signal**. The transmission and reception of signals between animals constitute **communication**, which often has a role in the proximate causation of behavior.

**Forms of Animal Communication**

Let’s consider the courtship behavior of the fruit fly, *Drosophila melanogaster*, as an introduction to the four 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 (Figure 51.4). In the first step, a male detects a female in his field of vision and orients his body toward hers. To confirm she belongs to his species, he uses his olfactory system to detect chemicals she releases into the air. The male then approaches and touches the female with a foreleg. This touching, or tactile communication, alerts the female to the male’s presence. In the third stage of courtship, the male extends and vibrates one of his wings, producing a courtship song. This auditory communication informs the female whether the male is of the same species. Only if all of these forms of communication are successful will the female allow the male to attempt copulation.

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.

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 honeybees. 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.

A returning bee quickly becomes the center of attention for other bees, called followers (Figure 51.5a). If the food source is close to the hive (less than 50 m away), the returning bee moves in tight circles while moving its abdomen from side to side (Figure 51.5b). 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 (Figure 51.5c). 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 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.

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**Figure 51.4 Courtship behavior of the fruit fly.**

Fruit fly courtship involves a fixed set of behaviors that follow one another in a rigid order.

1. **Orienting**
   - Male visually recognizes female.

2. **Tapping**
   - Female releases chemicals detected by the male’s sense of smell.
   - Male taps female’s abdomen with a foreleg.

3. **“Singing”**
   - Male extends and vibrates wing, producing a courtship song.
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 cm$^2$ of skin from a fathead minnow contains sufficient alarm substance to induce a reaction in 58,000 L of water.

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—involves the nervous, muscular, and skeletal systems: Stimuli activate sensory systems, are processed in the central nervous system, and result in motor outputs that constitute behavior. Thus, we are ready to focus on Tinbergen’s second question—how experience influences behavior.

**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).
CONCEPT CHECK 51.1

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.

2. WHAT IF? Suppose you exposed various fish species from the minnows’ environment to the alarm substance from minnows. Thinking about natural selection, suggest why some species might respond like minnows, some might increase their activity, and some might show no change.

3. MAKE CONNECTIONS How is the lunar-linked rhythm of fiddler crab courtship similar in mechanism and function to the seasonal timing of plant flowering? (See Concept 39.3.)

For suggested answers, see Appendix A.

CONCEPT 51.2

Learning establishes specific links between experience and behavior

For some behaviors—such as a fixed action pattern, a courtship stimulus-response chain, and pheromone signaling—nearly all individuals in a population behave alike. Behavior that is developmentally fixed in this way is known as innate behavior. Other behaviors, however, vary with experience and thus differ between individuals.

Experience and Behavior

Tinbergen’s second question asks how an animal’s experiences during growth and development influence the response to stimuli. One informative approach to this question 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 a measure of how the social and physical environment influences behavior.

Certain mouse species have behaviors well suited for cross-fostering studies. Male California mice (Peromyscus californicus) 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 disorders, such as schizophrenia, anxiety disorders, and alcoholism, that alter human behavior.

Learning

One powerful way that an animal’s environment can influence its behavior is through learning, the modification of behavior as a result of specific experiences. The capacity for learning depends on nervous system organization established during development following instructions encoded in the genome. Learning itself involves the formation of memories by specific changes in neuronal connectivity (see Concept 49.4). Therefore, the essential challenge for research into learning is not to decide between nature (genes) and nurture (environment), but rather to explore the contributions of both nature and nurture in shaping learning and, more generally, behavior.

Imprinting

In some species, the ability of offspring to recognize and be recognized by a parent is essential for survival. In the young, this learning often takes the form of imprinting, the establishment of a long-lasting behavioral response to a particular individual or object. Imprinting can take place only during a specific time period in development, called
the **sensitive period**. Among gulls, for instance, the sensitive period for a parent to bond with its young lasts one to two days. During the sensitive period, the young imprint on their parent and learn basic behaviors, while the parent learns to recognize its offspring. If bonding does not occur, the parent will not care for the offspring, leading to the death of the offspring and a decrease in the reproductive success of the parent.

How do the young know on whom—or what—to imprint? Experiments with many species of waterfowl indicate that young birds have no innate recognition of “mother.” Rather, they identify with the first object they encounter that has certain key characteristics. In the 1930s, the Austrian researcher Konrad 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 recognition of their biological mother.

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 pair-bond 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. When a wasp leaves her nest to go hunting, she hides the entrance from potential intruders by covering it with sand. When she returns, however, she flies directly to her hidden nest, despite the presence of hundreds of other burrows in the area. How does she accomplish this feat? Tinbergen hypothesized that a wasp locates her nest by learning its position relative to visible landmarks. To test his hypothesis, he carried out an experiment in the wasps’ natural habitat.
In some animals, spatial learning involves formulating a cognitive map, a representation in an animal’s nervous system of the spatial relationships between objects in its surroundings. One striking example is found in the Clark’s nutcracker (Nucifraga columbiana), a relative of ravens, crows, and jays. In the fall, nutcrackers hide pine seeds for retrieval during the winter. By experimentally varying the distance between landmarks in the birds’ environment, researchers discovered that the birds kept track of the halfway point between landmarks, rather than a fixed distance, to find their hidden food stores.

**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.

Associative learning is well suited to study in the laboratory. Such studies 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
each group 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 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 51.10 2), 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. 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.

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.

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 consider how behavior evolves, 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 provided evidence for abstract thinking in honeybees. 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. 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 51.10 1); the second group were rewarded for choosing the arm with the different color. Next, bees from
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 later on, 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 can be quite different in other bird species. 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.

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, and 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 (vervets 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.

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

1. How might associative learning explain why different species of distasteful or stinging insects have similar colors?
2. 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?
3. Make connections How might a learned behavior contribute to speciation? (See Concept 24.1.)

For suggested answers, see Appendix A.

CONCEPT 51.3

Selection for individual survival and reproductive success can explain diverse behaviors

Evolution We turn now to Tinbergen’s third question—how behavior enhances survival and reproduction in a population. The focus thus shifts from proximate causation—the “how” questions—to ultimate causation—the “why” questions. We’ll begin by considering the activity of gathering food. 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 allows us to examine one way that foraging behavior might have evolved. Variation in a gene called forager (for) dictates how far *Drosophila* larvae travel when foraging. On average, larvae carrying the *for* allele (“Rover”) travel nearly twice as far while foraging as do larvae with the *for* allele (“Sitter”).

Both the *for* and *for* alleles are present in natural populations. What circumstances might favor one or the other allele? The answer became apparent in experiments that maintained flies at either low or high population densities for many generations. Larvae in populations kept at a low density foraged over shorter distances than those in populations kept at high density (Figure 51.14). Furthermore, the *for* allele increased in frequency in the low-density populations, whereas the *for* allele increased in frequency in the high-density group. These changes make sense. At a low population density, short-distance foraging yields sufficient food, while long-distance foraging would result in unnecessary energy expenditure. Under crowded conditions, long-distance foraging could enable larvae to move beyond areas depleted of food. Thus, an interpretable evolutionary change in behavior occurred in the course of the experiment.

Optimal Foraging Model

To study the ultimate causation of 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. The **Scientific Skills Exercise** provides an example of how this model can be applied to animals in the wild.

**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

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**Do Crows Display Optimal Foraging Behavior?** On islands off British Columbia, Canada, Northwestern crows (*Corvus caurinus*) search rocky tide pools for sea snails called whelks. After spotting a whelk, the crow picks it 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? 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. In this exercise you’ll test how well this optimal foraging model predicts the average drop height observed in nature.

**How the Experiments Were Done** The height of drops made by crows in the wild was measured by referring to a marked pole erected nearby. In the test, the crow's behavior was simulated using a device that dropped a whelk onto the rocks from a fixed platform. The average number of drops required to break whelks from various platform heights was recorded and averaged over many trials with the device. Combining the data for each platform height, total “flight” height was calculated by multiplying the height times the average number of drops required.

**Data from the Experiment**

<table>
<thead>
<tr>
<th>Drop height (m)</th>
<th>Average number of drops</th>
<th>Total flight height (number of drops × drop height in m)</th>
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<td>12</td>
<td>180</td>
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**Interpret the Data**

1. How does the average number of drops required to break open a whelk depend on platform height for a drop of 5 meters or less? For drops of more than 5 meters?
2. Total flight height can be considered to be a measure of the total energy required to break open a whelk. Why is this value lower for a platform set at 5 meters than for one at 2 or 15 meters?
3. Compare the drop height preferred by crows with the graph of total flight height for the platform drops. Are the data consistent with the hypothesis of optimal foraging? Explain.
4. In testing the optimal foraging model, it was assumed that changing the height of the drop only changed the total energy required. Do you think this is a realistic limitation, or might other factors than total energy be affected by height?
5. Researchers observed that the crows only gather and drop the largest whelks. What are some reasons crows might favor larger whelks?
6. It turned out that the probability of a whelk breaking was the same for a whelk dropped for the first time as for an unbroken whelk dropped several times previously. If the probability of breaking instead increased, what change might you predict in the crow’s behavior?
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.

**Mating Systems and Sexual Dimorphism**

Although we tend to think of mating simply as the union of a male and female, species vary greatly with regard to mating systems, the length and number of relationships between males and females. In some animal species, mating is promiscuous, with no strong pair-bonds. In others, mates form a relationship of some duration that is monogamous (one male mating with one female) or polygamous (an individual of one sex mating with several of the other). Polygamous relationships involve polygyny, a single male and many females, or polyandry, a single female and multiple males.

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 51.14). Among monogamous species, males and females often look very similar. In contrast, among polygamous species, the sex that attracts multiple mating partners is typically showier and larger than the opposite sex. We’ll discuss the evolutionary basis of these differences shortly.

**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 many 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, and 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 cares for a harem of many females.
success among individuals are a consequence of differences in mating success (see Concept 23.4). 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.

**Mate Choice by Females** Mate preferences of females may play a central role in the evolution of male behavior and anatomy through intersexual selection. Consider, for example, 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. 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? Ornaments such as long eyestalks in these flies and bright coloration in birds correlate in general with health and vitality. A female whose mate choice is a healthy male is likely to produce more offspring that survive to reproduce. As a result, males may compete with each other in ritualized contests to attract female attention (Figure 51.16).

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 51.17). To explore whether parental

**Sexual Selection and Mate Choice** Sexual dimorphism results from sexual selection, a form of natural selection in which differences in reproductive

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**Figure 51.15** 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.

**Figure 51.16** Male stalk-eyed flies face off for female attention. In such ritual showdowns, the male whose eyestalk length is smaller usually retreats peacefully.

**Figure 51.17** Appearance of zebra finches in nature. The male zebra finch (left) is more highly patterned and colorful than the female zebra finch.
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, they were presented with prospective mates that were either artificially ornamented with a red feather or non-ornamented (Figure 51.18). Males showed no preference. Females raised by a male parent that was not ornamented also showed no preference. 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 51.19). 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. Similarly, male competition for mates can reduce variation among males. 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 51.20; see also Figure 51.16).

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.

As an example of applying game theory to mating behavior, let’s consider the side-blotched lizard (*Uta stansburiana*) of California. Genetic variations give rise to males with orange, blue, or yellow throats (Figure 51.21). One would expect that natural selection would favor one of the three color types, yet all three persist. Why? The answer appears to lie in the fact that 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. Thus, following the population over time,
one sees a persistence of all three color types and a periodic
shift in which type is most prevalent.

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

**CONCEPT CHECK 51.3**

1. Why does the mode of fertilization correlate with the presence or absence of male parental care?
2. **MAKE CONNECTIONS** Balancing selection can maintain variation at a locus (see Concept 23.4). Based on the foraging experiments described in this chapter, devise a simple hypothesis to explain the presence of both for" and for" alleles in natural fly populations.
3. **WHAT IF?** Suppose an infection in a side-blotched 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**

Genetic analyses and the concept of inclusive fitness provide a basis for studying the evolution of behavior

**EVOLUTION** We'll now explore issues related to Tinbergen's fourth question—the evolutionary history of behaviors. We will first look at the genetic control of a 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 genetic 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 different 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.

In many cases, differences in behavior arise not from gene inactivation, but from variation in the activity or amount of a gene product. One striking example comes from the study of two related species of voles, which are small, mouse-like rodents. Male meadow voles (Microtus pennsylvaniaicus) 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 51.22). Male prairie voles hover over their young pups, licking them and carrying them, while acting aggressively toward intruders.

A peptide neurotransmitter is critical for the partnering and parental behavior of male voles. Known as ADH or vasopressin (see Chapter 44), this peptide is released during mating and binds to a specific receptor in the central nervous system. When male prairie voles are given a drug that inhibits the brain receptor for vasopressin, they fail to form pair-bonds after mating.
The vasopressin receptor gene is much more highly expressed in the brain of prairie voles than in the brain of meadow voles. Testing the hypothesis that vasopressin receptor levels in the brain regulate postmating behavior, researchers inserted the vasopressin receptor gene from prairie voles into meadow voles. The male 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-bonding and parenting in voles, a change in vasopressin receptor levels is sufficient to alter the development of these behaviors.

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 correlates with variation in environmental conditions, it may reflect natural selection.

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 51.23). Inland populations feed on frogs, leeches, and fish, but not banana slugs. In fact, banana slugs are rare or absent in the inland habitats.

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 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. Was this change in the pattern of migration the outcome of natural selection? If so, the birds wintering in Britain must have a heritable difference in migratory behavior. To test this hypothesis, researchers at the Max Planck Research Center in Radolfzell, Germany, devised a strategy to study migratory orientation in the laboratory (Figure 51.24). The results demonstrated that the two patterns of migration—to the west and to the southwest—do in fact 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.

**Altruism**

We typically 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 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 consider how they 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, for example, the Belding’s ground squirrel, which lives in 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 51.25). 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 at times sacrifice themselves to protect the queen or kings from snakes or other predators that invade the colony.

**Inclusive Fitness**

With these examples from ground squirrels, honeybees, and mole rats in mind, let’s return to the question of how altruistic behavior arises during evolution. The easiest case to consider is that of parents sacrificing for their offspring. When parents sacrifice their own well-being to produce and aid offspring, this act actually increases the fitness of the parents because it maximizes their genetic representation in the population. By this logic, altruistic behavior can be maintained by evolution even though it does not enhance the survival and reproductive success of the self-sacrificing individuals.

What about circumstances when individuals help others who are not their offspring? By considering a broader group of relatives than just parents and offspring, biologist William Hamilton found an answer. He began by proposing that an animal could increase its genetic representation in the next generation by helping close relatives other than its own offspring. Like parents and offspring, full siblings share half their genes in common. Therefore, selection might also favor helping siblings or helping one’s parents produce more siblings. This thinking led Hamilton to the 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 to produce offspring.

**Hamilton’s Rule and Kin Selection**

The power of Hamilton’s hypothesis was that it provided a way to measure, or quantify, the effect of altruism on fitness. 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 recipient 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 man is thus two offspring \( (B = 2) \). What cost is incurred by his sister? Let’s say that she has a 25% chance of drowning in attempting the rescue. The cost of the altruistic act to the sister is then 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 51.26; 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.

Averaging over many individuals and generations, any particular gene in a sister faced with the situation described will be passed on to more offspring if she risks the rescue than if she does not. Among the genes propagated in this way may be some that contribute to altruistic behavior. Natural selection that thus favors altruism by enhancing the 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, \( r = 0.25 \) \( (¼) \), and between first cousins, \( r = 0.125 \) \( (⅛) \). 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 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 51.27). 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**

As animals, humans behave (and, sometimes, misbehave). Just as humans vary extensively in anatomical features, we display substantial variations in behavior. Environment intervenes in the path from genotype to phenotype for physical traits, but does so much more profoundly for behavioral traits. Furthermore, as a consequence of our marked capacity for learning, humans are probably more able than any other animal to acquire new behaviors and skills (Figure 51.28).

Some human activities have a less easily defined function in survival and reproduction than do, for example, foraging or courtship. One of these activities is play, which is sometimes defined as behavior that appears purposeless. We recognize play in children and what we think is play in the young of other vertebrates. Behavioral biologists describe “object play,” such as chimps playing with leaves, locomotor play, such as the acrobatics of an antelope, and “social play,” such as the interactions and antics of lion cubs. These categories, however, do little to inform us about the function of play. One idea is that, rather than generating specific skills or experience, play serves as preparation...
for unexpected events and for circumstances that cannot be controlled.

Human behavior and culture are 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 continues today.

Over our recent evolutionary history, we have built up 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 that at times make less apparent the continuum between humans and other animals. One such quality, our considerable capacity for reciprocal altruism, will be essential as we tackle current challenges, including global climate change, in which individual and collective interests often appear to be in conflict.

**CONCEPT CHECK 51.4**

1. Explain why geographic variation in garter snake prey choice might indicate that the behavior evolved by natural selection.
2. Suppose an individual organism aids the survival and reproductive success of the offspring of its sibling. How might this behavior result in indirect selection for certain genes carried by that individual?
3. Suppose you applied Hamilton’s logic to a situation in which one individual is past reproductive age. Could there still be selection for an altruistic act?

For suggested answers, see Appendix A.

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**Chapter Review**

**SUMMARY OF KEY CONCEPTS**

**CONCEPT 51.1**

Discrete sensory inputs can stimulate both simple and complex behaviors (pp. 1134–1138)

- **Behavior** is the sum of an animal's responses to external and internal stimuli. In behavior studies, proximate, or “how,” questions focus on the stimuli that trigger a behavior and on genetic, physiological, and anatomical mechanisms underlying a behavioral act. Ultimate, or “why,” questions address evolutionary significance.
- 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 often synchronized to the circadian cycle of light and dark in the environment or to cues that cycle over the seasons.
- The transmission and reception of signals constitute animal **communication**. Animals use visual, auditory, chemical, and tactile signals. Chemical substances called pheromones transmit species-specific information between members of a species 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. 1138–1143)

- Cross-fostering studies can be used to measure the influence of social environment and experience on behavior.

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

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**Learning**, the modification of behavior as a result of experience, can take many forms:
CONCEPT 51.3
Selection for individual survival and reproductive success can explain diverse behaviors (pp. 1143–1149)

- Controlled experiments in the laboratory can give rise to interpretable evolutionary changes in behavior.
- 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. Variations in mating system and 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
Genetic analyses and the concept of inclusive fitness provide a basis for studying the evolution of behavior (pp. 1149–1154)

- 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 on 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 correlates with 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.
- Altruism 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.

What insight about the genetic basis of behavior emerges from studying the effects of courtship mutations in fruit flies and of pair-bonding in voles?

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

a. addition of new syllables to a canary’s song repertoire.

b. crystallization of subsong into adult songs.

c. sensitive period in which canary parents imprint on new offspring.

d. 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

a. the behavioral difference is caused by genetic differences between populations.

b. members of different populations have different nutritional requirements.

c. the cultural tradition of using stones to crack nuts has arisen in only some populations.

d. members of different populations differ in learning ability.

6. Which of the following is not required for a behavioral trait to evolve by natural selection?

a. In each individual, the form of the behavior is determined entirely by genes.

b. The behavior varies among individuals.

c. An individual’s reproductive success depends in part on how the behavior is performed.

d. Some component of the behavior is genetically inherited.

LEVEL 3: SYNTHESIS/EVALUATION

7. 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, what observations and measurements would you make in this shorebird’s habitat to help determine which model is more accurate?
12. **SYNTHESIZE YOUR KNOWLEDGE**

Acorn woodpeckers (*Melanerpes formicivorus*) stash acorns in storage holes they drill in trees. When these woodpeckers breed, the offspring from previous years often help with parental duties. Activities of these nonbreeding helpers include incubating eggs and defending stashed acorns. What are some questions about the proximate and ultimate causation of these behaviors that a behavioral biologist might ask?

*For selected answers, see Appendix A.*

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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: INFORMATION**

Learning is defined as a change in behavior as a result of 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.

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