49 BEHAVIORAL ECOLOGY

My Pheromones Made Me Do It

A few years ago, as Toha Bererub walked down a street near her Las Vegas home, she felt a sharp pain above her right eye. Then another, and then another. Seconds later, hundreds of stinging bees covered the upper half of her body. Firefighters in protective gear rescued her, but not before she had been stung more than 500 times.

Bererub's tiny attackers were Africanized honeybees, a hybrid between the mild-tempered European honeybee and an African strain that is easy to provoke (Figure 49.1). Breeders had imported African bees to Brazil in the 1950s. They thought cross-breeding experiments would result in a mild-tempered but zippier pollinator for commercial orchards. However, some of the captive imports escaped and started mating with the locals.

Then, in a grand example of geographic dispersal, some descendant bees buzzed all the way from Brazil to Mexico and on into the United States. So far, the Africanized bees have established themselves in Texas, New Mexico, Nevada, California to the west, and Alabama, Virginia, and Florida to the east.

Honeybees sting only once. All species make the same kind of venom. Africanized bees make a bit less venom, but they get riled up faster and mount collective attacks. One squadron reportedly chased a perceived threat for a quarter of a mile.

The Africanized bees became known as “killer bees,” although they rarely kill their target. Their stings are extremely painful, but adults in good health usually can survive a collective attack. Bererub was seventy years old when attacked, and she recovered fully after spending a week in the hospital.

What makes the Africanized bees so testy? Isopentyl acetate. This chemical, which smells like bananas, is a key component of honeybee alarm pheromone.

A **pheromone**, remember, is a chemical signal released by one individual that may cause another individual of the species to alter its behavior. A honeybee releases an alarm pheromone when it recognizes and stings a perceived threat. The signaling molecules diffuse through air and form a concentration gradient, which guides other bees to the individual sounding the alarm.

Researchers once studied hundreds of colonies of Africanized honeybees and European honeybees to compare their responses to alarm pheromone. They positioned a tiny target in front of each colony and then released a small quantity of an artificial pheromone. The Africanized bees flew out of the colony and zeroed in on the perceived threat much faster. They also plunged six to eight times as many stingers into it.

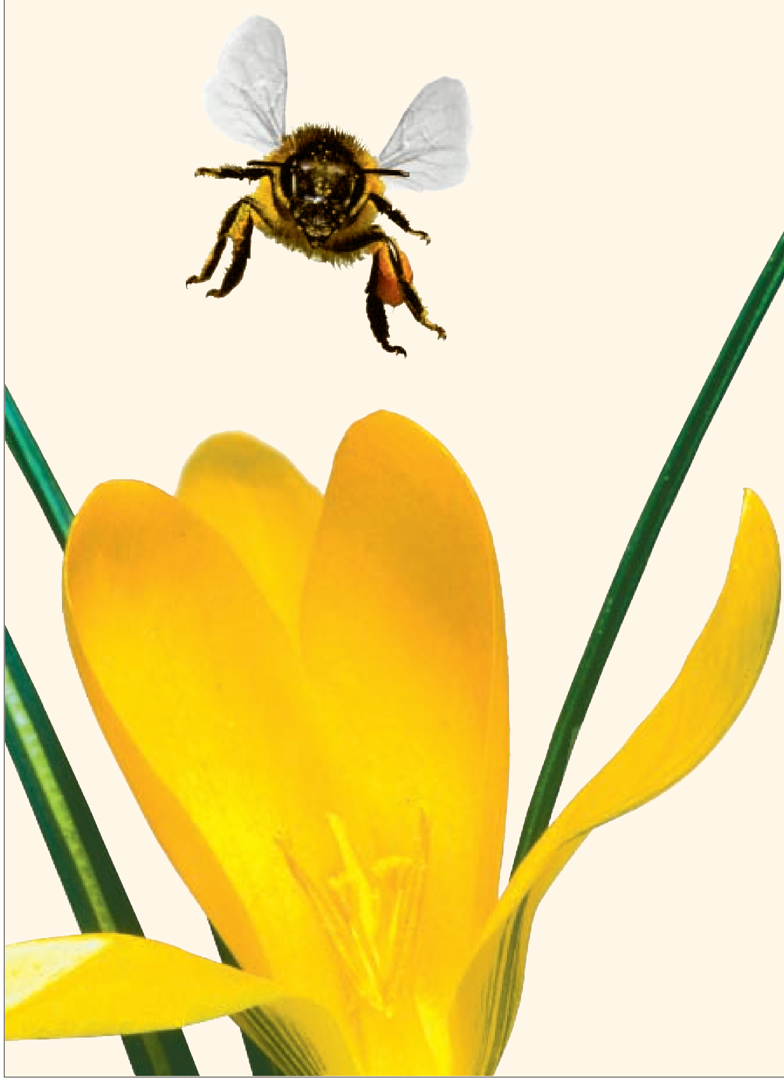


Figure 49.1 Good bee, bad bee. At left, a European honeybee about to pollinate a flower. *Facing page*, two of its aggressive relatives, Africanized honeybees, that stand guard at the entrance to their hive. If a potential intruder appears, they will release an alarm pheromone that stimulates hivemates to join an attack.

IMPACTS, ISSUES

Watch the video online!

The two kinds of honeybees show other differences in their behavior. Compared to European bees, Africanized bees are less picky about where they establish a colony. They are more likely to abandon their colony after being disturbed. Of more concern to beekeepers, they are less interested in stashing large amounts of honey.

Such differences among honeybees lead us into the world of **animal behavior**, to the coordinated responses that animal species make to stimuli. We invite you to reflect on the genetic basis of behavior before turning to the instinctive and learned mechanisms that arise from it. Along the way, we also will consider the adaptive value of behavior.

How Would You Vote?

Africanized bees are slowly expanding their range in North America. Some 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? See BiologyNow for details, then vote online.

Key Concepts

FOUNDATIONS FOR BEHAVIOR

An individual's behavior starts with interactions among gene products, such as hormones and pheromones. Most behavior has innate components but can be modified by environmental factors.

Behavioral traits that have a heritable basis and that enhance the individual's reproductive success can evolve by natural selection. Sections 49.1–49.3

CUES FOR SOCIAL BEHAVIOR

Evolved modes of communication underlie social behavior. Communication signals hold clear meaning for both the sender and the receiver of signals. Section 49.4

COSTS AND BENEFITS OF BEHAVIOR

Life in social groups has reproductive benefits and costs. Not every environment favors the evolution of such groups. Self-sacrificing behavior has evolved among a few kinds of animals that live in large family groups. Sections 49.5–49.7

FOUNDATIONS FOR HUMAN SOCIAL BEHAVIOR

The social behavior of all primates, including humans, has evolved in complex ways. Only humans consistently make moral choices about their behavior. Sections 49.8, 49.9

Links to Earlier Concepts

This chapter builds on your understanding of the nervous system and sensory systems (Sections 34.1, 35.1). You will consider the functions of neurotransmitters, hormones, and pheromones in behavior (36.1, 36.2). You will revisit the social parasites (46.7).

Be sure you understand the concepts of directional selection (18.4), sexual selection (18.6), and adaptation (18.9). You will see how predation (46.4) can exert selection pressure on the evolution of behavior. You may wish to review the sections on the evolution of primates and modern humans (26.12, 26.15).

FOUNDATIONS FOR BEHAVIOR

49.1 Behavior's Heritable Basis

LINKS TO SECTIONS 34.1, 35.1, 36.1

The nervous and endocrine systems govern behavioral responses to stimuli. Because genes specify the substances required for constructing and operating those systems, they are the heritable foundation for animal behavior.

GENES AND BEHAVIOR

Before an animal is even born or hatched, the nervous system becomes prewired to detect, interpret, and then issue commands for response to stimuli. A **stimulus**, recall, is a piece of information about the external or internal environment that a specific type of sensory receptor has detected. It takes gene products to build and operate sensory receptors, nerves and, in most species, a brain. Gene products also affect behavioral responses to stimuli.

Stevan Arnold found experimental evidence of the genetic basis for behavior in the feeding preferences of coastal and inland snake populations in California. Garter snakes living near the coast hunt banana slugs (Figure 49.2*a*). Snakes living inland hunt tadpoles and fishes. Offer them a banana slug and they ignore it.

Arnold offered captive newborn snakes a bit of slug as a first meal. Newborn coastal snakes usually ate it and flicked their tongue at cotton swabs drenched in essence of slug. (Snakes "smell" by tongue-flicking, which pulls odors into the mouth.) Newborn inland snakes ignored the swabs and rarely ate bits of slug. Here was a big difference between captive snakes that had no prior experience with slugs. These snakes are programmed before hatching to accept or reject slugs; they did not learn feeding preferences by taste trials.

Did allelic differences influence how odor-detecting mechanisms form in the garter snake embryo? Arnold crossed coastal with inland snakes. He predicted that hybrid offspring would make an *intermediate* response to slug chunks and odors, and they did. Many hybrid baby snakes tongue-flicked at slug-perfumed swabs more often than newborn inland snakes did—but not as often as newborn coastal snakes did (Figure 49.2*c*).

Some genes have been linked to specific behaviors. The *fruitless* gene controls male fruit fly courtship. A female will not mate unless a male waves his wings and licks and taps her body. Male flies that researchers induced to make the female version of the fruitless protein became more attracted to males than females. Female flies induced to make the male version of the protein waved their wings at females. These altered flies had no interest in ordinary males, but they did court males who had been made to smell like females.

This gene product is a master switch in the nervous system, with far-reaching effects on complex behavior.

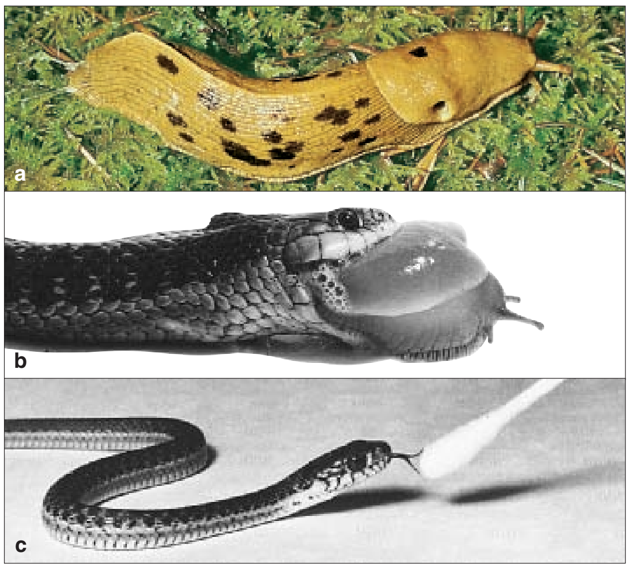


Figure 49.2 (**a**) Banana slug, food for (**b**) an adult garter snake of coastal California. (**c**) Newborn garter snake from a coastal population, tongue-flicking at a cotton swab drenched with tissue fluids from a banana slug.

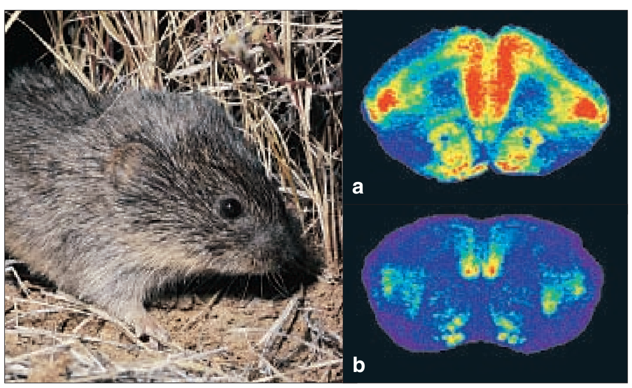


Figure 49.3 Distribution of oxytocin receptors (*red*) inside the brain of (**a**) a mate-for-life prairie vole and (**b**) a promiscuous mountain vole.

HORMONES AND BEHAVIOR

Some hormones are behavior-guiding gene products. For instance, all mammals make and secrete oxytocin, which affects more than labor and lactation (Section 44.14). In many species, it guides social behavior, such as pair bonding, aggression, and territoriality.

In prairie voles (*Microtus ochrogaster*), oxytocin is the hormonal key that unlocks the female's heart. The female of these small rodents bonds with a male after a night of repeated matings, and she mates for life. To test oxytocin's impact, researchers kept a female vole with a male for a few hours but blocked mating. They

Figure 49.4 Instinctive behavior of the European cuckoo. (**a**) This social parasite lays eggs in the nests of other birds. Even before a cuckoo hatchling opens its eyes, it reacts instinctually to anything round—typically the host bird's egg—and shoves it from the nest. (**b**) The clueless foster parents instinctually respond to a gaping mouth, not to a usurper's size or other traits that differ from their own species.

a

b

Figure 49.5 Instinctive behavior of a human baby who is imitating an adult's facial expression.

injected oxytocin into the female, and the pair bonded without the normally required sex act. By contrast, pair-bonded female prairie voles that were injected with an oxytocin blocker immediately dumped their former partners.

Whether a vole species is monogamous depends on the number and distribution of receptors for oxytocin. Monogamous prairie voles have more receptors than highly promiscuous mountain voles (Figure 49.3).

Monogamous voles also have more receptors in the brain for antidiuretic hormone (ADH). As you know, kidney cells have receptors for this hormone, but so do cells in the brain. Researchers isolated the gene for an ADH receptor in monogamous prairie voles. They transferred copies of the gene into some forebrain cells of male meadow voles (*M. pennsylvanicus*). Afterward, the males of this more promiscuous species showed an increased tendency to partner with one female only.

Male meadow voles used as a control group also got copies of the gene, but in a brain region not known to be involved in pair-bonding. Unlike the experimental group, the males retained their promiscuous ways.

INSTINCTIVE BEHAVIOR

Like many other animals, slug-loving garter snakes, wing-waving fruit flies, and pair-bonding voles offer us evidence of **instinctive behavior**—they perform a behavior without having first learned it through actual experience in the environment. They are prewired to recognize sign stimuli before being born or hatched. *Sign stimuli* are one or two simple, well-defined cues that trigger a suitable response. For garter snakes, the cue is a specific slug scent that calls for a *fixed action pattern*—a stereotyped motor program of coordinated muscle activity that runs to completion independently of feedback from the environment. The baby snake is compelled to strike, capture, and eat a slug.

Or consider cuckoos, a type of social parasite. Like cowbirds, the females lay eggs in nests of other birds. A newly hatched cuckoo is blind; skin covers its eyes. But contact with an egg (or any round object) triggers a fixed action pattern. That hatchling maneuvers the egg onto its back, then pushes it from the nest (Figure 49.4*a*). Its behavior helps the hatchling get undivided attention. Its "foster parents" are oblivious to the odd color and size of the usurper. They respond only to one sign stimulus—the gaping mouth of a chick—and continue with their parenting (Figure 49.4*b*).

Humans, too, display instinctive behavior. Three days after birth, a human infant already displays a capacity to mimic facial expressions of an adult who comes close to it (Figure 49.5). The infant cannot see its own face, nor can it feel which facial muscles the adult is using. Somehow it is able to open its mouth, protrude its tongue, or rotate its head the same way as the adult. Infants will also respond to a simplified stimulus—a flat, face-sized mask with two dark spots for eyes. One "eye" won't do the trick.

Behavior, or coordinated responses to stimuli, starts with genes. Some gene products construct and operate the nervous system, which governs behavior. Other products, such as hormones, help control the mechanisms required for specific forms of behavior.

Animals start out life neurally wired to recognize vital cues and to make an instinctively suitable response, one that has not been learned through actual experience.

Many animals execute a fixed action pattern, a stereotyped program of coordinated muscle activity in response to one or two simple, well-defined environmental cues.

49.2 Learned Behavior

With ***learned behavior****, an individual draws from past experiences and varies or changes its response to stimuli. A classic example, imprinting, occurs early in life, during a genetically determined period.*

Animals process information about experiences and then use it to change or adjust responses to stimuli. Learned behavior arises as the environment directly or indirectly influences gene expression. Sensory input and good or bad nutrition are typical factors that lead to alterations in how and what an animal learns.

Birdsong (Figure 49.6) is an instinctive behavior. Even so, songbirds can learn variations, or dialects, of the species song in different habitats. As Peter Marler demonstrated, many male birds learn the full song ten to fifty days after hatching by listening to other birds sing it. The male nervous system is prewired to recognize the species song; a learning mechanism is primed to select and respond to acoustical input. But what the male bird hears during a sensitive period shapes his *rendition* of the song.

In one study, Marler raised white-crown nestlings to maturity in soundproof chambers so they could not hear adult males. Their songs did not have the exact structure of a typical adult song. Marler also isolated captive nestlings and let them hear recorded songs of white-crown sparrows *and* song sparrows. When the captives matured, they sang just the white-crown song and mimicked the species dialect of the unseen tutor.

In another experiment, Marler did not use taped songs. He let young, hand-reared male white-crowns interact with a "social tutor" of the different species. The males tended to learn the tutor's song.

Results from many such experiments support this hypothesis: Birdsong starts with the genetically based capacity to learn from acoustical cues.

Imprinting is a classic case of learned behavior. This time-dependent form of learning is triggered by exposure to a sign stimulus. Exposure normally takes place during a sensitive period when the animal is young. Imprinting of baby geese on their mother is a favorite example of animal behaviorists (Figure 49.7).

Animals process information about experiences in the environment and use it to change or vary their response to a stimulus. This learned behavior involves interactions between gene products and environmental inputs.

Figure 49.6 Male marsh wren belting out a territorial song that has been likened to a loud gurgle. Males of this species start to imitate their species song when they are about fifteen days old. Unlike many species, marsh wrens continue to learn songs throughout their life.

a

b

Figure 49.7 No one can tell these imprinted baby geese that Konrad Lorenz is not Mother Goose!

(**a**) In response to a moving object and probably acoustical cues, baby geese imprint on the mother goose and follow her during a short, sensitive period right after hatching. They are neurally wired to learn crucial information—the identity of the one individual that will be most likely to protect them in the months ahead. Usually that will be their mother.

(**b**) Konrad Lorenz, one of the early investigators of animal behavior, presented these baby geese with sign stimuli that made them form an attachment to him.

49.3 The Adaptive Value of Behavior

If forms of behavior have a genetic basis, then they may evolve in various ways through natural selection. Alleles that encode the most adaptive versions of a trait tend to to increase in frequency in a population, and alternative alleles do not. In time, genetic changes in behavior that yield greater reproductive success are favored.

Natural selection theory helps us develop and test explanations of why some behavior persists and how it offers reproductive benefits that offset reproductive costs (disadvantages) associated with it. If a behavior is adaptive, it promotes the *individual's* production of offspring. Here are five definitions to keep in mind:

1. **Reproductive success**. An individual reproduces, and at least some offspring survive.
2. **Adaptive behavior**. A form of behavior that helps perpetuate the individual's genes. Its frequency in a population is maintained or increases over time.
3. **Social behavior**. Behavior expressed in the context of interactions among individuals of the same species.
4. **Selfish behavior**. Form of behavior that improves an individual's chance to produce or protect its own offspring regardless of the impact on the population.
5. **Altruism**. Self-sacrificing behavior. An individual behaves in a way that helps others in the population but reduces its own chance of producing offspring.

When biologists speak of selfish or altruistic behavior, they do not mean that the individual is consciously aware of some behavior or its reproductive goal. A hungry lion does not have to know that eating zebras is good for reproductive success. Its nervous system simply calls for *HUNTING BEHAVIOR!* when that lion sees a zebra. Hunting behavior persists in lion populations because genes for neural mechanisms that command hunting behavior are persisting.

To assess the adaptive value of any behavior, look for how it might promote reproductive success. For example, starlings (*Sturnus vulgaris*) nest in cavities of trees and decorate the nest bowl with sprigs of fresh leaves of pungent plants, such as wild carrot (*Daucus carota*). Larry Clark and Russell Mason hypothesized that nest decorating behavior suppresses populations of mites that infest nests and parasitize birds. Even a few mites produce thousands of descendants. In large numbers, mites suck enough blood from a nestling to weaken it and affect its growth and survival.

Clark and Mason tested their hypothesis with a set of experimental nests, some with fresh-cut wild carrot leaves and some without. They removed natural nests that starlings were using. Half of the nesting starling pairs got new nests with wild carrot sprigs. Swapped nests for the other pairs were sprigless. Figure 49.8*c* gives the results. Sprig-free nests had more mites than sprig-festooned nests. At the end of one experiment, sprig-free nests teemed with an average of 750,000 mites. Nests with sprigs had 8,000 mites. Why? Wild carrot sprigs contain an aromatic steroid compound that repels herbivores and helps plants survive. By coincidence, it prevents mites from maturing sexually.

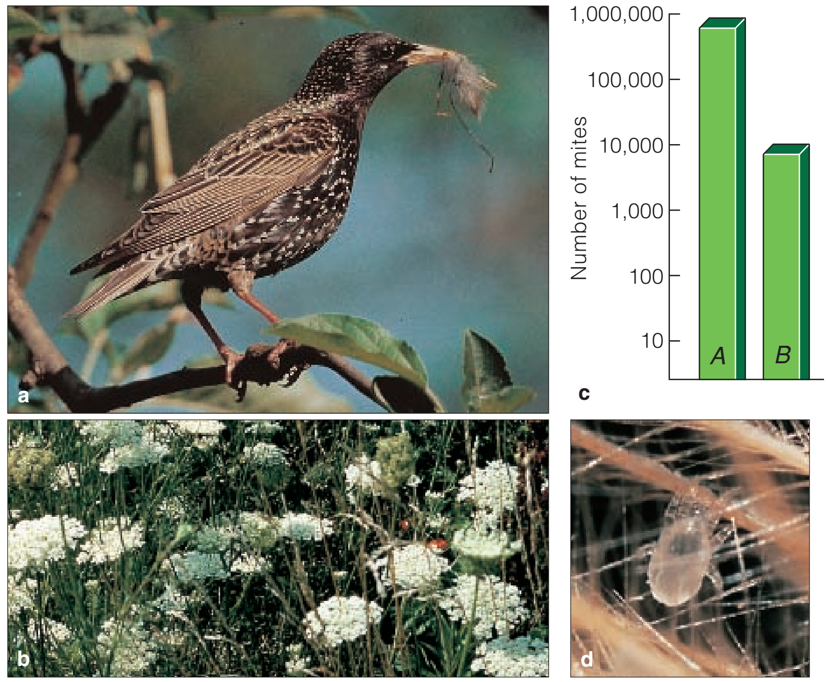


Figure 49.8 Experimental test of the adaptive value of starling nest-decorating behavior (**a**). Nests designated *A* did not have fresh sprigs of wild carrot (**b**) and other plants that make aromatic compounds. Nests designated *B* had fresh sprigs added every seven days. (**c**) Twenty-one days after the experiment started, the chicks left and researchers made counts of the mites (*Ornithonyssus sylviarum*) infesting each nest. The test results supported the hypothesis that aromatic compounds suppress development of juvenile mites into (**d**) adult mites.

Selection theory continues to guide experiments on this behavior. For instance, other researchers did not yield the same evidence that greenery reduces mite populations. Rather, their test results indicate that the decorating behavior may be adaptive either because it deters different kinds of parasites or because it boosts the immune function of the nestlings.

A genetically determined behavior may persist or increase in frequency in a population when it is adaptive. A behavior is adaptive when it increases the number of descendants that an individual successfully produces.

49.4 Communication Signals

LINKS TO SECTIONS 18.6. 35.1, 36.1

Competing for food, defending territory, alerting others to danger, advertising sexual readiness, forming bonds with a mate, caring for the offspring—such intraspecific behaviors require unambiguous forms of communication.

THE NATURE OF COMMUNICATION SIGNALS

Communication signals are unambiguous cues sent and received among individuals of a species, and they involve instinctive and learned forms of behavior. Information-laden cues from a signaler are meant to change the behavior of receivers. Chemical, acoustical, and visual cues are among the most common.

Pheromones, again, are communication signals. The *signaling* pheromones induce the receiver to respond fast. They include chemical alarms, such as honeybee calls to action against potential threats. They include sex attractants. Bombykol is one of them. Bombykol molecules released by a female silk moth can attract males that are kilometers away. *Priming* pheromones bring about physiological (not behavioral) responses. As one example, a volatile odor in the urine of certain male mice can trigger and enhance estrus in female mice of the same species.

Acoustical signals are common. Male birds, frogs, grasshoppers, whales, and many other animals make sounds that attract females. Prairie dogs bark alarms. Wolves howl and kangaroo rats drum their feet on the ground when advertising possession of territory.

Some signals never vary. Zebra ears pressed flat to the head convey hostility; ears pointing up convey its absence. Different signals convey the intensity of the message. A zebra with ears laid back is not too riled up as long as its mouth is open only a bit. When the ears are laid back and its mouth gapes, watch out. That combination is a type of *composite* signal. Such signals have information encoded in two or more cues.

Signals often take on different meaning in different contexts. A lion emits a spine-tingling roar to keep in touch with its pride *or* to threaten rivals. Also, a signal can convey information about signals to follow. Dogs and wolves solicit play behavior with their play bow, as in Figure 49.9*a*. Without the bow, the signal receiver may construe the behaviors that follow as aggressive, sexual, or even exploratory—but not playful.

Signals evolve or persist in a population when they promote reproductive success of both the sender *and* receiver. If a signal is harmful, natural selection will favor individuals that don't send it or respond to it.

COMMUNICATION DISPLAYS

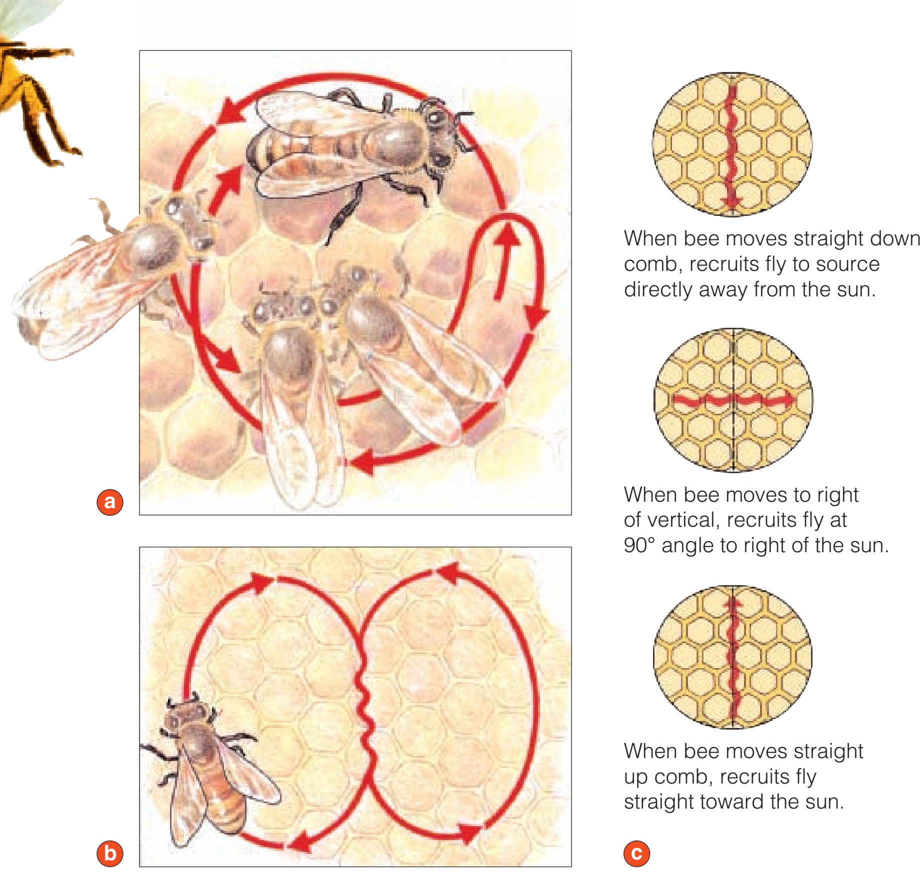
The play bow is a *communication* display, a pattern of behavior that is a social signal. The *threat* display is another common pattern. It announces that a signaler is prepared to attack a signal receiver. If a rival for a receptive female confronts a dominant male baboon, the dominant animal will roll his eyes upward and "yawn," which exposes sharp canines (Figure 49.9*b*). The signaler can benefit when the rival backs down, because he can control access to the female without having to fight. The signal receiver benefits because he can avoid a serious beating, infected wounds, and possibly death.

Figure 49.9 Communication displays. (**a**) Play bow of a young male wolf soliciting a romp. (**b**) Part of a male baboon's threat display: exposed canines. (**c**) Courtship display of Adelé penguins.

Figure 49.10 ***Animated!*** Honeybee dances, a classic example of a tactile display. (**a**) Honeybees that have visited a source of food close to their hive return and perform a *round* dance on the hive's honeycomb. Worker bees that maintain contact with the foraging bee throughout the dance will fly out and search for food near the hive.

(**b**) A bee that visits a feeding station more than 100 meters distant from the hive performs a *waggle* dance. During the dance, it makes a straight run and waggles its abdomen. A waggle dancer also varies the dance speed to convey more information about distance to a food source. For example, when food is 150 meters away, a bee dances much faster, and with more waggles per straight run, compared to a dance about a food source that is 500 meters away.

(**c**) As Karl von Frisch discovered, a *straight* run's orientation varies, depending on the direction in which a food source is located. He put one dish of honey on a direct line between a hive and the sun. Foragers that located it returned to the hive and oriented their straight runs right up the honeycomb. He put another dish of honey at right angles to a line between the hive and the sun. Foraging bees made their straight runs 90 degrees to vertical on the honeycomb. Thus, a honeybee "recruited" into foraging orients its flight *with respect to the sun and the hive*. By doing so, it wastes less time and energy during its food-gathering expedition.



Such displays are ritualized, with intended changes in the function of common behavior patterns. Normal movements might be exaggerated or frozen. Feathers, manes, claws, and other body parts are often notably enlarged, patterned, and colored. Ritualization is well developed in *courtship* displays—the steps that must precede pair formation. Courtship displays are well developed among birds (Section 18.6 and Figure 49.9*c*).

With *tactile* displays, a signaler touches the receiver in ritualized ways. After locating a source of pollen or nectar, a foraging honeybee returns to its colony (the hive) and performs a complex dance. It moves in a defined pattern, jostling a crowd of workers that stay in close physical contact with it. Its signals give other bees information about the general location, distance, and direction of a food source (Figure 49.10).

ILLEGITIMATE SIGNALERS AND RECEIVERS

Unintended recipients can intercept communication signals. Male tungara frogs make two kinds of calls—one simple, the other complex. The calls mean "come on over" to female frogs, but they mean "dinner over here" to fringe-lipped bats. Complex calls are more inviting to females but make it easier for bats to find the caller. When bats are near, male frogs vocalize less and are more likely to make the simpler call.

There are illegitimate signalers, too. Some assassin bugs can borrow the scent of their prey—termites—by hooking a dead termite on their back. By signaling that they "belong" to a termite colony, they can more easily hunt termites. As another example, if a female of certain predatory firefly species sees a flash from a male of a different species, she will flash back. If she lures him into attack range, she will capture and eat him. Getting eaten is an evolutionary cost of having an otherwise useful response to a come-hither signal.

A communication signal transfers information from one individual to another individual of the same species. Such signals benefit both the signaler and the receiver.

Some individuals of a different species act illegitimately as a communication signaler or receiver.

49.5 Mates, Offspring, and Reproductive Success

LINKS TO SECTIONS 18.6, 26.10

For reasons we need not explore here, many people find mating and parenting behaviors of animals fascinating. How useful is selection theory in helping us interpret such behavior? Take a look.

SEXUAL SELECTION AND MATING BEHAVIOR

Competition among members of one sex for access to mates is common. So is choosiness in selecting a mate. Such activities, recall, are forms of **sexual selection**. This microevolutionary process favors traits that give the individual a competitive advantage in attracting and often holding on to mates (Section 18.6).

But *whose* reproductive success is it—the male's or the female's? Male animals, remember, produce many tiny sperm, and females produce far larger but fewer eggs. For the male, success generally depends on how many eggs he can fertilize. For the female, it depends more on how many eggs she produces or how many offspring she can raise. Usually, the most important factor in a female's sexual preference is the quality of the mate, not the quantity of partners.

Female hangingflies (*Harpobittacus apicalis*) provide an instructive example. They choose males that offer superior food. A male hunts and kills a moth or some other insect. Then he releases a sex pheromone, which attracts females to him and his "nuptial gift" (Figure 49.11*a*). A female tends to select the male that offers a large calorie-rich gift. Only after the female has been eating the gift for five minutes or so does she start to accept sperm from her partner. She lets the male continue inseminating her—but only for as long as it takes for her to devour the gift.

Before twenty minutes are up, a female hangingfly can break off the mating at any point. If she does, she might well mate with a different male hangingfly and accept his sperm. Doing so dilutes the reproductive success of her first partner.

Females of different species shop around for males with the best burrows. Consider the fiddler crabs that live along muddy shores from Massachusetts down to Florida. In males, one of the two claws is enlarged. Some of those claws are enlarged enough to make up more than half the body weight (Figure 49.11*b*). When spring tides are favorable, the male crabs build their elaborate mating burrows in the same area. Each male stands beside his burrow, waving his oversized claw. Females stroll by, checking out details of the burrows. When a female likes what she sees, she will follow the male into his burrow and engage in sex.

Many female birds are choosy. Male sage grouse (*Centrocercus urophasianus*) converge at a **lek**, a type of communal display ground. Each male stakes out a few square meters. With tail feathers erect, males use their large, puffed-out neck pouches to emit booming calls (Figure 49.11*d*). As they do, they stamp about on

Figure 49.11 (**a**) Male hangingfly dangling a moth as a nuptial gift for a potential mate. Females of some hangingfly species choose sexual partners that offer the largest gift to them. By waving his enlarged claw, a male fiddler crab (**b**) may attract the eye of a female fiddler crab (**c**). A male sage grouse (**d**) showing off as he competes for female attention at a communal display ground.

their patch of prairie, a bit like wind-up toys. Females tend to select and mate with one male sage grouse. Afterward, they go off to nest and raise the young by themselves. Many females often select the same male, so most of the males never do mate.

In another behavioral pattern, sexually receptive females of some species cluster in defendable groups. Where you come across such a group, you are likely to observe males competing for access to clusters. The competition for ready-made harems has resulted in combative male lions, sheep, elk, elephant seals, and bison, to name a few types of animals (Figure 49.12).

Figure 49.12 Male bison locked in combat during the breeding season.

PARENTAL CARE

When females fight for males, then we can expect that the males provide more than sperm delivery. Some help with parenting. Midwife toads are an example. A male wraps strings of fertilized eggs around his legs until the eggs hatch (Figure 49.13*a*). With her eggs being cared for, a female can mate with other males, if she can find some that are not already caring for eggs. Late in the breeding season, unencumbered males are rare, and female toads fight for access to them. The females even attempt to pry mating pairs apart.

Parental behavior uses up time and energy, which parents otherwise might spend on living long enough to reproduce again. However, for many species, the benefit of immediate reproductive success outweighs the cost of parenting. Reproductive success might be more chancy later on.

For amphibians and reptiles, parenting is rare once the young are hatched. Crocodilians are an exception. Crocodilian parents construct a nest, as birds do. Their young call out when they are ready to hatch. Parents dig up the young and care for them for some time.

Most birds are monogamous, and both parents often care for the young (Figure 49.13*b*). In mammals, males typically leave after mating. Females raise the young alone, and males attempt to mate again or conserve energy for the next breeding season (Figure 49.13*c*). Mammalian species in which males do help care for the young tend to be monogamous. About 5 percent of all mammals fall into this category.

Researchers use selection theory to explain some aspects of mating behavior.

Male or female preferences for certain behavioral traits can provide the individual with a competitive edge and promote its reproductive success.

Figure 49.13 (**a**) Male midwife toad with developing eggs wrapped around his legs. (**b**) Male and female Caspian terns cooperate in the care of their chick. (**c**) A female grizzly will care for her cub for as long as two years. The male takes no part in its upbringing.

49.6 Costs and Benefits of Social Groups

LINKS TO SECTIONS 45.1, 46.4

Survey the animal kingdom and you will find a range of social groups, with evolutionary costs and benefits.

COOPERATIVE PREDATOR AVOIDANCE

Cooperative responses to predators help some groups reduce the net risk to all. Vulnerable individuals, too, can be on the alert for predators, join a counterattack, or engage in more effective defenses (Figure 49.14).

Vervet monkeys, meerkats, prairie dogs, and many other mammals cooperate with their alarm calls, as in Figure 49.14*a*. A prairie dog makes a particular bark when it sights an eagle and a different signal when it sights a coyote. Others dive into burrows to escape an eagle's attack or they stand erect, the better to scan the horizon and zero in on the threat.

Ecologist Birgitta Sillén-Tullberg observed group benefits for Australian sawfly caterpillars that live in clumps on branches (Figure 49.14*b*). When disturbed, individuals collectively rear back, writhe, and vomit partly digested eucalyptus leaves, which are toxic to songbirds and other animals that prey on them.

As Sillén-Tullberg hypothesized, individual sawfly caterpillars benefit from their coordinated repulsion of predatory birds. She used her hypothesis to predict that birds are more likely to eat a lone caterpillar. She tested her prediction with young hand-reared birds. Birds that were offered one caterpillar at a time ate an average of 5.6 caterpillars. Birds that were offered a clump of caterpillars ate an average of 4.1. Individuals were safer in a group, as predicted.

THE SELFISH HERD

Simply by their physical position in the group, some individuals form a living shield against predation on others. They belong to a **selfish herd**, a simple society that benefits their reproductive self-interest. Selfish-herd behavior has been studied in bluegill sunfishes. Male sunfishes build adjacent nests on the bottom of a lake. Then females deposit their eggs where males have used their fins to scoop out depressions in mud.

If a colony of bluegill males is a selfish herd, then we can predict competition for the "safe" sites—at the center of a colony. Compared to eggs at the periphery, eggs in nests at the center are less likely to be eaten by snails and largemouth bass. Competition does indeed occur. The largest, most powerful males tend to claim centermost locations. Other, smaller males assemble around them and bear the brunt of predatory attacks. Even so, they are better off in the group than on their own, fending off a bass single-handedly, so to speak.

COOPERATIVE HUNTING

Many predatory mammals, including wolves, lions, and wild dogs, live in social groups and cooperate in hunts (Figure 49.15). Are group hunts more successful than solitary hunts? Often they are not. Researchers observed a solitary lion that captured prey about 15 percent of the time. Two lions hunting together did capture prey twice as often, but they had to share it, so the number of successful hunts per lion balanced

Figure 49.14 Group defenses. (**a**) Black-tailed prairie dogs bark an alarm call that warns others of predators. Does this put the caller at risk? Not much. Prairie dogs usually act as sentries only if they are done feeding and are standing beside their burrows. (**b**) Australian sawfly caterpillars form clumps and collectively regurgitate a fluid (the yellow blobs) that is toxic to most predators. (**c**) Musk oxen adults (*Ovibos moshatus*) form a ring of horns, often around the young.

Figure 49.15 Members of a wolf pack (*Canis lupus*). Wolves cooperate in hunting, caring for the young, and defending a territory. Benefits are not distributed equally. Only the highest ranking individuals, the alpha male and alpha female, breed.

out. When more lions joined the hunt, the success rate per lion fell. Wolves show a similar pattern. Among many cooperative hunters, hunting success in itself might not explain group living. Individuals do hunt together, but they also may fend off scavengers, care for one another's young, and protect territory.

DOMINANCE HIERARCHIES

Many social groups share resources unequally among some individuals that are subordinate to others. Most wolf packs, for instance, have one dominant male that breeds with just one dominant female. Other wolves in the pack are nonbreeding brothers and sisters, or aunts and uncles. They all hunt and bring food to the individuals that guard the young in their den.

Baboons live in large troops. A female stays with the group into which she was born and inherits social standing from her mother. Dominant females get more food, water, and grooming. Their young grow and mature faster than those of lower-ranking females.

Why would a subordinate give up resources and, often, breeding privileges? It might get injured or die if it challenges a strong individual. It might not be able to survive on its own. A subordinate might even get a chance to reproduce if it lives long enough or if its dominant peers are taken out by a predator or old age. Some subordinate wolves and baboons do move up the social ladder when the opportunity arises.

REGARDING THE COSTS

If social behavior is advantageous, *then why are there so few social species?* In most habitats, the costs outweigh benefits. For instance, packed-together individuals do compete more for a share of resources (Section 45.1). Cormorants, puffins, and many other seabirds form dense breeding colonies, as in Figure 49.16. All must compete for a share of the same ecological pie.

Figure 49.16 Nearly uniform spacing in a crowded cormorant colony.

Large social groups also attract more predators. If individuals are crowded together, they invite parasites and contagious diseases that jump from host to host. The individuals may also be at risk of being killed or exploited by others. Given the opportunity, breeding pairs of herring gulls cannibalize a neighbor's eggs and any chicks that wander away from their nest.

Living in a social group can provide benefits, as through cooperative defenses or shielding against predators.

Group living has costs, in terms of increased competition, increased vulnerability to infections, and exploitation by others of the group.

49.7 Why Sacrifice Yourself?

LINK TO CHAPTER 46 INTRODUCTION

Extreme cases of sterility and self-sacrifice have evolved in only two groups of insects and one group of mammals. How are genes of the nonreproducers perpetuated?

SOCIAL INSECTS

Honeybees and fire ants (Chapter 46) are among the true social (eusocial) insects. Like termites, they stay together for generations in a group that has a division of labor. Many permanently sterile individuals care cooperatively for the offspring of just a few breeding individuals. Often they are highly specialized in form and function (Figure 49.17).

Consider a honeybee hive. The only fertile female, a queen, secretes a pheromone that other female bees distribute through the hive. This signaling molecule suppresses the development of ovaries in all the other females, which makes them sterile. The queen bee is larger than worker bees partly because of her enlarged egg-producing ovaries (Figure 49.18*a*).

About 30,000 to 50,000 female workers feed larvae, clean and maintain the hive, and build honeycomb from waxy secretions. Adult worker bees live for about six weeks in the spring and summer. When foragers return to the hive after finding a rich source of nectar or pollen, they engage others in a dance. This tactile display recruits more foragers (Figure 49.10). Workers also cooperate through the transfer of food from one to another. They guard the entrance to the hive and will sacrifice themselves to repel intruders.

Males, the stingless drones, develop only in spring and in summer. They have no part in the day-to-day work and subsist on food gathered by their worker sisters. Drones live for sex. Each day, they fly out in search of a mate. If one is lucky, he will find a virgin queen on her single flight away from her colony. The sole function of her flight is to meet up with and mate with a drone. A drone dies right after he inseminates a virgin queen, which then founds a new colony. She will store and use his sperm for years, perpetuating his genes and those of his original colony.

Like honeybees, termites live in enormous family groups with a queen specialized for producing eggs (Figure 49.18*c*). Unlike a honeybee hive, each termite colony holds sterile individuals of both sexes. A king supplies the female with sperm. Winged reproductive termites of both sexes develop seasonally.

SOCIAL MOLE-RATS

Vertebrates are not known for sterility and extreme self-sacrifice. The only eusocial mammals are African mole-rats. The best studied is *Heterocephalus glaber*, the naked mole-rat. Clans of this nearly hairless rodent build and occupy burrows in arid parts of East Africa.

A reproducing female dominates the clan, and she mates with one to three males (Figure 49.18*b*). Other, nonbreeding members live just to protect and care for the "queen" and "king" (or kings) and their offspring. The sterile diggers excavate subterranean tunnels and chambers that are living rooms or dumps for wastes. When a digger comes across a tasty tuber or root, it hauls some back to the main chamber, where it emits a series of chirps. Its chirps recruit others, which help carry the tuber back to the chamber. In this way, the queen, her retinue of males, and her offspring get fed. Digger mole-rats also deliver food to other helpers that seem to loaf about, shoulder to shoulder and belly to back, with the reproductive royals. These "loafers" actually spring to action when a snake or some other enemy threatens the clan. Collectively, and at great risk, they chase away or attack and kill the predator.

Figure 49.17 Specialized ways of serving and defending the colony. (**a**) An Australian honeypot ant worker. This sterile female is a living container for her colony's food reserves. (**b**) Army ant soldier (*Eciton burchelli*) with formidable mandibles. (**c**) Eyeless soldier termite (*Nasutitermes*). It bombards intruders with a stream of sticky goo from its nozzle-shaped head.

Figure 49.18 Three queens. (**a**) A queen honeybee with her court of sterile worker daughters. (**b**) This queen naked mole-rat has twelve mammary glands, the better to feed her many offspring. In a laboratory colony at Cornell University, one female produced a litter of twenty-eight pups. She gave birth to more than 900 offspring during her lifetime. (**c**) A termite queen (*Macrotermes*) dwarfs her offspring and her mate. Her body pumps out thousands of eggs a day.

Figure 49.19 Damaraland mole-rats in a burrow. Like their relatives, the naked mole-rats, they live in colonies having nonbreeding workers. Unlike naked mole-rats, these fuzzy burrowers are not highly inbred.

INDIRECT SELECTION FOR ALTRUISM

None of the altruistic individuals of a honeybee hive, termite colony, or naked mole-rat clan directly passes genes to the next generation. So how are genes that underlie altruistic behavior perpetuated? According to William Hamilton's theory of **inclusive fitness**, genes associated with altruism can be favored by selection if they lead to behavior that will increase the number of offspring produced by an altruist's closest relatives.

A sexually reproducing, diploid parent caring for offspring is not helping exact genetic copies of itself. Each of its gametes, and each of its offspring, inherits one-half of its genes. Other individuals of the social group that have the same ancestors also share genes with their parents. Two siblings (brothers or sisters) are as genetically similar as a parent and its offspring. Nephews and nieces share about one-fourth of their uncle's genes.

Sterile workers may be indirectly promoting genes for "self-sacrifice" through altruistic behavior that will benefit their close relatives. All of the individuals in honeybee, termite, and ant colonies are members of a great extended family. Nonbreeding family members support siblings, a few of which are future kings and queens. Although a guard bee dies after driving her stinger into a bear, siblings in the hive will perpetuate some of her genes.

Does close kinship explain why naked mole-rats are the only eusocial mammals? DNA fingerprinting studies of one naked mole-rat clan revealed that all of the individuals are *very* close relatives and genetically different from individuals of other clans. Each clan is highly inbred after many generations of brother–sister, mother–son, and father–daughter matings.

However, inbreeding might not even be necessary for mole-rat eusociality. The social organization of the Damaraland mole-rat (*Cryptomys damarensis*) resembles that of *H. glaber* (Figure 49.19). Nonbreeding members of both sexes cooperatively assist one breeding pair. Even so, breeding pairs of wild Damaraland mole-rat colonies usually are unrelated.

Researchers are now searching for other factors that select for eusocial behavior in mole-rats. According to one hypothesis, arid habitats and patchy food sources favor mole-rat genes that give rise to cooperation in digging burrows, searching for food, and fending off competitors of other species for resources.

Altruistic behavior may persist when individuals pass on genes indirectly, by helping relatives survive and reproduce.

By the theory of inclusive fitness, genes associated with altruistic behavior that is directed toward relatives may spread through a population in certain situations.

49.8 A Look at Primate Social Behavior

LINKS TO SECTIONS 26.12, 26.15

Primates, especially chimpanzees and bonobos, live in groups. Their social environment is a significant factor in determining an individual's reproductive success.

In the 1960s Jane Goodall, a young primatologist, set out on her lifelong study of chimpanzees in Tanzania. One of her earliest discoveries was the chimpanzee's capacity to make and use simple tools—"fishing sticks"—by stripping leaves from branches. The long, flexible sticks are inserted into a termite mound, as shown in Figure 49.20*a*, which agitates the termites. The stick is carefully withdrawn after termites swarm on it, and the chimpanzee gets a high-protein snack. Thicker sticks are used to make holes in the mound, then the fishing sticks are inserted into the holes.

Different chimpanzee groups use slightly different tool-shaping and termite-fishing methods. Youngsters of each group learn by imitating the adults.

Male chimpanzees spend their lives in the group in which they are born and form strong social bonds. The females are often unrelated and interact little with one another. A female's status is dictated mostly by how she gets along with the males. Before the rainy season, mature females that are entering their fertile cycle go through hormone-driven physiological and behavioral changes. Their external genitalia become swollen and vivid pink. The swellings are strong visual signals to males. They are flags for sexual jamborees—for great gatherings of highly stimulated chimpanzees in which any males present may have a turn at copulating with the same female.

Male chimpanzees cooperatively hunt for monkeys, small pigs, and antelopes. They may also cooperate in attacks on neighboring groups. Males sometimes even kill infants. By one hypothesis, infanticidal behavior of males may exert selection pressure for promiscuity in females. A female who mates with many males might protect her offspring by obscuring their paternity. A male would be expected to avoid killing an infant that might carry his genes.

Comparative studies of the closely related bonobo reveal contrasting sexual and social behavior (Figure 49.20*b*). As with chimpanzees, adult males are related and females are not. Yet bonobo females form strong social bonds. Unlike female chimpanzees, they can be receptive to sex at any time, not just during the fertile cycle. Male bonobos display less social cohesion than male chimpanzees do. They do not hunt together, and no one has come across an infanticidal male.

What explains the differences? Does a higher level of interaction help female bonobos deter potentially infanticidal males? Does unlimited access to sexually receptive females interfere with male–male bonding or diffuse male aggression? We do not know. Hormones that affect pair bonding may play a role. Like prairie voles and mountain voles, chimpanzees and bonobos differ in a regulatory region near a gene that encodes one ADH receptor. In voles, a longer sequence in this region correlates with more family-oriented behavior. Interestingly, the bonobo sequence for this region is about 360 bases longer than the chimpanzee sequence. What about humans? Our sequence in this region is nearly identical to that of the bonobos—and with this in mind, we turn briefly to human behavior.

Chimpanzees and bonobos both live in social groups. They differ in the details of social organization, degree of female cooperation, and extent of male aggression.

Figure 49.20 (**a**) Chimpanzees (*Pan troglodytes*) using sticks as tools for extracting tasty termites from a nest.

(**b**) Female bonobo (*Pan paniscus*) with her offspring. Like humans, bonobos are bipedal; they often walk on two legs. Also like humans, and unlike chimpanzees, the bonobo females have sexual organs that allow them to copulate facing their partner, and they can be sexually receptive at any time of year. They use sex as a means of strengthening social bonds.

49.9 An Evolutionary View of Human Social Behavior

Evolutionary forces shaped animal behavior—but humans alone consistently make moral choices about their behavior.

EXAMPLES OF BEHAVIORAL CUES

Is it possible that molecular cues help humans form social attachments, as they do in other animals? Think of how oxytocin and ADH help control pair bonding in voles. Now think about *autism*. Someone affected by this behavioral disorder cannot enter normal social relationships. An autistic child has significantly low levels of oxytocin in blood. Also, a control sequence near the gene for one ADH receptor is shorter than normal. This same sequence is shorter in chimpanzees than in bonobos and humans.

Researchers are studying how hormones influence mother–infant bonding and romantic bonds. Nursing stimulates oxytocin secretion. So does orgasm, even a friendly massage. Does the brief increase in oxytocin or other hormonal responses contribute to what we perceive as love? That is an open question.

Also, human pheromones may be present in sweat or other secretions. When females live in proximity, as they do in college dormitories, their menstrual cycles typically become synchronized. Martha McClintock and Kathleen Stern demonstrated that one woman's menstrual cycle will lengthen or shorten after she has become exposed to sweat secreted by a woman who was in a different phase of the cycle.

Men and women secrete different chemicals and respond differently to them. PET scans reveal that one chemical component in male sweat activates certain brain areas in women but not in most men. Similarly, a chemical component of female urine activates brain areas in most males more than it does in females. Intriguingly, male homosexuals show the same brain response to male sweat as women do.

In most mammals, pheromones bind to receptors in a vomeronasal organ, or VNO. Neurons connect it to parts of the brain that control behavior. In humans, the VNO is a tiny, ductlike structure on the septum, a tissue that divides the nose into two nostrils. Many scientists hypothesize that human VNOs are vestigial structures—no longer functional. Others suspect that the human VNO does connect to the brain, by way of some pathway that has not yet been discovered.

EVOLUTIONARY QUESTIONS

If we are comfortable with studying the evolutionary basis of the behavior of termites, naked mole-rats, and other animals, why do so many people resist the idea of analyzing human behavior in the same way? Often they fear that attempts to identify the adaptive value of some human trait will be used to define its morality. However, there is a clear difference between trying to explain behavior in terms of its evolutionary history and attempting to justify it. To a biologist, "adaptive" does not mean "morally right." It simply means useful in perpetuating an individual's genes.

LINK TO CHAPTER 43 INTRODUCTION

An example: Infanticide is morally repugnant. Is it unnatural? No. It happens in many animal groups and all human cultures. Male lions often kill the offspring of other males when they take over a pride. Doing so frees up the lionesses to breed with them, which can increase the infanticidal male's reproductive success.

Biologists may predict that unrelated human males are a threat to infants, and evidence supports this. The absence of a biological father and the presence of an unrelated male increases risk of death for an American child under age two by seventy times.

What about parents who kill their own offspring? In her book on maternal behavior, primatologist Sarah Blaffer Hrdy cites a study of a village in Papua New Guinea in which about 40 percent of the newborns were killed by parents. She argues that when resources or social support are hard to come by, a mother might increase her fitness by killing a newborn. She can then allocate child-rearing energy to her other offspring or save it for children she may have in the future.

Do most of us find such behavior appalling? Yes. Does such behavior warrant attention? Think about all you have learned in this book, then decide.

A behavior that might be adaptive in the evolutionary sense may still be judged by society to be morally wrong.

http://biology.brookscole.com/starr11

Summary

Section 49.1 Animal behavior starts with genes that specify products required for development of the nervous, endocrine, and muscular systems. Hormones are among the gene products that affect behavior.

Instinctive behavior is performed without having been learned by experience in the environment. It is a prewired response to one or two simple, well-defined environmental cues.

Section 49.2 An animal learns when it processes and integrates information from experiences, then uses that information to vary or change responses to stimuli. Imprinting is one form of learning that happens only during a sensitive period early in life.

Section 49.3 A behavior that has a genetic basis is subject to evolution by natural selection. Adaptive forms of behavior evolved as a result of individual differences in reproductive success in past generations. A behavior persists when its reproductive benefits exceed the reproductive costs.

Section 49.4 Communication signals are meant to change the behavior of individuals of the same species. Pheromones are signaling molecules that have roles in social communication.

Visual signals are key components of courtship displays and threat displays. Acoustical signals are sounds that have precise, species-specific information. Tactile signals are specific forms of physical contact between a signaler and a receiver.

BiologyNow

Explore the honeybee dance language with the animation on BiologyNow.

Section 49.5 Sexual selection favors traits that give an individual a competitive edge in attracting and often holding on to mates. Females of many species select for males that have traits or engage in behaviors they find attractive. When large numbers of females cluster in defensible areas, males may compete with one another to control the areas.

Parental care has reproductive costs in terms of future reproduction and survival. It is adaptive when benefits to a present set of offspring offset the costs.

BiologyNow

Read the InfoTrac article "Something Fishy in the Nest," Bryan Neff, Natural History, *February 2004.*

Section 49.6 Animals that live in social groups may benefit by cooperating in predator detection, defense, and rearing the young. Benefits of group living are often distributed unequally. Species that live in large groups incur costs, including increased disease and parasitism, and increased competition for resources.

BiologyNow

Read the InfoTrac article "Caterpillars as Social Insects," James Costa, American Scientist, *March–April 1997.*

Section 49.7 Ants, termites, and some other insects as well as two species of mole-rats are eusocial. They live in colonies with overlapping generations and have a reproductive division of labor. Most colony members do not reproduce; they assist their relatives and rear their offspring.

According to the theory of inclusive fitness, such extreme altruism is perpetuated because altruistic individuals have some number of genes in common with their reproducing relatives. Altruistic individuals in the social group pass on "by proxy" the genes that underlie this behavior.

Sections 49.8, 49.9 Researchers are identifying the mechanisms and adaptive significance of primate social behavior. With respect to humans, a behavior that is adaptive in the evolutionary sense may still be judged by society to be morally wrong.

Self-Quiz

Answers in Appendix II

1. Genes affect the behavior of individuals by ______ .
   a. influencing the development of nervous systems
   b. affecting the kinds of hormones in individuals
   c. governing development of muscles and skeletons
   d. all of the above

2. A behavior is defined as adaptive if it ______ .
   a. varies among individuals of a population
   b. occurs without prior learning
   c. increases an individual's reproductive success
   d. is widespread across a species
   e. benefits unrelated members of the species

3. Steven Arnold offered slug meat to newborn garter snakes from different populations to test his hypothesis that the snakes' response to slugs ______ .
   a. was shaped by indirect selection
   b. is an instinctive behavior
   c. is based on pheromones
   d. is adaptive

4. Generally, living in a social group costs the individual, in terms of ______ .
   a. competition for food, other resources
   b. vulnerability to contagious diseases
   c. competition for mates
   d. all of the above

5. Social behavior evolves because ______ .
   a. social animals are more advanced than solitary ones
   b. under some conditions, the costs of social life to individuals are offset by benefits to the species
   c. under some conditions, the benefits of social life to an individual offset the costs to that individual
   d. under most conditions, social life has no costs to an individual.

6. Eusocial insects ______ .
   a. live in extended family groups
   b. are found among almost all insect orders
   c. show a reproductive division of labor
   d. a and c
   e. all of the above

7. Helping other individuals at a reproductive cost to oneself might be adaptive if those helped are ______ .
   a. members of another species
   b. competitors for mates
   c. close relatives
   d. illegitimate signalers

8. Match the terms with their most suitable description.
   ____ fixed action pattern
   ____ altruism
   ____ basis of instinctive and learned behavior
   ____ imprinting
   ____ pheromone

   a. time-dependent form of learning requiring exposure to key stimulus
   b. genes plus actual experience
   c. stereotyped motor program that runs to completion independently of feedback from environment
   d. assisting another individual at one's own expense
   e. one communication signal

Additional questions are available on **Biology Now™**

Figure 49.21 Behaviorally confused rooster.

Figure 49.22 A Nazca booby attends to its single surviving chick.

Critical Thinking

1. Sexual imprinting is common in birds. During a short sensitive period in early life, the bird learns features that it will seek later, when ready to mate. Figure 49.21 shows an amorous rooster wading into the water after ducks. Speculate on what might have caused this behavior.

2. Nazca boobies (*Sula granti*) lay two eggs, several days apart. No matter how much food is available, only one chick survives to adulthood (Figure 49.22). The first chick to hatch pushes its younger sibling from the nest, and that sibling dies of starvation and neglect. Formulate a hypothesis on how it might be adaptive for parents of this species to lay two eggs if one of the hatchlings tends to kill the other. Design an experiment to test your hypothesis.

3. In 2002 Svante Paabo proposed how one gene, *FOXP2*, might have been pivotal in the evolution of *language*. Humans who have a base-pair substitution in this gene cannot speak intelligibly, understand complex sentences, or make certain movements of the mouth and face.

All mammals have the *FOXP2* gene, which has a 715 base-pair sequence. The gene has mutated very little over evolutionary time. The one in chimpanzees differs from the one in mice by a single base pair. But two more base pairs mutated after the ancestors of humans diverged from the lineage that led to chimpanzees. This altered version of the gene became fixed in the lineage that led to modern humans. Why? By one hypothesis, language-related traits that arose from the two recent substitutions were favored by directional selection. Speculate on how a capacity to make and comprehend more complex auditory signals shaped the social behavior of the forerunners of humans.

4. A cheetah scent-marks plants in its territory with certain exocrine gland secretions. What evidence would you require to demonstrate that the cheetah's action is an evolved communication signal?

5. Among primates, differences in sexual behavior tend to be related to the size of a male's gonads. Gorillas have relatively tiny testicles. In a 450-pound male, they may weigh about an ounce. Gorillas live in groups consisting of a male, a few females, and offspring. This is the most typical kind of primate social group. When a female is ready to mate, there usually is only one adult male around to inseminate her.

In contrast, a female chimpanzee advertises her fertile period and mates with many males (Section 49.8). A 100-pound chimpanzee male has testicles about four times as weighty as a gorilla's. By making far more sperm, a male chimpanzee increases the odds that his sperm, not a rival's, will fertilize a female's egg.

An adult human male is larger than a chimpanzee, but his testicles are only about half the weight. What might this suggest about female promiscuity and male competition to fertilize eggs in the lineage that led to humans?

6. In moths and many other insects, potential mates find one another with the help of species-specific pheromones. The pheromones are usually mixes of chemicals derived from fatty acids. Explain how a mutation could result in a change in the mix of chemicals in a moth pheromone. How might such mutations encourage speciation?

Epilogue

BIOLOGICAL PRINCIPLES AND THE HUMAN IMPERATIVE

Molecules, single cells, tissues, organs, organ systems, multicelled organisms, populations, communities, ecosystems, and the biosphere. These are architectural systems of life, assembled in increasingly complex ways over the past 3.8 billion years. We are latecomers to this immense biological building program. And yet, within the relatively short span of 10,000 years, many of our activities have been changing the character of the land, ocean, and atmosphere, even the genetic character of species.

It would be presumptuous to think that we alone have had profound impact on the world of life. As long ago as the Proterozoic, photosynthetic organisms were irrevocably changing the course of biological evolution by enriching the atmosphere with oxygen. During the past as well as the present, competitive adaptations led to the rise of some groups, whose dominance assured the decline of others. Change is nothing new. What *is* new is the capacity of one species to comprehend what might be going on.

We now have the population size, technology, and cultural inclination to use up energy and modify the environment at rapid rates. Where will this end? Will feedback controls operate as they do, for instance, when population growth exceeds carrying capacity? In other words, will negative feedback controls come into play and keep things from getting too far out of hand?

Feedback control will not be enough, for it does not get under way until the deviation has reached a critical

threshold. Our patterns of resource consumption and our population growth are founded on an illusion of unlimited resources and a forgiving environment. A prolonged, global shortage of food or the passing of a critical threshold for the global climate can come too fast to be corrected; in which case the impact of the deviation may be too great to be reversed.

What about feedforward mechanisms, which might serve as early warning systems? For example, when sensory receptors near the surface of skin detect a drop in outside air temperature, each sends messages to the nervous system. That system responds by triggering mechanisms that raise the body's core temperature before the body itself becomes dangerously chilled. Extrapolating from this, if we develop feedforward control mechanisms, would it not be possible to start corrective measures before we do too much harm?

Feedforward controls alone will not work, for they operate after change is under way. Think of the DEW line—the Distant Early Warning system. It is like a vast sensory receptor for detecting missiles launched against North America. By the time it does what it is supposed to, it may be too late to stop widespread destruction.

It would be naive to assume we can ever reverse who we are at this point in evolutionary time, to de-evolve ourselves culturally and biologically into becoming less complex in the hope of averting disaster. Yet there is reason to believe we can avert disaster by using a third kind of control mechanism—a capacity to anticipate events even before they happen. We are not locked into responding only after irreversible change has begun. We have the capacity to anticipate the future—it is the essence of our visions of utopia and hell. *We all have the capacity to adapt to a future that we can partly shape*.

For instance, we can stop trying to "beat nature" and learn to work with it. Individually and collectively, we can work to develop long-term policies that take into account biotic and abiotic limits on population growth. Far from being a surrender, this would be one of the most intelligent behaviors of which we are capable.

Having a capacity to adapt and using it are not the same thing. We have already put the world of life on dangerous ground because we have not yet mobilized ourselves as a species to work toward self-control.

Our survival depends on predicting possible futures. It depends on preserving, restoring, and constructing ecosystems that fit with our definition of basic human values and available biological models. Human values can change; our expectations can and must be adapted to biological reality. *For the principles of energy flow and resource utilization, which govern the survival of all systems of life, do not change*.

It is our biological and cultural imperative that we come to terms with these principles, and ask ourselves this: What will be our long-term contribution to the world of life?