

Musk oxen (*Ovibos moschatus*). The social behavior of a herd of musk oxen includes encircling their young to protect them from predators.

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55 The Ecology and Evolution of Animal Behavior

WHY IT MATTERS

In early spring, male white-crowned sparrows leave their wintering grounds in Mexico and fly thousands of kilometers to their northern breeding range. There, they select patches of habitat that contain the resources necessary for breeding—suitable cover, potential nesting sites, and abundant food. Then, they start to sing and sing, repeating their song thousands of times every day. The songs are a form of communication through which males announce their presence to rival males and to females. Males also perform elaborate courtship behaviors. And once the young hatch, they communicate with their parents, eliciting the care they need before leaving the nest.

All of these behaviors carry significant costs and risks. For example, migration requires enormous energy expenditure, and many migrating birds die before completing their trip. Moreover, singing males are conspicuous, and they may attract the attention of a hawk or some other predator. Given the costs and dangers associated with these behaviors, what benefits do the birds gain from performing them? The ultimate evolutionary benefit is obvious: with luck, individuals performing these complex and diverse behaviors may leave surviving offspring (**Figure 55.1**).



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Figure 55.1
Reproductive success. Parental care is just one of many behaviors required for successful reproduction in white-crowned sparrows (*Zonotrichia leucophrys*) and many other animal species. The number of surviving nestlings will determine the reproductive success of their parents.

Questions about ultimate benefits are fundamentally different from the questions we considered in the previous chapter, where we focused on *how* underlying physiological and genetic mechanisms enable animals to behave. In this chapter, we try to explain *why* animals behave as they do. Why do sparrows migrate to their breeding grounds, breed in certain habitats but not others, and expose themselves to predation by singing? The behavior of animals is closely tied to ecological circumstances, and evolutionary biologists view most behaviors as an individual's responses to its environment. Moreover, like morphological traits, behaviors are subject to microevolutionary change (see Chapter 20). If particular alleles contribute even slightly to the development of a behavior that enhances an animal's fitness, natural selection will cause the frequency of those alleles to increase in the next generation.

Behavioral biologists apply ecological and evolutionary analyses to all forms of animal behavior, including those described above. In this chapter, we examine the ecology and evolution of several categories of animal behavior: orientation, navigation, and migration; habitat selection and territoriality; communication; reproductive behavior and mating systems; and social behavior, including behaviors described as altruistic. We close the chapter with a brief look at human behavior.

55.1 Migration and Wayfinding

Most animals move through their environments at some stage of their life cycles. Although some species move only short distances to find suitable environmen-

tal conditions, many others undertake large-scale movements on a seasonal schedule.

Migrating Animals Make Long Round-Trips on a Seasonal Cycle

Many animal species undertake a seasonal **migration**, traveling from the area where they were born to a distant and initially unfamiliar destination, and returning to their birth site later. The Arctic tern (*Sterna paradisaea*), a seabird, makes an annual round-trip migration of 40,000 km (**Figure 55.2**). Many other vertebrate species, including gray whales and salmon, also undertake long and predictable journeys. Even some arthropods migrate long distances. For example, spiny lobsters (*Panulirus* species) form long conga lines as they move between coral reefs and the open ocean floor on a seasonal cycle (**Figure 55.3**).

Animals Use Wayfinding Mechanisms to Guide Their Movements

Moving animals use various wayfinding mechanisms to arrive at their destination. Biologists group these mechanisms into three general categories: *piloting*, *compass orientation*, and *navigation*. Many species probably use a combination of these mechanisms to guide their movements.

The simplest wayfinding mechanism is **piloting**, in which animals use familiar landmarks to guide their journey. For example, gray whales (*Eschrichtius robustus*) migrate from Alaska to Baja California and back using visual cues provided by the Pacific coastline of North America. When it is time to breed and lay eggs, Pacific salmon (genus *Oncorhynchus*) use olfactory cues to pilot their way from the ocean back to the stream where they themselves hatched.

Animals that do not undertake long migrations also use specific landmarks to identify their nest site or places where they have stashed food. In a famous experiment published in 1938, Niko Tinbergen showed that female digger wasps (*Philanthus triangulum*), which nest in soil, use visual landmarks to find their nests after flying off in search of food (**Figure 55.4**). Tinbergen arranged pinecones in a circle around one nest while the female was still inside. As she left, she flew around the area, apparently noting nearby landmarks. Tinbergen then moved the circle of pinecones a short distance away. Each time a female returned, she searched for her nest within the pinecone circle—and never once found it unless the pinecones were returned to their original position. In a follow-up study, Tinbergen rearranged the circle of pinecones into a triangle after females left their nests and added a ring of stones nearby. The returning females looked for their nest in the stone circle. Tinbergen concluded that digger wasps respond to the general outline or geom-

etry of landmarks around their nests and not to the specific objects that create those landmarks.

A more sophisticated wayfinding mechanism, **compass orientation**, allows animals to move in a particular direction, often over a specific distance or for a prescribed length of time. Some day-flying migratory birds, for example, orient themselves using the sun's position in the sky in conjunction with an internal biological clock (see Section 40.4). The internal clock allows the bird to use the sun as a compass, compensating for changes in its position through the day; the clock may also allow some birds to estimate how far they have traveled since beginning their journey. Other migratory animals use polarized light or Earth's magnetic field as a compass.

Some birds that migrate at night use the positions of stars to determine their direction. The indigo bunting (*Passerina cyanea*), for example, flies about 3500 km from the northeastern United States to the Caribbean or Central America each fall and makes the return journey each spring. Stephen Emlen of Cornell University demonstrated that these birds use celestial cues to direct their migration (**Figure 55.5**). Emlen confined individual buntings in cone-shaped test cages. He lined the sides of the cages with blotting paper, placed inkpads on the bottom, and kept the cages in an outdoor enclosure so that the birds had a full view of the sky. Whenever a bird made a directed movement, its inky footprints indicated the direction in which it was trying to fly. Emlen found that on clear nights in fall, the footprints pointed to the south; on clear nights in spring, they pointed north. On cloudy nights, when the buntings could not see the stars, their footprints were evenly distributed in all directions, indicating that their compass required a view of the stars.

The most complex wayfinding mechanism is **navigation**, in which an animal moves toward a specific destination, using both a compass and a “mental map” of where it is in relation to the destination. Human hikers in unfamiliar surroundings routinely use navigation to find their way home: they use a map to determine their current position and the necessary direction of movement and a compass to orient themselves in that direction. Scientists have documented true navigation in only a few animal species. Perhaps the most notable is the homing pigeon (*Columba livia*), which can navigate to its home coop from any direction. Recent research suggests that homing pigeons probably use the sun's position as their compass and olfactory cues as their map.

Environmental Cues Trigger Hormonal Changes That Induce Seasonal Migration

For white-crowned sparrows and many other species, researchers have shown that decreasing (or increasing) day length, a correlate of the approaching autumn (or

Figure 55.2

Long-distance migration. Arctic terns (*Sterna paradisaea*) migrate from the high Arctic to Antarctica each year, a round-trip journey of 40,000 km. This species' summer breeding range is shaded on the map.

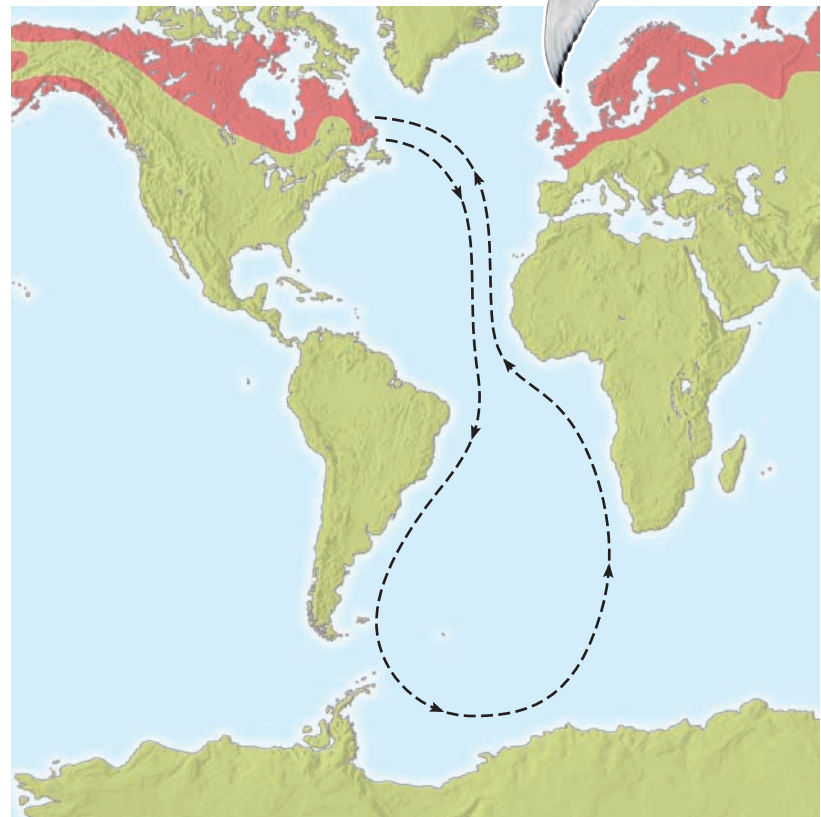


Figure 55.3

Migrating arthropods. Spiny lobsters (*Panulirus argus*) make seasonal migrations between coral reefs and the open ocean floor. As many as 50 individuals march in single file for several days.

Figure 55.4 Experimental Research

Using Landmarks to Find the Way Home

QUESTION: How do female digger wasps (*Philanthus triangulum*) relocate their nests after flying off to search for food?

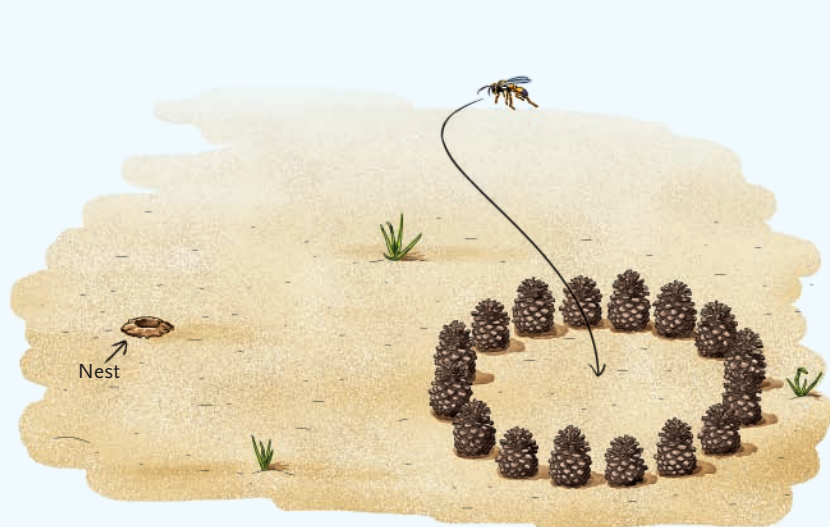
EXPERIMENT: Tinbergen arranged pinecones in a circle around the nest of a female digger wasp while she was still inside. After leaving the nest, she circled the area a few times, apparently noting nearby landmarks. Tinbergen then moved the circle of pinecones a short distance away.

RESULT: Each time the female returned, she searched for her nest within the pinecone circle. She was unable to find the nest unless Tinbergen replaced the pinecones in their original position.

Wasp's flight pattern on leaving nest



Wasp's return, looking for nest



CONCLUSION: Female digger wasps use the location of local landmarks to find the entrances to their underground nests.

spring), stimulates the anterior pituitary of the bird's brain to generate a series of hormonal changes. The birds then feed heavily and accumulate the fat reserves necessary to fuel the long journey. Sparrows also become increasingly restless at night, until one evening they launch themselves into their nocturnal migration. Their ability to adopt and maintain a southerly orientation in autumn (and a northerly one in spring) rests in part on their capacity to use the positions of stars to provide them with directional information.

Seasonal Variation in Food Supply May Explain the Evolution of Migratory Behavior

Migratory behavior entails obvious costs, such as the time and energy devoted to the journey and the risk of death from exhaustion or predator attack. Why then do some species migrate? What benefits accrue to an individual that undertakes a costly migration?

For migratory birds, the most widely accepted hypothesis focuses on seasonal changes in food supplies. The amount of insect food available in northern forests

increases explosively during the warm spring and summer, providing abundant resources to produce eggs and rear offspring. Then, during the late fall and winter, insects all but disappear. A few bird species that forage on seeds and dormant insects do not head south. However, energy supplies are more predictably available in tropical overwintering grounds, and migratory birds may have a better chance of surviving there. The following spring they return north to exploit the food bonanza on their summer breeding grounds.

The two-way migratory journeys may provide other benefits as well. Avoiding the northern winter is probably adaptive because endotherms must increase their metabolic rates just to stay warm in cold climates (see Section 46.8). But in summer the days are longer at high latitudes than they are in the tropics (see Section 52.1), giving adult birds more time to collect enough food to rear a brood.

Seasonal changes in food supply also underlie the migration of monarch butterflies (*Danaus plexippus*), which eat milkweed (*Asclepias* species) leaves as larvae and the nectar of milkweeds and other plants as adults.

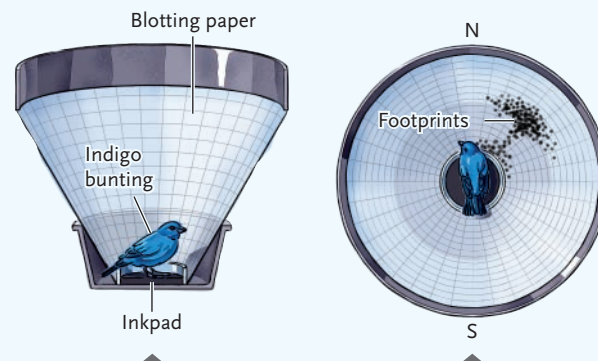
Figure 55.5 Experimental Research

Experimental Analysis of the Indigo Bunting's Star Compass

Indigo bunting

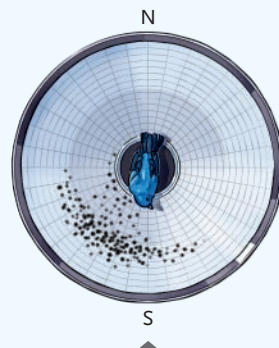


R. & N. Bowers/VIREO

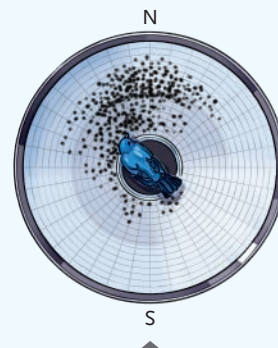


Side (left) and overhead (right) views of the test cage with blotting paper on the sides and an inkpad on the bottom

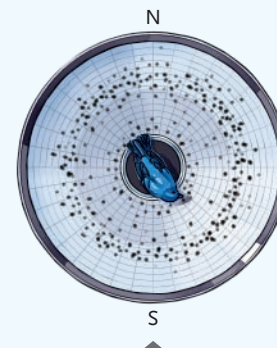
RESULTS: On clear nights in autumn, the footprints pointed to the south; on clear nights in spring, they pointed north. On cloudy nights, when buntings could not see the stars, their footprints were evenly distributed in all directions.



In autumn, the bunting footprints indicated that they were trying to fly south.



In spring, the bunting footprints indicated that they were trying to fly north.



On cloudy nights, when buntings could not see the stars, their footprints indicated a random pattern of movement.

CONCLUSION: Indigo buntings use the positions of the stars to direct their seasonal migrations. When they could see the stars above their test cages, they moved in the predicted direction; but when clouds obscured their view of the stars, they moved in random directions.

In eastern North America, milkweed plants grow only during spring and summer. Many adult monarchs head south in late summer, when milkweeds are beginning to die, migrating as much as 4000 km from eastern and central North America to central Mexico, where they cluster in spectacular numbers (**Figure 55.6**). Unlike migrant birds, these insects do not feed on their overwintering grounds. Instead, their metabolic rate

decreases in the cool mountain air, and the butterflies become inactive for months, thereby conserving precious energy reserves. When spring arrives, the butterflies become active again and begin the return migration to northern breeding habitats. The northward migration is slow, however, and many individuals stop along the way to feed and lay eggs. But their offspring, and their offspring's offspring, continue the northward

a. Monarch larva and adult



b. Migrating monarch adults



c. Monarch migration routes



Figure 55.6

Monarch butterfly migrations. (a) Monarch butterflies (*Danaus plexippus*) feed primarily on milkweed plants. (b) When milkweed plants in their breeding range die back at the end of summer, millions of monarchs begin a southward migration. (c) Butterflies that live and breed east of the Rocky Mountains migrate to Mexico. After passing the winter in a semidormant state, they migrate northward the following spring. Monarchs living west of the Rocky Mountains winter in coastal California.

migration through the summer; some descendants eventually reach Canada for a final round of breeding. The summer's last generation then returns south to the spot where their ancestors, two to five generations removed, spent the previous winter.

For other animals, the migration to breeding grounds may provide special conditions necessary for reproduction. For example, gray whales migrate south to breeding grounds in quiet, shallow lagoons where predators are rare and warm water temperatures will not stress their calves.

STUDY BREAK

1. What is the difference between piloting, compass orientation, and navigation?
2. What is the most probable selection pressure that has fostered seasonal migrations in birds?

55.2 Habitat Selection and Territoriality

The geographical range of nearly every animal species includes a mosaic of habitat types. The breeding range of white-crowned sparrows, for example, encompasses forests, meadows, housing developments, and city dumps. An animal's choice of habitat is critically important because the habitat provides food, shelter, nesting sites, and the other organisms with which it interacts. If an animal chooses a habitat that does not provide appropriate resources, it will not survive and reproduce.

Animals Use Multiple Criteria for Selecting Habitats

On a large spatial scale, animals almost certainly use multiple criteria to select the habitats they occupy, but no research has yet established any general principles

about how animals make these choices. When a migrating bird arrives at its breeding range, for example, it probably cues on large-scale geographical features, such as a pond or a patch of large trees. If it does not find the food or nesting resources it needs—or if other individuals have already depleted those resources—it may move to another habitat patch.

On a very fine spatial scale, basic responses to physical factors enable some animals to find suitable habitats. The simplest such mechanism is called a **kinesis** (*kinesis* = movement), a change in the rate of movement or the frequency of turning movements in response to environmental stimuli. For example, the terrestrial crustaceans known as wood lice (Isopoda) typically live under rocks and logs or in other damp places. Although these arthropods are not attracted to moisture per se, laboratory experiments have shown that when a wood louse encounters dry soil, it exhibits a kinesis, scrambling around and turning frequently; when it reaches a patch of moist soil, it moves much less. As a result, these animals accumulate in moist habitats. Biologists infer that this behavior is adaptive because wood lice exposed to dry soil quickly dehydrate and die. Other animals may exhibit a **taxis** (*taxis* = ordered movement), a response that is directed either toward or away from a specific stimulus. For example, cockroaches (order Blattodea) exhibit negative phototaxis: they actively avoid light and seek darkness, a behavior that makes them harder for visually oriented predators to detect.

Genetics and Learning Influence Habitat Selection

Biologists generally assume that habitat selection is adaptive and has been shaped by natural selection in most animal species. For example, some animals instinctively select habitats where they are well camouflaged, a means of avoiding detection by predators (see Figure 50.3); predators would discover and eliminate any individual that fails to select a matching background—along with any alleles responsible for the mismatch. Many insects have a genetically determined preference for the plants that they eat during their larval stage. Adults often restrict their mating and egg-laying activities to these food plants, effectively selecting the habitats where their offspring will live and feed, as described in the discussion of sympatric speciation (see Section 21.3).

Even vertebrates sometimes exhibit such innate preferences, as demonstrated by two closely related European bird species, blue tits (*Parus caeruleus*) and coal tits (*Parus ater*). Adult blue tits feed mostly in oak trees, whereas coal tits prefer to feed in pines. When researchers reared the young of both species in cages without any vegetation at all and then offered them a choice between oak branches and pine branches, coal tits immediately gravitated toward pines and blue tits toward oaks, strongly suggesting that the preference is

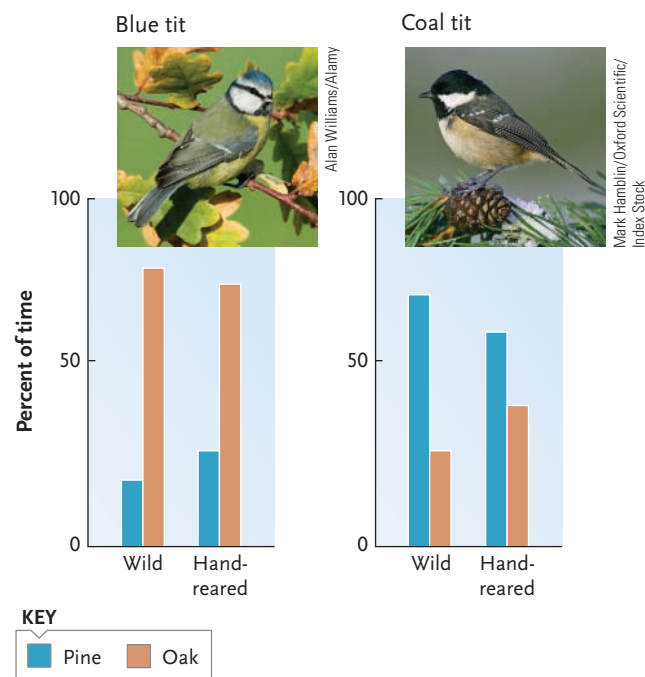


Figure 55.7 Habitat selection by birds. Wild blue tits (*Parus caeruleus*) show a strong preference for oak trees, and coal tits (*Parus ater*) show a strong preference for pine trees. Hand-reared birds that were raised in a vegetation-free environment showed identical, though slightly weaker, preferences.

innate (Figure 55.7). Further research demonstrated that each species feeds most successfully in the tree species it prefers. Thus, natural selection probably fostered these preferences.

Habitat preferences can be molded by experiences early in life, however. For example, the tadpoles of red-legged frogs (*Rana aurora*) usually live in aquatic habitats cluttered with sticks, strands of algae, and plant stems; when given a choice in the laboratory, they prefer striped backgrounds to plain ones. By contrast, tadpoles of the closely related cascade frog (*Rana cascadae*) live over gravel bottoms, and they prefer plain substrates over striped ones. However, when red-legged frogs are reared over plain substrates and cascade frogs over striped substrates, they no longer exhibit preferences for their usual substrates.

Animals Sometimes Defend Patches of Habitat for Their Exclusive Use

Under some circumstances, animals may defend a **territory** from other members of their species, retaining more or less exclusive use of the resources it contains. Territorial behavior occurs in all major groups of vertebrates, many insects, and some other invertebrates, but it is by no means universal. In many organisms, territorial behavior occurs only during the breeding season.

Animals establish and defend territories only when some critical resource is in short supply. More-

over, the resource must be fixed in space so that the area around it can be defended. For example, during the breeding season, most songbirds defend a territory within which they build a nest and collect food for their young. By contrast, many sea bird species, such as terns and penguins, do not defend a feeding territory. They catch fish in the ocean and build nests on the shore. Although they defend a tiny area around the nest, they never attempt to defend a section of ocean; fishes come and go at will and thus do not constitute a defendable resource.

Territorial defense is always a costly activity. Patrolling territory borders, performing displays hundreds of times per day, and chasing intruders take time and energy. Moreover, territorial displays increase an animal's likelihood of being injured or detected and captured by a predator.

Experiments conducted by Catherine Marler and Michael Moore of Arizona State University illustrate the cost of territorial behavior in Jarrow's spiny lizard (*Sceloporus jarrovi*). Male lizards ordinarily exhibit strong territoriality only during the autumn mating season, when elevated blood levels of testosterone stimulate their aggressive behavior. The researchers implanted small doses of testosterone under the skin of experimental animals in June and July, during the nonmating season; controls received a placebo treatment. Testosterone-enhanced males were more active and displayed more often than control males. But experimental males spent less time feeding, even though they used about 30% more energy per day than control males. Over the course of about 7 weeks, a significantly higher percentage of experimental males died—a clear sign that engaging in territorial behavior is costly.

On the other hand, the benefits of maintaining a territory include having access to nesting sites, food supplies, and refuges from predators. For example, the surgeonfish (*Acanthurus lineatus*), which lives in the coral reefs around American Samoa, may engage in as many as 1900 chases per day to defend a small territory from other algae-eating fish species. But territory holders may consume up to five times as much food as nonterritory holders.

Figure 55.8

Visual displays. The courtship display of a male wandering albatross (*Diomedea exulans*) includes ritualized postures and movements of the wings and body.



STUDY BREAK

1. Why do wood lice tend to occur in moist parts of their habitat?
2. What are the costs of maintaining a territory, and what are the benefits?

55.3 The Evolution of Communication

When resident animals advertise their presence in their territories, they are communicating information to nearby animals. In the formal language of animal behavior studies, all communication systems involve an interaction between a *signaler*, the animal that transmits information, and a *signal receiver*, the animal that intercepts the information and makes a behavioral response. Natural selection has adjusted the ability of signalers to transmit information and the ability of receivers to get the message.

Animal Signals Can Activate Different Sensory Receptors in Receivers

Biologists categorize animal signals according to the sensory receptors, or “channels,” through which the signal acts: *acoustical*, *visual*, *chemical*, *tactile*, or *electrical*. Each channel has specific advantages.

Bird songs are examples of **acoustical signals**; a signaler produces a sound that is heard by a signal receiver. Many animals use the acoustical channel, including a host of nocturnal and burrow-dwelling insects and amphibians. These signals reach distant receivers, even at night and in cluttered environments where visual signals are less effective.

Because humans frequently use facial expressions and body language to send messages, **visual signals** are a familiar form of communication. In many animals, visual signals are *ritualized*; in other words, they have become exaggerated and stereotyped over evolutionary time, forming an easily recognized visual display (**Figure 55.8**). Visual displays can even be useful at night or in the darkness of the deep sea; some animals, such as fireflies and certain fishes, send bioluminescent signals to distant receivers.

Many species release **chemical signals**, which carry messages to signal receivers through the olfactory channel. Scent marking (spraying) by male cats is an example. In particular, mammals and insects often communicate through **pheromones**, distinctive volatile chemicals released in minute amounts to influence the behavior of members of the same species. For example, a worker ant's body contains a battery of glands, each releasing a different pheromone (**Figure 55.9**). One set of pheromones recruits fellow workers to battle colony invaders; another set stimulates workers to col-

lect food that has been discovered outside the colony. Other animals release pheromones to attract mates. Female silkworm moths (*Bombyx mori*) produce bombykol, a single molecule of which can generate a message in specialized receptors on the antennae of any male silkworm moth that is downwind (see Figure 39.19).

In many species, touch conveys important messages from a signaler to a receiver. **Tactile signals** can operate only over very short distances, but for social animals living in close company, they play a significant role in the development of friendly bonds between individuals (**Figure 55.10**).

Some freshwater fish species, especially those that occupy murky tropical rivers where visual signals could not be seen, use weak **electrical signals** to communicate. These fishes have electric organs that can release charges of variable intensity, duration, and frequency, allowing substantial modulation of the message that a signaler sends. Among the New World knifefishes (order Gymnotiformes), including the electric eel (*Electrophorus electricus*), electrical discharges can signal threats, submission, or a readiness to breed.

Honeybees Use Several Communication Channels to Transmit Complex Messages

When animals need to convey a complex message, they may use several channels of communication simultaneously. For example, as Karl von Frisch demonstrated, the famous dance of the honeybee (*Apis mellifera*) involves tactile, acoustical, and chemical communication (**Figure 55.11**). When a foraging honeybee discovers pollen or nectar, it returns to its colony and performs a complex dance on the vertical surface of the honeycomb in the complete darkness of the hive. The dancer moves in a circle, attracting a crowd of workers, some of which follow and maintain physical contact with the dancer. From the dance, they acquire information about the distance and direction they will need to fly to locate the food source.

When the food source is less than about 75 m from the hive, the bee performs a “round dance” (see Figure 55.11a). It moves in tight circles, swinging its abdomen back and forth. Bees surrounding the dancer produce a brief acoustical signal, which stimulates the dancer to regurgitate a sample of the food it discovered. The regurgitated sample serves as a chemical cue to other workers, which then leave the hive to search for that type of food.

If the food source is more distant, the forager performs what von Frisch described as the “waggle dance.” The bee dances a half circle in one direction and then dances in a straight line while wagging its abdomen before dancing a half circle in the other direction (see Figure 55.11b). With each waggle, the dancer produces a brief buzzing sound. Von Frisch determined that the angle of the straight run relative

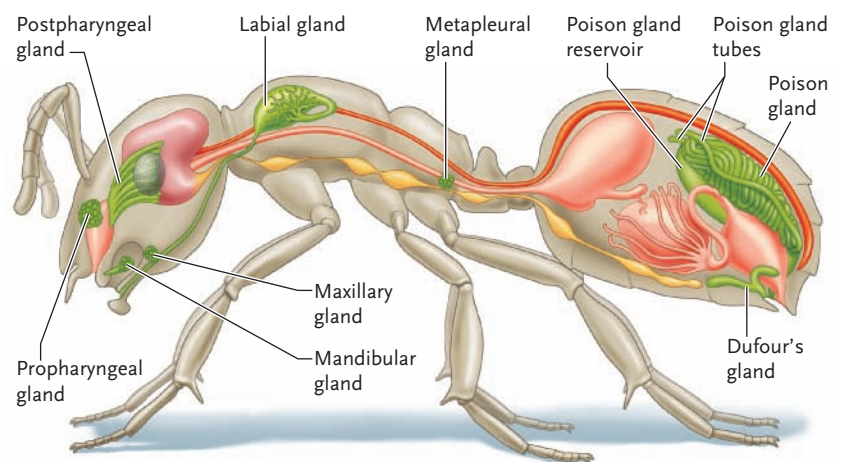


Figure 55.9
Chemical signals. An ant's body contains a host of pheromone-producing glands, each of which manufactures and releases its own volatile chemical or chemicals.

to the vertical honeycomb indicates the direction of the food source relative to the position of the sun (see Figure 55.11c). The duration of the waggles and buzzes that the bee makes on the straight run carries information about the distance to the food: the longer the time spent wagging and buzzing, the further the food is from the hive.

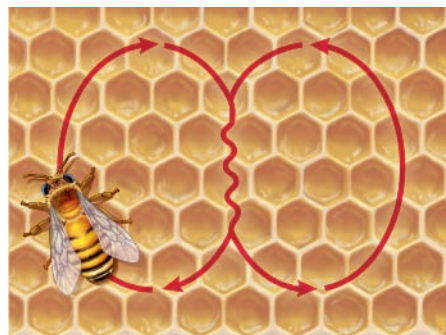


Figure 55.10
Tactile signals. Grooming by hyacinth macaws (*Anodorhynchus hyacinthinus*) removes parasites and dirt from feathers. The close physical contact also promotes friendly relations between groomer and groomee.

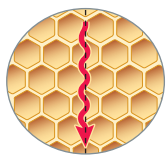
a. Round dance



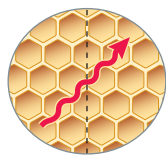
b. Waggle dance



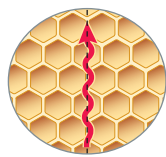
c. Coding direction in the waggle dance



When the bee moves straight down the comb, other bees fly to the source directly away from the sun.



When the bee moves 45° to the right of vertical, other bees fly at a 45° angle to the right of the sun.



When the bee moves straight up the comb, other bees fly straight toward the sun.

Figure 55.11

Dance communication by honeybees. Foraging honey bees (*Apis mellifera*) transmit information about the location of a food source by dancing on the vertical honeycomb.

(a) If the food source is close to the hive, the forager performs a “round dance.” (b) If the food source is more than about 75 m from the hive, the forager performs a “waggle dance,” which indicates the distance to the food source. (c) The dancing bee indicates the direction to a distant food source by the angle of the waggle run.

Figure 55.12

Threat displays.

The threat display of a dominant male mandrill (*Mandrillus sphinx*), used to drive away rival males, features exposed canines.



Tom and Pat Leeson

Biologists Use Evolutionary Hypotheses to Analyze Communication Systems

Signal receivers often respond to communication from signalers in predictable ways. For example, a male white-crowned sparrow generally avoids entering a neighboring territory simply because it hears the song of the resident male. Similarly, young male baboons often retreat without a fight when they see an older male’s visual threat display (Figure 55.12), even though they may lose the chance to mate with a female. Why do these receivers behave in ways that appear to be beneficial to their rivals, but not to themselves?

When biologists try to explain behavioral interactions, their hypotheses focus on how an animal’s actions may allow it to contribute more offspring to the next generation. In our first example, the retreating male sparrow avoids wasting time and energy on a battle he

is likely to lose—as well as the possibility of being injured or killed by another male. Moreover, ousting the current resident might be more tiring and risky than finding a suitable unoccupied breeding site. This hypothesis predicts that resident males should almost always win physical contests. In cases when an intruder wins a territory from a resident, it may do so only after a prolonged series of exhausting clashes. Observations of territorial species—whether birds, lizards, frogs, fish, or insects—generally support these predictions.

Applying a similar argument to competition among male baboons, we can predict that smaller or younger males will concede females to threatening older rivals without fighting. The signal receiver retreats after receiving the threat because he judges that he would be demolished in real combat—after all, a male baboon’s canine teeth are not just for show. Evolutionary analyses therefore suggest that both the signaler and the signal receiver benefit from the transfer of information in their communication system.

An evolutionary analysis also helps to explain the strange yell of ravens (*Corvus corax*), which scavenge carcasses of deer, elk, or moose in northern forests during winter. When one of these large birds comes across a food bonanza, it may call loudly, attracting a crowd of hungry ravens. The calling behavior puzzled Bernd Heinrich of the University of Vermont. Wouldn’t a quiet raven eat more, survive longer, and produce more offspring than a noisy bird? If natural selection favored the raven’s calling behavior, we might expect that the cost of calling (in terms of lost food) would be offset by a reproductive benefit for the individual caller. Heinrich noticed that paired, territory-owning adults did not yell loudly when they found goat carcasses that he had hauled into the Maine woods; instead, they fed quietly. Only young, wandering ravens that happened upon a carcass in another bird’s territory advertised their discovery. The signals of these birds attracted other nonterritorial ravens, which collectively overwhelmed the resident pair’s attempts to defend their territory. Only then was a wanderer likely to have a chance to feed in an area that would otherwise be off-limits.

STUDY BREAK

1. Which channels do humans consciously use to communicate with each other?
2. How does a honeybee tell its hive-mates that it has discovered a distant food source?
3. Why do ravens sometimes announce their discovery of food?

55.4 The Evolution of Reproductive Behavior and Mating Systems

In many animal species, communication coordinates the reproductive activities of males and females and governs the interactions between parents and offspring. In this section, we examine how several elements of behavior contribute to the reproductive success of individuals.

Males and Females Use Different Reproductive Strategies

In sexually reproducing species, males and females often differ in their overall **reproductive strategies**, the set of behaviors that lead to reproductive success. This difference arises in part from a fundamental difference in the amount of **parental investment**, the time and energy devoted to the production and rearing of offspring, provided by the two sexes. Because eggs are much larger than sperm, females almost always contribute more energy than males to the production of a gamete.

A male might increase the number of offspring that carry his alleles simply by mating with multiple females, especially if he does not spend time and energy providing parental care to his offspring. Thus, in many animal species, males compete intensely for access to females, and any trait that increases a male's access or attractiveness to females has a big reproductive payoff.

Entirely different selection pressures operate on females, whose reproductive output is generally limited by the number of eggs they can produce. Mating with multiple males will not increase that number. But the success of her offspring may depend on the attributes of their father or the territory he holds. Thus, the females of many species choose their mates carefully. In some cases, females mate with males whose territories include abundant resources, ensuring an ample food supply for their young. In other cases, females choose robust males that will contribute “good genes” (that is, alleles that confer a high likelihood of surviving and reproducing) to her offspring, increasing their chances of long-term success.

Male Competition for Females and Female Mate Choice Foster Sexual Selection

Male competition for access to females coupled with the females' choice of mates establishes a form of natural selection called **sexual selection**, that is, selection for mating success (see Section 20.3). As a result of sexual selection, males are larger than females in many species, and males have ornaments and weapons, such as horns and antlers, that are useful for attracting fe-

males as well as for butting, stabbing, or intimidating rival males. Males typically show off these elaborate structures in complex **courtship displays** to attract the attention of females. For example, male peafowl (*Pavo cristatus*) strut in front of females while spreading a gigantic fan of tail feathers, which they shake, rattle, and roll.

Why should females choose males with exaggerated structures that they display conspicuously? Biologists have developed several hypotheses to explain the attraction. First, a male's large size, bright feathers, or large horns might indicate that he is particularly healthy, that he can harvest resources efficiently, or simply that he has managed to survive to an advanced age. These traits are, in effect, signals of male quality; and if they reflect a male's genetic makeup, he is likely to fertilize a female's eggs with sperm containing successful alleles. In some cases, big, showy males hold large, rich territories, and females that choose them gain access to the resources their territories contain.

The degree to which females *actively* choose genetically superior mates varies among species. In the northern elephant seal (*Mirounga angustirostris*), for example, female choice is more or less passive. Large numbers of females gather on beaches to give birth to their pups before becoming sexually receptive again. Males locate these clusters of females and fight to keep other males away (see Figure 20.8). Males that win have exceptional reproductive success, but only after engaging in violent and relentless combat with rival males. In this kind of mating system, females are practically guaranteed to receive sperm from large and powerful males in superb physiological condition, attributes that may well be associated with alleles that will increase their offspring's chances of living long enough to reproduce.

In other species, females exercise more active mate choice, copulating only after inspecting a group of potential partners. Among birds, active female mate choice is most apparent at **leks**, display grounds where each male possesses a small territory from which it courts attentive females. Male sage grouse (*Centrocercus urophasianus*), a lekking bird of western North America, gather in open areas among stands of sagebrush. Each male defends just a few square meters, where it struts in circles while emitting booming calls and showing off its elegant tail feathers and big neck pouches (**Figure 55.13**). Females wander among the displaying males, presumably analyzing the males' visual and acoustical displays. Eventually, each female selects a mate from among the dozens of males present. Females repeatedly favor males that come to the lek daily, defend their small area vigorously, and display more frequently than the average lek participant. In other words, favored males can sustain their territorial defense and high display rate over long periods, an ability that may correlate with useful genetic traits.



Figure 55.13
Lekking behavior. Male sage grouse (*Centrocercus urophasianus*) use their ornamental feathers in visual courtship displays performed at a lek, where each male has his own small territory. The smaller brown females observe the prancing males before choosing a mate.

Experimental studies of peafowl suggest that the top peacocks at a lek may indeed supply advantageous alleles to their offspring. In nature, peahens prefer males whose tails have many ornamental eyespots (**Figure 55.14**). In an experiment on captive birds, some females were mated to males with highly attractive tails, but others were paired with males whose tails were less impressive. The offspring of both groups were reared under uniform conditions for several months and then released into an English woodland. After 3 months on their own, the offspring of fathers with impressive tails survived better and weighed significantly more than did those whose fathers had less



Figure 55.14
Sexual selection for ornamentation. The attractiveness of a peacock (*Pavo cristatus*) to females depends in part on the number of eyespots on his extraordinary tail. The offspring of males with elaborate tails are more successful than the offspring of males with plainer tails.

attractive tails. Apparently, a peahen's mate choice does provide her offspring with a survival advantage.

Another hypothesis argues that females select showy males even though their ornate structures may impede their locomotion or their elaborate displays may attract the attention of a predator. According to this hypothesis, any male that survives *despite* carrying such a handicap must have a very strong constitution indeed, and he will pass those successful alleles—as well as the alleles responsible for the ornamental handicap—to the female's offspring.

Patterns of Parental Care and Territoriality Influence Mating Systems

In the examples of mate choice just described, successful males inseminate many females, increasing their reproductive success dramatically. But one male mating with many females is only one of several **mating systems**, the ways in which males and females pair up. Some species are **promiscuous**: individuals do not form close pair bonds, and both males and females mate with multiple partners. Other species are **monogamous**: one male and one female form a long-term association. Finally, some species are **polygamous**: *either* males *or* females may have many mating partners. If one male mates with many females, the relationship is called **polygyny**; if one female mates with multiple males, it is described as **polyandry**.

Mating systems appear to have evolved to maximize reproductive success, partly in response to the amount of parental care that offspring require and partly in response to other aspects of a species' ecology. For example, the young of most songbird species, like the white-crowned sparrow, are helpless upon hatching; all they can do is open their mouths and peep, signaling to their parents that they are ready to be fed. These young require lots of parental care, and they are more likely to flourish if both parents bring food to the nest. As you might expect, nearly all songbirds are monogamous, and males and females team up to provide parental care to their offspring.

In some other bird species, such as red-winged blackbirds (*Agelaius phoeniceus*), males establish large, resource-filled territories, and females select mates largely by the quality of the real estate a male holds. Any male with an exceptionally fine territory will be desirable, even if another female has already established herself there. A second female may judge that more resources are available in his territory than in a neighboring one, despite competition with the other female. However, if many females have already settled in a male's territory, intense competition from them may make it less attractive. Given this pattern of habitat and mate choice by females, red-winged blackbirds have a polygynous mating system; males may fertilize the eggs of multiple females and provide little if any direct care to their offspring.

STUDY BREAK

1. For monogamous species, what characteristics of males should increase their attractiveness to females?
2. What activities do male and female sage grouse perform at a lek?
3. Why might a female red-winged blackbird settle on a territory that was already occupied by another female?

55.5 The Evolution of Social Behavior

Social behavior, the interactions that animals have with other members of their species, has profound effects on an individual's reproductive success. Some animals are solitary, getting together only briefly to mate (rhinoceroses and leopards); others spend most of their lives in small family groups (gorillas); still others live in groups with thousands of relatives (termites and honey bees). Some species, such as some African antelopes and humans, live in large social units composed primarily of nonrelatives.

Group Living Carries both Benefits and Costs

Ecological factors have a large impact on the reproductive benefits and costs of social living. Groups of cooperating predators frequently capture prey more effectively than they would on their own. For example, white pelicans (*Pelecanus erythrorhynchos*) often encircle a school of fish before moving in for the kill. Conversely, prey that are subject to intense predation often gain safety in numbers. Those living in groups have more watchful eyes to detect an approaching predator. In ad-

dition, a predator may be confused when multiple prey scatter in many directions. Finally, few predators have the capacity to capture every individual in a prey cluster, so that some prey escape while the predator pursues others.

Some prey species, such as musk oxen (*Ovibos moschatus*), join forces to defend themselves actively (see the photo that opens this chapter). Even some insects, such as Australian sawfly caterpillars (*Perga dorsalis*), exhibit cooperative defensive behavior (Figure 55.15). When

predators disturb the caterpillars, all members of the group rear up and writhe about, regurgitating sticky, pungent oils that they have collected from the eucalyptus leaves they eat. Although the caterpillars can store these oils safely, they are toxic and repellent to bird predators.

A group of sawflies regurgitates more repellent eucalyptus oils than a single individual, which may explain why these insects form their simple societies. If this hypothesis is correct, solitary individuals should be at greater risk of being eaten than those that live communally. Birgitta Sillén-Tullberg of the University of Stockholm, Sweden, tested this prediction by offering sawfly caterpillars to young great tits (*Parus major*), a songbird species. Birds that received caterpillars one at a time consumed an average of 5.6, but those that received them in groups of 20 ate an average of only 4.1 caterpillars. As Sillén-Tullberg had predicted, the caterpillars were somewhat safer in a group than on their own.

In some environments, the costs of social clumping can be significant. These costs may include increased competition for food. For example, when thousands of royal penguins (*Eudyptes schlegeli*) crowd together in huge colonies (Figure 55.16), the pressure



John Alcock/Arizona State University

Figure 55.15 Social defensive behavior. Australian sawfly (*Perga dorsalis*) caterpillars clump together on tree branches. These larvae each regurgitate yellow blobs of sticky, aromatic fluid. The accumulation of fluid from a large group of caterpillars successfully deters some predators.



A. E. Zuckerman/Tom Stack & Associates

Figure 55.16 Colonial living. Royal penguins (*Eudyptes schlegeli*) on Macquarie Island, between New Zealand and Antarctica, experience both benefits and costs from living together in huge colonies.

on the local food supplies is great, increasing the risk of starvation. Communal living also facilitates the spread of contagious diseases and parasites. Nestlings in large colonies of cliff swallows (*Petrochelidon pyrrhonota*) are often stunted in growth because their nests are swarming with blood-feeding parasites, which move easily from nest to nest under crowded conditions. Such costs are probably why the vast majority of animals do not live in large, complex societies.

Fitness Varies among the Members of a Dominance Hierarchy

Recognizing the costs as well as the benefits of social living, biologists have examined features of social living that appear to reduce the fitness of some individuals. For example, some animal species form **dominance hierarchies**, social systems in which each individual's behavior is governed by its place in a highly structured social ranking. In a typical dominance hierarchy, the dominant or *alpha* individual rules the roost; subordinate individuals typically concede valuable resources to more dominant animals without so much as a peep of protest.

Although dominant individuals gain first access to resources, they also incur costs. Frequent challenges from lower ranking individuals may induce a stress response in dominant animals, which must constantly defend their status. For example, in some primates, wild dogs, and other mammals, dominant males have higher blood levels of cortisol and other stress-related hormones (see Section 40.4) than do subordinates. Elevated cortisol levels may induce high blood pressure, the disruption of sugar metabolism, and other pathological conditions.

Why does a subordinate remain in the group when dominant companions reduce its chances for reproductive success? A possible explanation is that survival rates and reproductive success may be even lower for animals that live by themselves: a solitary baboon surely quickens the pulse of a passing leopard (**Figure**

55.17). A subordinate member of a group gains the benefits, such as protection against predators, that come from being part of the group. Low-ranking males may even have the chance to copulate with one of the group's females when dominant males are not watching, thus ensuring some representation of their alleles in the next generation. And if a low-ranking individual can live long enough, its social superiors may be toppled by predation, accidents, or old age, and a one-time subordinate may find itself high on the social register with food and mates galore.

In Some Animal Societies, Individuals Exhibit Altruistic Behavior

In some species, group members appear to sacrifice their own reproductive success to help individuals that are not their direct descendants; such behaviors are collectively called **altruism**. For example, subordinate members of a wolf pack do not reproduce, but they share captured prey with the dominant pair and that pair's offspring. Altruistic behavior, by its very definition, appears to contradict a basic premise of Darwinian evolutionary theory, namely that natural selection favors traits that increase an *individual's* relative fitness. Why don't subordinate wolves simply save the energy spent on helping, bide their time until they can become dominant, and then produce their own offspring?

Behavioral ecologist William D. Hamilton of University College, London, provided a solution to this puzzle. He recognized that alleles favoring altruism could be propagated indirectly if altruistic individuals sacrificed personal reproduction to help their relatives reproduce. Helping relatives in this way can propagate the helper's own genes because the family shares alleles inherited from their ancestors.

We can quantify the average percentage of alleles that relatives are likely share by calculating their degree of relatedness (**Figure 55.18**). We start by considering half siblings who, by definition, share only one genetic parent. Half siblings share on average 25% of their alleles by inheritance from their shared parent, making their degree of relatedness 0.25. By contrast, full siblings, who share the same genetic mother *and* father, share 25% of their alleles through the mother and 25% of their alleles through the father, for a total, on average, of $25\% + 25\% = 50\%$ of their alleles. In other words, the degree of relatedness for full siblings is 0.50. The degree of relatedness between a nephew or niece and an aunt or uncle is 0.25, and the degree of relatedness between first cousins is 0.125. Thus, individuals should be more likely to help close relatives because, by increasing a close relative's fitness, the individual is helping to propagate some of its own alleles.

If altruistic behavior reduces the reproductive success of an individual exhibiting that behavior, how could an allele that promotes altruistic behavior persist

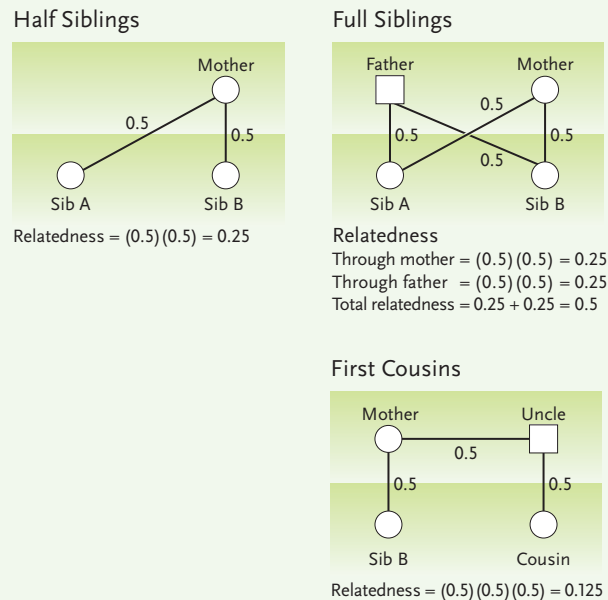
Figure 55.17
The cost of living alone. A solitary olive baboon (*Papio anubis*) confronts a leopard (*Felis pardalis*) bravely but without much chance of survival.



John Dominis/Time & Life Pictures/Getty Images

Figure 55.18 Research Method

Calculating Degrees of Relatedness



PURPOSE: The kin-selection hypothesis suggests that the extent of altruistic behavior exhibited by one individual to another is directly proportional to the percentage of alleles that they share. The hypothesis therefore predicts that individuals are more likely to help close relatives because, by increasing a close relative's fitness, the individual is helping to propagate some of its own alleles. Researchers calculate the degree of relatedness between individuals to test this prediction.

PROTOCOL: To calculate the degree of relatedness between any two individuals, we first draw a family tree that shows all of the genetic links between them. The alleles of a parent are shuffled by recombination and independent assortment in the gametes they produce, so we can calculate only the average percentage of a parent's alleles that offspring are likely to share.

We start by considering *half* siblings, those who share only one genetic parent. Each sibling receives half of its alleles from its mother. Because a parent has only two alleles at each gene locus, the probability of sibling A getting a particular allele from its mother is 0.5 (decimal notation for 50%). Similarly, the probability of sibling B getting the same allele from its mother is also 0.5. Statistically, the probability that two independent events—in this case, the transfer of an allele to sibling A and the transfer of *the same* allele to sibling B—will both occur is the product of their separate probabilities. Thus, the likelihood that both siblings receive the same allele from their mother is $0.5 \times 0.5 = 0.25$.

Now consider two *full* siblings, who share the same genetic mother *and* father. They share 25% of their alleles through the mother *plus* 25% of their alleles through the father, for a total of 50% (half their alleles). In other words, the degree of relatedness for full siblings is 0.50.

INTERPRETING THE RESULTS: Each link drawn between a parent and an offspring or between full siblings indicates that those two individuals share, on average, 50% of their alleles. We can calculate the total relatedness between any two individuals by multiplying out the probabilities across all of the links between them. Thus, the degree of relatedness between a niece and an uncle is 0.25, and the degree of relatedness between first cousins is 0.125.

or even increase in frequency in a population? The answer depends on the overall number of offspring that carry the allele in the next generation. Altruistic behavior may increase the survival of the altruist's relatives—and they may share the allele in question. If the altruistic behavior allows the assisted relatives to produce proportionately more offspring than the altruist might have produced without helping them, the allele for altruism can increase in frequency in the population. This form of natural selection is aptly called **kin selection**.

For example, suppose a male wolf helps his parents rear four pups to adulthood, pups that would have died without the extra assistance provided by the altruist. Because the pups are his siblings, they share 50% of his genes; thus, on average the helper wolf has created “by proxy” two ($0.50 \times 4 = 2$) copies of any allele that contributed to his altruistic behavior. The costs of his altruism must be measured against this indirect reproductive success. If he had abstained from altruism, the helper wolf might have raised, say, two surviving offspring of his own. Each of his offspring would

carry half of his alleles, preserving just one ($0.50 \times 2 = 1$) copy of a given allele. Under these hypothetical circumstances, reproducing on his own would have produced fewer copies of his alleles in the next generation than helping to raise his siblings.

Although our example of the altruistic wolf is hypothetical, biologists have observed sibling helpers in many bird and mammal species. The phenomenon is especially common among animals in which inexperienced young adults are unable to control sufficient resources to reproduce successfully on their own. Their altruistic behavior not only assists reproduction by their close relatives, but it may also provide useful practice for rearing their own future offspring.

Hamilton's kin-selection hypothesis explains altruistic behavior between closely related individuals, but behavioral biologists have also observed examples of altruism between nonrelatives. For example, the common vampire bat (*Desmodus rotundus*), which feeds on the blood of sleeping mammals, must consume a meal every 2 days to avoid starving to death. Bats that have consumed a large meal often share

a. Queen with sterile workers



Kenneth Lorenzen

b. Workers sharing food and passing pheromones



Kenneth Lorenzen

Figure 55.19

Life in a honeybee (*Apis mellifera*) colony. (a) A court of sterile worker daughters surrounds a queen bee, the only female of the colony that reproduces. (b) Worker bees routinely share food and transfer pheromones to one another.

their bounty with unrelated members of their group. Why would one bat share its resources with a non-relative? Robert Trivers, then of Harvard University, proposed that individuals will help nonrelatives if they are likely to return the favor in the future. Trivers called this form of altruistic behavior **reciprocal altruism**, because each member of the partnership can potentially benefit from the relationship. Trivers hypothesized that reciprocal altruism would be favored by natural selection as long as individuals that do *not* reciprocate—called “cheaters” by behavioral biologists—are denied future aid. Observations of vampire bats and some other animals have confirmed Trivers’ hypothesis: when a vampire bat accepts a “blood donation” from another bat, but then refuses to share food that it has collected, the other bats refuse to share their food with it in the future.

An Unusual Genetic System May Explain Altruism in Eusocial Insects

Hamilton’s insights lead to a critical prediction about the occurrence of self-sacrificing behavior: altruism should usually be directed to close relatives. The evidence from many animal species overwhelmingly supports this prediction, but some species of ants, bees, wasps, and termites, those known as eusocial insects, provide a truly remarkable example. In **eusocial** insects, thousands of related individuals—a large percentage of them sterile female workers—live and work together in a colony for the reproductive benefit of a single queen and her mate(s). The workers may even die in defense of their colonies. How did this self-sacrificing social behavior evolve, and why does it persist over time? The failure of altruistic workers to reproduce should doom any alleles that promote altruism to early extinction.

For example, in a honeybee (*Apis mellifera*) colony, which may contain 30,000 to 50,000 related individuals, the only fertile female is the queen bee; all of the workers are her daughters (**Figure 55.19**). The queen’s role in the colony is to reproduce. The workers perform all other tasks in maintaining the hive, from feeding the queen and her larvae to constructing new honeycomb and foraging for nectar and pollen. They also transfer food to one another and sometimes guard the entrance to the hive. Some pay the ultimate sacrifice when they sting intruders: this act of defense tears open the bee’s abdomen, leaving the stinger and the poison sac behind in the intruder’s skin, but killing the bee.

Why do bees and other eusocial insects devote their entire lives to helping their mother produce hundreds of thousands of eggs? One answer may lie in a genetic phenomenon called **haplodiploidy**, an unusual pattern of sex determination in these insects (**Figure 55.20**). Like many other organisms, female

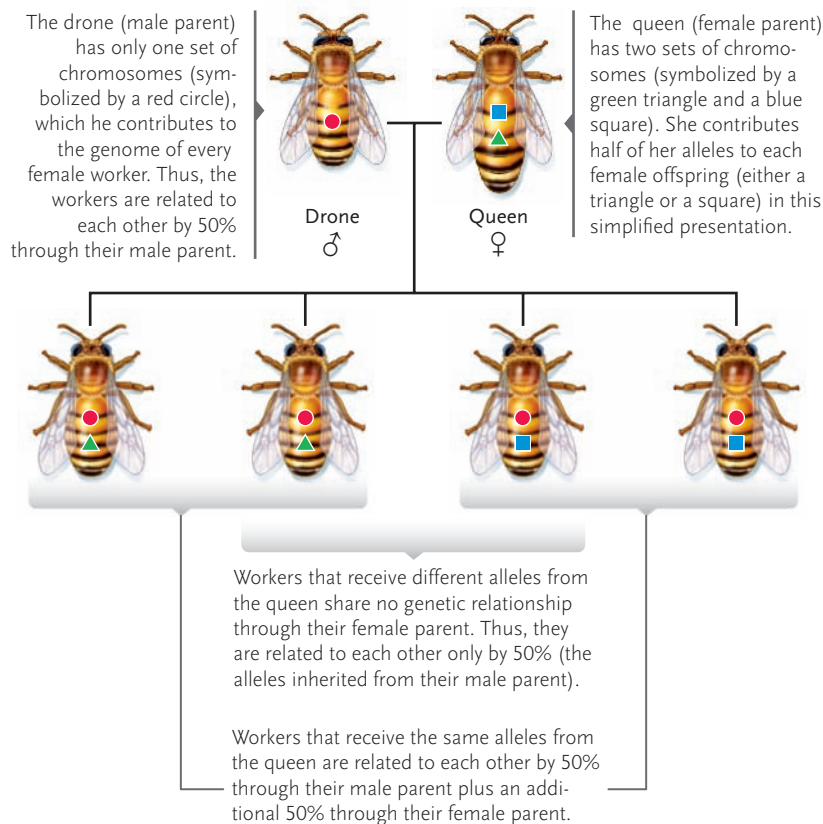


Figure 55.20

Haplodiploidy. The genetic system of eusocial insects produces full siblings that have an exceptionally high degree of relatedness. Although this simplified model ignores recombination between the queen’s two sets of chromosomes, it demonstrates how half the workers are related to each other by 50% and half are related to each other by 100%. Thus, the average degree of relatedness among workers is 75%. Including recombination would complicate the illustration, but the conclusion would be the same.

bees are diploid, receiving one set of chromosomes from each parent. But male bees are haploid: they hatch from unfertilized eggs. When a queen bee mates with one drone (a male), all of the sperm he delivers are genetically identical because males have only one set of chromosomes. Thus, all workers inherit exactly the same set of alleles from their male parent, producing a 50% degree of relatedness among them. Like other diploid organisms, the workers are also related to each other by an average of 25% through their female parent. Adding these two components of relatedness, we see that workers are related to each other by an average of 75%, a higher degree of relatedness than they would have to any offspring they produced if they were fertile.

This extremely high degree of relatedness among the workers in some eusocial insect colonies may explain their exceptional level of cooperation. When Hamilton first worked out this explanation of social behavior in these insects, he suggested that the workers devote their lives to caring for their siblings—the queen’s other offspring—because a few of those siblings, which carry 75% of the workers’ alleles, may become future queens producing enormous numbers of offspring themselves.

Nonbreeding workers also exist in a mammalian species, the naked mole-rat (*Heterocephalus glaber*), a small, almost hairless animal that lives in underground colonies of 70 to 80 individuals in eastern Africa. As described in *Insights from the Molecular Revolution*, recent studies have shown that the highly cooperative individuals occupying a colony share an exceptionally high proportion of their alleles.

STUDY BREAK

1. What do the social behaviors of musk oxen and sawfly larvae have in common?
2. Which animals in a dominance hierarchy are most likely to reproduce?
3. Why might the genetic system of many eusocial insects promote altruistic behavior?

55.6 An Evolutionary View of Human Social Behavior

Evolutionary Analyses May Help to Explain Human Social Behavior

If we can analyze the evolutionary basis of the behavior of honeybees, naked mole-rats, and other animals, perhaps we can do the same for human behavior. According to Hamilton’s kin selection hypothesis, we would

expect human altruism toward nonrelatives to be rare. And it is true that *most* acts of human altruism are directed toward family members; huge sacrifices to help nonrelatives are relatively uncommon. But why, from an evolutionary perspective, do such charitable acts toward strangers occur at all?

Many behavioral biologists believe that reciprocal altruism can explain why humans have an evolved willingness to engage in low-cost acts of charity. Such behavior demonstrates their capacity for cooperation, and generosity is a socially approved trait that may confer benefits on those who exhibit it. This hypothesis yields the prediction that people who engage in charity will usually let others know about it. That prediction is supported by data showing that when organizers of blood drives offer small participation pins to donors, more people sign up to give blood.

Sometimes researchers employ an evolutionary perspective to study difficult or painful societal issues, such as the occurrence of child abuse within families. Evolutionary theory leads us to predict that family members should generally help, not harm, one another. Margo Wilson and Martin Daly of McMaster University wondered if child abuse might be more common in reconstituted families, those with stepparents who are *not* genetically related to all the children in their care. To test this hypothesis, they examined data on criminal child abuse within families, made available by the police department of a Canadian city. In this city, the chance that a young child would be subject to criminal abuse was 40 times higher for children living with one stepparent and one genetic parent than for children who lived with both genetic parents (**Figure 55.21**).

This example illustrates the sort of insights that an evolutionary analysis of human behavior can provide. Wilson and Daly are not justifying or excusing child abusers. Neither are they claiming that abusive stepparenting is evolutionarily adaptive. Instead, their point is that humans may have some genetic characteristic that makes it more difficult to invest in children that they know are not their own, particularly if they also care for their own genetic children. These results are not just academic. Although a large majority of stepparents cope well with the difficulties of their role, a few do not. Knowledge of familial circumstances under which child abuse is more likely to occur may allow us to provide social assistance that would prevent some children from being abused in the future.

In recent years, the application of evolutionary thinking to human behavior has produced research on all sorts of questions. Sometimes the questions are interesting or even profound. Why do some tightly knit ethnic groups discourage intermarriage with members of other groups? At other times the issues may seem frivolous. Why do men often find women with certain physical characteristics attractive? Although evolution-



INSIGHTS FROM THE MOLECULAR REVOLUTION

Unadorned Truths about Naked Mole-Rat Workers

Naked mole-rats (*Heterocephalus glaber*) are sightless and essentially hairless burrowing mammals (see the accompanying photo) that live in mazes of subterranean tunnels in parts of Ethiopia, Somalia, and Kenya. Mole-rat colonies, which may include from 25 to several hundred individuals, contain a single “queen” and one to three males as the only breeding individuals. The remaining males and females are nonbreeding workers that, like the worker bees, ants, and termites of insect colonies, do all the labor: digging and defending the tunnels and caring for the queen and her mates.

One of the many unanswered questions about these colonial mammals is the genetic structure of a colony. Is close kinship one of the relationships underlying the altruistic behavior of the workers? In other words, do they cooperate because they are all brothers and sisters?

H. Kern Reeve and his colleagues at Cornell University investigated this

question using molecular techniques resembling the DNA fingerprinting analysis often used to determine human kinship. The technique (see Section 18.2) depends on a group of repeated DNA sequences that vary to a greater or lesser extent among individuals; that is, they are *polymorphic*. No two individuals (except identical twins) are likely to have exactly the same combination of sequences. Brothers and sisters with the same parents have the most closely related sequences; as relationships become more distant, the differences in the sequences increase.

The researchers began their work by capturing mole-rats living in four colonies in Kenya. Individuals from the same colony were placed together in a system of artificial tunnels. Samples of DNA, taken from individuals that died naturally in the artificial colonies, were subjected to DNA fingerprinting analysis (see Section 18.2). First, the extracted DNA was fragmented by treating with a restriction endonuclease. The DNA fragments were separated by agarose gel electrophoresis, then transferred to a membrane filter by the Southern blot technique (see Figure 18.9). Next, the DNA fragments on the filter were hybridized independently with three radioactively labeled probes that identify three distinct groups of polymorphic sequences in the mole-rat DNA. The hybridization patterns were visualized by autoradiography. The pattern of bands, different for each individual (other than twins), is the DNA fingerprint.

The fingerprint of each mole-rat was compared with the fingerprints of other members of the same and other colonies. In the comparisons, bands that were the same in two individuals were scored as “hits.” The number of hits was then analyzed to assign relatedness by noting which individuals shared the greatest number of bands.

The comparisons revealed that individuals in the same mole-rat colony were indeed closely related—they shared an unusually high number of bands, higher than human siblings and approaching the band similarity of identical twins. The number of bands shared between individuals of different colonies was significantly lower, but still higher than that noted between unrelated individuals of other vertebrate species. The close relatedness of even separate colonies, as the investigators point out, may be due to similar selection pressures or to recent common ancestry among colonies in the same geographical region.

On the basis of their results, the researchers propose that the close genetic relatedness among individuals in a colony, which is assumed to increase the degree of altruistic behavior, is one of two major factors underlying the evolution and maintenance of the nonbreeding worker caste in the colonies. The second major factor, they propose, is the chance of survival, which is greater for mole-rats remaining in colonies than for those that attempt to live and breed on their own.



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Naked mole-rats (*Heterocephalus glaber*) live in colonies containing many workers that are effectively sterile.

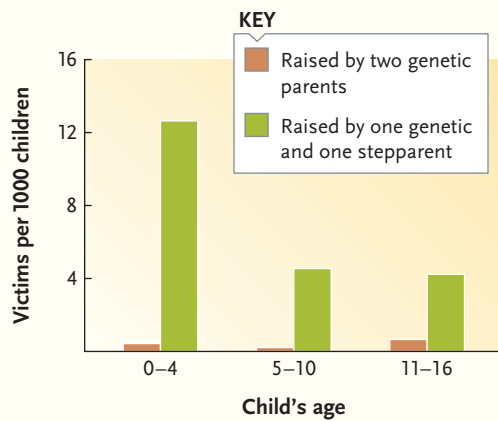
ary hypotheses about the adaptive value of behavior can be tested, helping us to understand why we behave as we do, they should never be used to *justify* behavior that is harmful to other individuals. Understanding why we get along or fail to get along with each other and the ability to make moral judgments about our behavior are uniquely human characteristics that set us apart from other animals.

STUDY BREAK

1. How might evolutionary biologists explain altruistic behavior that people exhibit to non-relatives?
2. Why might stepparents provide fewer resources to their children than birth parents do?

Figure 55.21 Observational Research

An Evolutionary Analysis of Human Cruelty



HYPOTHESIS: Wilson and Daly hypothesized that child abuse would be more common in families in which parents and children were not genetically related than in families in which parents raise their biological offspring.

PREDICTION: Stepparents abuse their stepchildren more frequently than birth parents abuse their biological children.

METHOD: The researchers analyzed data on criminal child abuse within families that had been collected by the police department of a large Canadian city.

RESULT: The data indicated that children living with one stepparent and one genetic parent were 40 times more likely to suffer criminal abuse than children living with two genetic parents.

CONCLUSION: Children raised by one genetic parent and one stepparent are significantly more likely to suffer abuse than those raised by two genetic parents.

UNANSWERED QUESTIONS

Who else is watching and listening?

Studies of communication have typically concentrated on the signaler and the intended receiver. But others are lurking in the background—eavesdroppers who are also attending to these signals. These third parties often use the signal to the signaler's detriment. Some flies, for example, listen for calling male crickets and deposit their larvae on the caller; the larvae eventually kill the cricket as they use him for a food source. Sometimes the signal that makes a male more attractive to females has the same effect on eavesdroppers. Male túngara frogs, for example, can add a "chuck" to the "whine" component of their call. These more complex calls make them more attractive to female frogs but also increase their risk of being captured by frog-eating bats or found by blood-sucking flies. Other animals circumvent this cruel bind by evolving signals in "private channels" to which intended receivers, but not predators, are privy. Ultraviolet signals in swordtail fishes and electrical signals in weakly electric fish are two examples. Increasingly, communication systems are being analyzed from the perspective of a complex communication network rather than the more simple two-way interactions.

Why do females prefer attractive mates?

One reason that females prefer attractive mates is that females can use the ornaments of males to judge their quality in terms of performance and survivorship. A superior male might provide better resources for the female and her offspring, or even pass on better genes to their young. Alternatively, male courtship traits must stand out against a sometimes chaotic background of environmental noise and signals from competing males. To stand out more than others, males might evolve signals that are better at stimulating the female's sensory, neural, and cognitive systems. If a species has evolved visual pigments that allow individuals to locate orange fruit, for example, males should

evolve orange colors, because they will better stimulate the female's visual system. Such a scenario has been suggested for guppies. Researchers who study *sensory drive* try to understand how selection on sensory systems in one context, such as feeding, can influence functions in other contexts, such as mate choice.

To what degree is human behavior influenced by natural selection?

Cooperative and altruistic behavior sometimes evolve in animal societies. Since all societies face similar basic challenges, it is not surprising that cooperation can also be important in human societies. Strong evidence suggests that cooperation has evolved under selection in animal societies, but does logic demand that it has evolved under selection in humans as well? If not, what data would provide strong evidence for the evolution of human social behavior?

The field of evolutionary psychology, which poses these questions, is constrained because the invasive experimental approaches that have been so successful in animal biology cannot be applied to humans. Here the cross-cultural, comparative approach has made some important advances. These questions are being pursued by researchers in biology and psychology as well as anthropology and sociology. This mix of researchers with different approaches guarantees excitement and controversy about these very basic questions that ask why we are who we are.



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Review

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55.1 Migration and Wayfinding

- Some animals—including some arthropods, fishes, birds, and mammals—migrate seasonally, traveling from their birthplace to a distant locality and back again (Figures 55.2 and 55.3).
- Migrating animals may use piloting, compass orientation, or navigation to find their way. In piloting, animals use familiar landmarks to guide their journey (Figure 55.4). In compass orientation, animals use the position of the sun or stars, polarized light, or the Earth's magnetic field as a guide (Figure 55.5). In navigation, animals use mental maps of their position to find their destination.
- Biologists frequently interpret migratory behavior as an adaptive response to changing food supplies (Figure 55.6). Some animals occupy northern habitats when food is plentiful during the spring and summer breeding season. They generally head south to seasonally more productive habitats before the onset of winter.

55.2 Habitat Selection and Territoriality

- Animals use multiple criteria when selecting their habitats.
- Kineses and taxes help animals orient to appropriate portions of the habitats they occupy.
- Habitat selection often has a largely genetic basis, but learning and prior experience influence habitat selection in some species (Figure 55.7).
- Animals may establish and defend territories to gain exclusive use of defendable resources that are in short supply. The costs of territoriality include the time and energy devoted to territory defense and the risk of injury from fights or exposure to predators.

55.3 The Evolution of Communication

- Animal communication occurs between a signaler, which sends a message, and a signal receiver, which receives and interprets the message.
- Animals communicate using acoustical, visual, chemical, tactile, or electrical signals (Figures 55.8–55.10). Each sensory channel provides specific advantages. Animals may use more than one channel simultaneously.
- Honeybees use a combination of tactile, acoustical, and chemical channels to share information about the location of food sources (Figure 55.11).

Animation: Honeybee dances

55.4 The Evolution of Reproductive Behavior and Mating Systems

- Males and females exhibit different reproductive strategies. Males can increase their reproductive success by inseminating the eggs of many females. Females generally seek mates that provide successful alleles to offspring, have access to abundant resources, or help care for young.
- Males often compete for access to females (Figure 55.12). Sexual selection has produced elaborate structures that males use for displays and for aggressive interactions with other males (Figures 55.13 and 55.14). Females may choose to mate with males that have showy structures and great stamina, which may function as signs that they possess successful alleles.
- The type of mating system a species uses is tied to its pattern of territoriality and the amount of parental care the male parent provides.

55.5 The Evolution of Social Behavior

- Social interactions between individuals of the same species provide both benefits and costs. Group living may provide better protection from predators, more efficient feeding, and communal care of young (Figures 55.15 and 55.17). The costs of living in a group include increased competition for scarce resources and an increase in the spread of contagious diseases (Figure 55.16).
- Dominance hierarchies are highly structured societies in which some individuals have high status and first access to resources.
- Altruistic behavior appears to contradict a basic premise of Darwinian evolutionary theory, because altruistic individuals sacrifice their own fitness for the benefit of others. However, individuals generally display altruistic behavior to close relatives that share some of their alleles (Figures 55.18).
- An unusual mechanism of sex determination, haplodiploidy, makes the workers in some eusocial insect colonies more closely related to each other than siblings are in most species (Figures 55.19 and 55.20). Haplodiploidy may have fostered the evolution of highly altruistic behavior.

Animation: Sawfly defense

55.6 An Evolutionary View of Human Social Behavior

- Although humans are more likely to provide assistance to close relatives than to nonrelatives, acts of charity to strangers are common, especially if the altruist can advertise the generosity.
- An analysis of child abuse suggests that humans are more likely to abuse children to whom they are not genetically related than they are to abuse their biological children (Figure 55.21).

Questions

Self-Test Questions

1. Which of the following statements about animal migration is true?
 - a. Piloting animals use the position of the sun to acquire information about their direction of travel.
 - b. Animals migrating by compass orientation use mental maps of their position in space.
 - c. Navigating animals use familiar landmarks to guide their journey.
 - d. Navigating animals use a compass and a mental map of their position to reach a destination.
 - e. Most migrating birds use olfactory cues to return to the place where they hatched from eggs.
2. In Marler and Moore's experiment with Jarro's spiny lizard, what evidence from males that had received testosterone implants suggested that engaging in territorial behavior carries a heavy cost?
 - a. They had to consume more water than control males.
 - b. They mated with fewer females than control males.

- c. They ate more frequently than control males.
 d. They had higher death rates than control males.
 e. They weighed more than control males.
3. Which signal type would provide the fastest communication between bats flying in a dark forest?
 a. chemical signals d. tactile signals
 b. acoustical signals e. electrical signals
 c. visual signals
4. Squashing an ant on a picnic blanket often attracts many other ants to its “funeral.” What kind of signal did squashing the ant likely produce?
 a. an electrical signal d. a chemical signal
 b. a visual signal e. a tactile signal
 c. an acoustical signal
5. Which of the following behaviors might have been produced by sexual selection?
 a. A male frog calls loudly and clearly from a pond during the breeding season.
 b. A young male goat bleats plaintively when left by its mother.
 c. A hen clucks to call its chicks closer when a predator approaches.
 d. A female lion ignores the sexual advances of a young male.
 e. A male dog is attracted to the odor of a female dog.
6. In comparison to males, the females of many animal species:
 a. compete for mates.
 b. choose mates that are well camouflaged in their habitats.
 c. choose to mate with many partners.
 d. are always monogamous.
 e. choose their mates carefully.
7. Social behavior:
 a. is exhibited *only* by animals that live in groups with close relatives.
 b. cannot evolve in animals that maintain territories.
 c. evolved because group living provides benefits to individuals in the group.
 d. is never observed in insects and other invertebrate animals.
 e. can be explained only by the hypothesis of kin selection.
8. Altruism is a behavior that:
 a. cannot evolve.
 b. has been observed only in insects.
 c. increases the number of offspring an individual produces.
 d. can indirectly spread the altruist’s alleles.
 e. can evolve only in animals with a haplodiploid genetic system.
9. The degree of relatedness between a parent and its biological offspring:
 a. is the same as that between brother and sister.
 b. is less than that between brother and sister.
 c. depends on how many siblings the parent has.
 d. promotes an individual’s reproductive success.
 e. is the same as between first cousins.
10. The tendency for humans to be charitable to perfect strangers can be explained by the hypothesis of:
 a. sexual selection. d. polyandry.
 b. kin selection. e. navigation.
 c. reciprocal altruism.

Questions for Discussion

- In Chapter 53, you learned about some of the environmental changes associated with global warming. What effects might global warming have on animal species that undertake seasonal migrations?
- The yellow-rumped whippersnapper, an imaginary species of songbird, always established breeding territories in forests where trees are interspersed among many small ponds. Design an experiment to determine what features of the environment this species uses to select its habitat.
- Although females provide parental care far more often than males in the animal kingdom as a whole, exceptions exist, especially among birds and fishes. Develop three evolutionary hypotheses to explain why male birds are so likely to involve themselves in caring for their broods.

Experimental Analysis

You discover that a particular butterfly species almost always lives in open meadows and almost never lives in nearby shaded forests. Design an experiment to test whether or not habitat selection by this species is adaptive.

Evolution Link

African honeyguides (family Indicatoridae) are birds that call to humans and other mammals, leading them to honeybee colonies in woodlands. The mammals then open the hives to extract the honey, and the honeyguide feeds on the beeswax. How could a communication system between two species evolve?

How Would You Vote?

Africanized bees are slowly expanding their range in North America. Some researchers think the more we know about them, the better we will be able to protect ourselves. Should we fund more research into the genetic basis of their behavior? Go to www.thomsonedu.com/login to investigate both sides of the issue and then vote.

