Chapter 51

Animal Behavior

Lecture Outline

Overview: Shall We Dance?

- Red-crowned cranes *(Grus japonensis)* gather in groups to dance, prance, stretch, bow, and leap. They grab bits of plants, sticks, and feathers with their bills and toss them into the air.
- How does a crane decide that it is time to dance? In fact, why does it dance at all?
- Animal behavior is based on physiological systems and processes.
- An individual **behavior** is an action carried out by the muscular or hormonal system under the control of the nervous system in response to a stimulus.
- Behavior contributes to homeostasis; an animal must acquire nutrients for digestion and find a partner for sexual reproduction.
- All of animal physiology contributes to behavior, while animal behavior influences all of physiology.
- Being essential for survival and reproduction, animal behavior is subject to substantial selective pressure during evolution.
- Behavioral selection also acts on anatomy because body form and appearance contribute directly to the recognition and communication that underlie many behaviors.

Concept 51.1: A discrete sensory input is the stimulus for a wide range of animal behaviors.

- An animal's behavior is the sum of its responses to external and internal stimuli.

Classical ethology presaged an evolutionary approach to behavioral biology.

- In the mid-20th century, pioneering behavioral biologists developed the discipline of **ethology**, the scientific study of how animals behave in their natural environments.
- Niko Tinbergen, of the Netherlands, suggested four questions that must be answered to fully understand any behavior.
    1. What stimulus elicits the behavior, and what physiological mechanisms mediate the response?
    2. How does the animal's experience during growth and development influence the response mechanisms?
    3. How does the behavior aid survival and reproduction?
    4. What is the behavior's evolutionary history?
- The first two questions are **proximate questions**, directed at "how" a behavior occurs.

- The last two are **ultimate questions**, addressing "why" a behavior occurs.
- To explain the distinction between proximate and ultimate questions, let's consider the red-crowned cranes, which breed in spring and early summer.
- A proximate question about the timing of breeding by this species might be How does day length influence breeding by red-crowned cranes?
    - A reasonable hypothesis is that breeding is triggered by the effect of increased day length on the crane's production of and response to particular hormones.
- An ultimate question might be Why do red-crowned cranes reproduce in the spring and early summer?
    - A reasonable hypothesis is that red-crowned cranes reproduce in spring and early summer because that is when breeding is most likely to be successful.
    - In the summer, parent birds can find an ample supply of food for their rapidly growing offspring, providing an advantage in reproductive success compared to birds that breed in other seasons.

A fixed action pattern is a type of behavior linked to a simple stimulus.

- A **fixed action pattern (FAP)** is a sequence of unlearned behavioral acts that is essentially unchangeable and, once initiated, is usually carried to completion.
- A FAP is triggered by an external sensory stimulus called a **sign stimulus**.
- Tinbergen studied what has become a classic example of a sign stimulus and fixed action pattern in the male three-spined stickleback fish.
    - The male stickleback attacks other males that invade his nesting territory.
    - The stimulus for the attack is the red underside of the intruder; a male stickleback will attack any model that has some red visible on it.

Environmental cues provide stimuli that animals use to orient both simple and complex movements.

- A **kinesis** is a simple change in activity or turning rate in response to a stimulus.
    - For example, sow bugs exhibit a kinesis in response to variations in humidity.
    - These terrestrial crustaceans are more active in dry areas and less active in humid areas, so the kinesis increases the chance that they will leave a dry area and encounter a moist area.
- A **taxis** is an oriented movement toward (positive taxis) or away from (negative taxis) a stimulus.
    - For example, many stream fishes automatically swim or orient themselves in an upstream direction (toward the current).
    - This taxis keeps the fish from being swept away and keeps them facing in the direction from which food is coming.
- Many birds, fish, and other animals undergo **migration**, a regular, long-distance change in location.
- How do migrating animals find their way? Many migrating animals track their position relative to the sun.
- The sun's position relative to Earth changes throughout the day. Animals adjust for these changes by means of a *circadian*, or 24-hour, clock that is an integral part of the nervous system.
    - Experiments with controlled cycles of light and dark find that birds orient differently relative to the sun at different times of the day.

- At night, animals may orient relative to the North Star, which has a constant position in the night sky.

- Clouds can obscure both the sun and stars, but by tracking their position relative to Earth's magnetic field, pigeons and other animals can navigate without solar or astral cues.
- How do animals detect Earth's magnetic field in navigating long-distance movements?
- One hypothesis is based on the discovery of magnetite, a magnetic iron ore, in the heads of migrating fish and birds.
    - Earth's pull on magnetite-containing structures may trigger the transmission of nerve impulses to the brain.
    - Placing a small magnet on the head of a homing pigeon prevents it from navigating efficiently to its roost on an overcast day.
- Another hypothesis suggests that animals are guided by magnetic field effects on photoreceptors in the visual system.
    - Birds can orient themselves effectively in a magnetic field only when their environment contains at least faint light of particular wavelengths.

Animals display circadian, cirannual, and lunar behavioral rhythms.

- The output of the circadian clock is a circadian rhythm, a daily cycle of rest and activity.
- The clock is synchronized with the light and dark cycles of the environment but can maintain rhythmic activity under constant environment conditions, such as during hibernation.
- Behavioral rhythms such as migration and reproduction are *circannual* rhythms, linked to the yearly cycle of seasons.
    - Although migration and reproduction typically correlate with food availability, these behaviors are not a direct response to changes in food intake.
    - Circannual rhythms, like circadian rhythms, are directly influenced by the periods of daylight and darkness in the environment.
    - Placing a bird in an environment with extended daylight can induce out-of-season migratory behavior in some species.
- Not all biological rhythms are linked to the light and dark cycles in the environment.
    - Fiddler crabs live along the shore in burrows in mud and sand flats that are covered and uncovered by the tides.
    - During courtship, male fiddler crabs position themselves at the entrance to their burrows, waving one massively enlarged claw to attract potential mates.
    - Male courtship is linked not to day length but to lunar cycles, linking reproduction to times of maximal tidal movement of water and thus enhancing reproductive success.

Signals function in animal communication.

- Animals may generate environmental stimuli that guide other animals' behavior.
- A stimulus transmitted from one animal to another is called a **signal**.
- The transmission and reception of signals constitute animal **communication**.
- Courtship behavior in the fruit fly, *Drosophila melanogaster*, constitutes a *stimulus response chain*, in which the response to each stimulus serves as the stimulus for the next behavior.
- In the first stage of fruit fly courtship, the male identifies a female of the same species based on visual and chemical communication.
    - **Visual communication** is the recognition of the female by appearance.

- **Chemical communication** is the transmission and reception of signals in the form of specific chemicals released by the female and detected by the male's olfactory system.

- In the second stage of courtship, the male approaches and taps the female with a foreleg.
  - This touching, or **tactile communication**, alerts the female to the male's presence.
  - In the process, chemicals present on her abdomen are transferred to the male, providing further chemical confirmation of her species identity.
- In the third stage of courtship, the male extends and vibrates his wing, producing a specific courtship song.
  - This singing, an example of **auditory communication**, tells the female whether the male is the same species.
- Only when all these forms of communication are successful does a receptive female allow the male to attempt copulation.
- The type of signal used to transmit information is closely related to an animal's lifestyle and environment.
- Most terrestrial mammals are nocturnal, which makes visual displays relatively ineffective; they rely on olfactory and auditory signals.
- Birds are mostly diurnal and have a relatively poor olfactory sense; they communicate primarily by visual and auditory signals.
- Like birds, humans are diurnal and use mainly visual and auditory communication.
  - Humans detect and appreciate the songs and bright colors used in avian communication but miss many of the chemical cues on which other mammals base their behavior.
- The information content of animal communication varies considerably.
- Honeybees use a symbolic language to share information about the location of food sources.
  - The language was discovered in the 1940s by ethologist Karl von Frisch, who studied the behavior of the European honeybee *(Apis mellifera carnica)*.
- A bee returning from a foraging trip is the center of attention for other follower bees.
- If the food source is close to the hive (less than 50 m away), the returning bee displays a "round dance," moving in tight circles while waggling its abdomen from side to side.
  - This behavior motivates follower bees to leave the hive and search for food that is nearby.
- When a source of food is farther from the nest, the returning bee performs a "waggle dance," consisting of a half-circle swing in one direction, a straight run, and a half-circle swing in the other direction to communicate the direction and distance of the food source from the hive.
  - The angle of the straight run relative to the hive's vertical surface is the same as the horizontal angle of the food in relation to the sun.
  - If the returning bee runs at a 30° angle to the right of vertical, follower bees leaving the hive fly 30° to the right of the horizontal direction of the sun.
  - A dance with a longer straight run, and therefore more abdominal waggles per run, indicates a greater distance to the food source.
  - As follower bees exit the hive, they fly almost directly to the area indicated by the waggle dance.
  - Using flower odor and other clues, they search for and locate the food source.

Many animals communicate through chemical substances called pheromones.

- **Pheromones** are especially common among mammals and insects and often relate to reproductive behavior.
  - For example, moth pheromones can attract a mate from several kilometers away and also serve to trigger specific courtship behaviors.
- The context of a chemical signal can be as important as the chemical itself.
  - In a honeybee colony, pheromones produced by the queen and the workers maintain the hive's complex social order.
  - When male honeybees (drones) are outside the hive, where they can mate with a queen, they are attracted to her pheromone; when drones are inside the hive, they are unaffected by it.
- Pheromones may also function in nonreproductive behavior.
  - For example, when a minnow or catfish is injured, an alarm substance in the fish's skin disperses in the water, inducing a fright response in other fish.
  - Nearby fish become more vigilant and form tightly packed schools, often near the bottom, where they are safer from attack.
- Pheromones can be very effective at remarkably low concentrations.
  - For instance, just 1 cm^2 of skin from a fathead minnow contains sufficient alarm substance to induce a reaction in 58,000 L of water.

Concept 51.2: Learning establishes specific links between experience and behavior.

- For behaviors such as fixed action patterns, taxis, and pheromone signals, all individuals in a population exhibit virtually the same behavior, despite internal differences and environmental differences during development and throughout life.
- Behavior that is *developmentally fixed* in this way is called **innate behavior**.
- Environmental conditions can influence behavior through **learning**, the modification of behavior based on specific experiences.
- **Habituation**, one of the simplest forms of learning, is a loss of responsiveness to stimuli that convey little or no new information.
  - Many animals recognize the alarm calls of members of their species, but they eventually stop responding if these calls are not followed by an actual attack (the "cry-wolf" effect).
- Habituation prevents the wasting of time and energy on stimuli that are irrelevant to the animal's survival and reproduction, thus increasing an individual's evolutionary fitness.***Imprinting takes place early in life.***
- **Imprinting**, the formation early in life of a long-lasting behavioral response to a specific individual or object, includes both learning and innate components.
- Imprinting is limited to a **sensitive period**, a specific developmental phase when certain behaviors can be learned.
- An example of imprinting is young geese bonding to their mother.
- Among gulls, the sensitive period for a parent to bond with its young lasts one to two days.
  - If bonding does not occur in the first days, the parent will not care for the infant.
- How do the young know on whom—or what—to imprint?
- The tendency to respond is innate; the outside world provides the *imprinting stimulus* to which the response will be directed.

- Waterfowl have no innate recognition of "mother"; they respond to and identify with the first object they encounter that has certain key characteristics.
    - In classic experiments in the 1930s, Konrad Lorenz showed that the principal imprinting stimulus in graylag geese is a nearby object that is moving away from the young.
    - Incubator-hatched goslings imprinted on Lorenz and steadfastly followed him, showing no recognition of their biological mother or other adults of their own species.
- Cranes also imprint as hatchlings, creating both problems and opportunities in programs designed to save endangered crane species.
    - A group of 77 endangered whooping cranes were hatched and raised by sandhill cranes.
    - Because the whooping cranes imprinted on their foster parents, none formed a mating-pair bond with another whooping crane.
    - Captive breeding programs now isolate young cranes and expose them to the sights and sounds of members of their own species.
- Imprinting has been used to aid crane conservation.
    - Young whooping cranes imprinted on humans in "crane suits" have been taught to follow these "parents" flying ultralight aircraft along new migration routes.
    - Most important, such cranes have formed mating-pair bonds with other whooping cranes.

Many animals are capable of spatial learning.

- Every natural environment shows spatial variation in the locations of nest sites, hazards, food, and prospective mates.
- An organism's fitness may be enhanced by its capacity for **spatial learning**, establishing a memory that reflects the environment's spatial structure.
- As a graduate student, Niko Tinbergen studied spatial learning behavior in the female digger wasp *Philanthus triangulum*, which nests in small burrows dug in sand dunes.
- When a wasp leaves her nest to go hunting, she covers up the entrance with sand.
- Upon her return, she flies directly to her hidden nest, despite the presence of hundreds of other burrows in the area.
- Tinbergen hypothesized that a wasp locates her nest by learning its position relative to visible **landmarks**, or location indicators.
    - To test this hypothesis, Tinbergen manipulated objects around nest entrances and demonstrated that digger wasps engage in visual learning.

Animals may use cognitive maps to navigate efficiently within their surroundings.

- In place of landmark orientation, some animals guide their activity by a **cognitive map**, a neural representation of the spatial relationships between objects in an animal's surroundings.
- Clark's nutcracker *(Nucifraga columbiana)* uses cognitive maps to locate stored food.
    - Nutcrackers are corvids, a bird family that also includes ravens, crows, and jays.
- In the fall, a nutcracker may store up to 30,000 pine seeds in thousands of hiding places called caches, distributed over an area as large as 35 km^2.
- During the winter, the birds relocate a large fraction of their caches.
- In experiments in which the distance between landmarks was varied, researchers demonstrated that birds learn the halfway point between landmarks.

- Such behavior suggests that the birds use a general abstract geometric rule, which we can approximate as "Seed caches are found halfway between particular landmarks."
- Such rules, a fundamental property of cognitive maps, reduce the amount of detail required to remember an object's location.

Some animals can learn to associate one environmental feature with another.

- Learning leads to an animal modifying its behavior based on information from the environment.
  - For instance, an inexperienced white-footed mouse that attacks the brightly colored but distasteful caterpillar of a monarch butterfly learns to avoid insects with similar coloration and behavior.
- The ability to associate one environmental feature (such as a color) with another (such as a foul taste) is called **associative learning**.
- Associative learning is often divided into two types: classical conditioning and operant conditioning.
- In **classical conditioning**, an arbitrary stimulus becomes associated with a particular outcome.
  - Russian scientist Ivan Pavlov carried out early experiments in classical conditioning, demonstrating that if he rang a bell each time just before feeding a dog, the dog would salivate in anticipation of food at the bell's sound.
- In **operant conditioning**, also called *trial-and-error learning*, an animal learns to associate one of its own behaviors with a reward or punishment and then tends to repeat or avoid that behavior.
  - A predator may learn to avoid potential prey associated with painful experiences.
  - B. F. Skinner, a pioneer in the study of operant conditioning, explored this type of learning by having a rat learn through repeated trials to obtain food by pressing a lever.
- Although it was once thought that animals could learn to link any stimulus with any behavior, that idea was proven incorrect.
  - For example, pigeons can associate danger with a particular sound but not with a particular color.
  - Although pigeons can learn to associate a color with food, the development and organization of the pigeon nervous system apparently restrict the associations that can be formed.
  - Such restrictions are not specific to birds: Rats can learn to avoid illness-inducing food on the basis of smells but not sights or sounds.
- The associations that an animal forms readily often reflect relationships likely to appear in nature.
  - In the case of a rat's diet, for example, a harmful food is far more likely to have a certain odor than to be associated with a particular sound.
- Experiments regarding associative learning need to be interpreted carefully: What we define in the laboratory as a limitation in learning may be of little or no consequence to the animal in its natural habitat.

Some animals are capable of cognition and problem solving.

- The most complex forms of learning involve **cognition**—the ability of an animal's nervous system to perceive, store, process, and use information gathered by sensory receptors.
- Many animal species besides humans and other primates display cognition.
- Insects can categorize objects according to abstract concepts.

- In one experiment, honeybees exposed to a sample color were rewarded for flying into the arm of a Y-shaped maze marked with the same color.
- After repeated trials, the bees were challenged with black-and-white patterns.
- If shown a sample with bars oriented either vertically or horizontally, the bees most often chose the arm of the maze with bars matching that orientation.
- When bees were initially trained to choose a different color, they chose bars of different orientation in the follow-up experiment.
- Honeybees are thus able to distinguish on the basis of "same" and "different."

- **Problem solving** is the cognitive activity of devising a method to proceed from one state to another in the face of real or apparent obstacles.
- Problem-solving behavior is highly developed in primates and dolphins.
  - If a chimpanzee is placed in a room with several boxes on the floor and a banana hung high out of reach, the chimp will stack the boxes and climb up to reach the food.
- Corvids are also capable of problem solving.
  - In one study, ravens were confronted with food hanging from a branch by a string.
  - Several ravens flew to the branch and alternately pulled up and stepped on the string until they reached the food.
  - Some ravens failed to solve the problem, indicating that problem-solving success varies with individual experience and abilities.
- Many animals learn to solve problems by observing the behaviors of other individuals.
  - Young wild chimpanzees learn how to crack oil palm nuts with two stones by watching and copying experienced chimpanzees.

Some behaviors are learned in distinct stages.

- Development of some behaviors, such as singing in some bird species, occurs in distinct stages.
- The first stage of song learning for white-crowned sparrows takes place early in life.
  - If a fledgling sparrow does not hear sparrow songs during the first 50 days of its life, it fails to develop the adult song of its species.
  - Although the young bird does not sing during the sensitive period, it memorizes the song of its species by listening to other white-crowned sparrows sing.
  - During the sensitive period, fledglings chirp more in response to songs of their own species than to songs of other species.
  - Thus, although young white-crowned sparrows *learn* the songs they will sing as adults, learning appears to be bounded by genetically controlled preferences.
- The sensitive period when a white-crowned sparrow memorizes its species' song is followed by a second learning stage when the juvenile bird sings tentative notes called a subsong.
  - The juvenile bird hears its own singing and compares it with the song memorized during the sensitive period.
  - Once a sparrow's own song matches the one it memorized, the song "crystallizes" as the final song, and the bird sings only this song for the rest of its adult life.
- Canaries do not have a single sensitive period for song learning.
  - A young canary begins with a subsong, but the full song it develops does not crystallize.
  - Between breeding seasons, the song becomes flexible again, and an adult male may learn new song "syllables" each year, adding to the song it already sings.

- These examples of song learning illustrate how both experience and genetics influence development of a behavior.

Concept 51.3: Genetic makeup and environment both contribute to the development of behavior.

- Animal behavior is based on complex interactions between genetic and environmental factors.
- This finding contrasts with the popular conception that behavior is due *either* to genes (nature) *or* to environment (nurture).

Behaviors vary in the extent of contribution of genetic and environmental factors.

- One informative approach to identifying environmental contributions to behavior is a **cross-fostering study**, in which the young of one species are placed in the care of adults from another species.
- The extent to which the offspring's behavior changes indicates how the social and physical environment influences behavior.
- Cross-fostering experiments between mouse species illuminate the relative roles of nature and nurture in parental care.
  - Males of the California mouse species *(Peromyscus californicus)* are highly aggressive toward other mice and provide extensive parental care.
  - In contrast, male white-footed mice *(Peromyscus leucopus)* are less aggressive and engage in little parental care.
- When the pups of each species were cross-fostered in the nests of the other species, the behavior of both species was altered.
  - Male California mice raised by white-footed mice were less aggressive toward intruders.
  - Cross-fostered male California mice that strayed from the nest were not retrieved as frequently as those raised by their own species.
- Experience during development influences both parental and aggressive behaviors in these rodents.
  - The cross-fostering effects were greater for California mice than for white-footed mice.
- The influence of experience on behavior was not limited to a single generation.
  - When the cross-fostered California mice became parents, they spent less time retrieving their offspring.
  - Experience during development had modified physiology in a way that altered parental behavior, extending the influence of environment to a subsequent generation.
- For humans, the influence of genetics and environment on behavior can be explored by a **twin study**, in which researchers compare the behavior of identical twins raised apart with those raised in the same household.
- Twin studies of a wide range of behavioral disorders, such as schizophrenia, anxiety disorders, and alcoholism, have shown that the fraction of susceptibility governed by genetic differences between individuals varies among mental diseases but is almost always greater than 20% and less than 80%.
- Environment and genetics thus contribute significantly to these disorders in humans.

Experience can modify genetic programs that underlie behaviors.

- The courtship behavior of male fruit flies involves a complex series of actions in response to multiple sensory stimuli.
- Recent evidence indicates that a single gene called *fru* controls the entire male courtship ritual.
  - Males lacking a functional *fru* (for *fruitless*) gene fail to court and mate with females.
  - Normal male and female flies produce distinct forms of the *fru* gene product.
  - When females are genetically manipulated to produce the male form of *fru*, they court other females just as males do.
- How can a single gene control so many behaviors and actions?
  - *fru* codes for a regulatory protein that directs the expression and activity of many other genes with narrower functions.
  - In effect, *fru* programs the fly for male courtship behavior by overseeing a male-specific wiring of the central nervous system.
- Charles Henry, of the University of Connecticut, has studied the genetic basis for species-specific differences in the courtship song of the green lacewing.
  - These insects live throughout central to northern Eurasia and North America.
  - The 15 species of green lacewing are identical in appearance but differ in courtship songs.
- Henry showed that lacewings reared in isolation in the laboratory performed the song specific to their species. Thus, the courtship song is genetically controlled.
- Henry then crossed different green lacewing species in the laboratory and analyzed the songs produced by the hybrid offspring.
- These experiments demonstrated that each component or property of the courtship song is governed by a different gene.
  - The distinct courtship song of each green lacewing species reflects genetic differences at multiple, independent loci.
- Behavioral differences between closely related species, such as green lacewings, are common.
- Though less obvious, significant differences in behavior can also be found *within* a species.
- When behavioral variation between populations of a species corresponds to variation in environmental conditions, it may be evidence of past evolution.

The blackcap provides a case study of variation in migratory patterns.

- The blackcap *(Sylvia atricapilla)* is a small migratory warbler that bred in Germany, migrating southwest to Spain and then south to Africa for the winter.
- In the 1950s, a few blackcaps began to spend their winters in Britain. Over time, the population of blackcaps wintering in Britain grew to many thousands.
  - Some of these birds had migrated westward from central Germany.
- Why were there now two patterns of migration from Germany?
- Peter Berthold, at the Max Planck Research Center in Radolfzell, Germany, who studied blackcap migratory orientation in the laboratory, found that the two patterns of migration reflect genetic differences between the two populations.
- The change in migratory behavior in western European blackcaps is both recent and rapid.
  - Before 1950, there were no known westward-migrating blackcaps in Germany.
  - By the 1990s, westward migrants made up 7–11% of the blackcap populations of Germany.

- Once westward migration began, it persisted and increased in frequency, perhaps due to Britain's milder winters and widespread winter bird feeders.

Garter snakes provide a case study of genetically based variation in prey selection.

- A well-known example of genetically based variation in behavior within a species is prey selection by the western garter snake *Thamnophis elegans*.
  - The natural diet of this species differs widely across its range in California.
  - Coastal garter snakes feed on salamanders, frogs, and toads, but mainly on slugs. Inland snakes eat frogs, leeches, and fish, but not slugs.
- Researchers offered slugs to snakes from both populations, but only coastal snakes readily accepted the slugs.
- To what extent do experience and genetics contribute to the willingness of snakes to eat slugs?
- To answer this question, pregnant snakes were collected from each wild population and housed in separate cages in the laboratory.
- Newborn snakes born in the laboratory were offered ten opportunities to eat pieces of slug.
- More than 60% of young snakes from coastal mothers readily ate pieces of slug, but fewer than 20% of naïve snakes from inland mothers ate pieces of slug even once.
- Clearly, slugs are a genetically acquired taste.
- Researchers suggest that when inland snakes colonized coastal environments 10,000 years ago, a small fraction of the population had the ability to recognize slugs by scent.
- These snakes took advantage of the abundant food source that slugs represented and had higher fitness than snakes that ignored slugs.
- The capacity to recognize slugs as prey increased in frequency in coastal populations.
- Behavior is usually shaped by a large number of genes that individually have small effects.
- Variation at a single gene may also have observable effects.
- In some cases, differences at a single locus can cause dramatic differences in behavior, even if the behavior requires the activity of many other genes.

Mating and parental behaviors in voles are under strong genetic influence.

- Parental behavior differs in two closely related species of voles.
  - Male meadow voles *(Microtus pennsylvanicus)* are solitary and do not form lasting relationships with mates. Following mating, they pay little attention to their pups.
  - Male prairie voles *(Microtus ochrogaster)* form a strong attachment, or *pair-bond,* with a single female after they mate. Male prairie voles care for their young pups while acting aggressively toward intruders.
- Research suggests that a neurotransmitter released during mating is critical for the partnering and parental behavior of male voles.
- This peptide, arginine-vasopressin, binds to a specific receptor in the central nervous system.
- When male prairie voles are treated with a drug that inhibits the brain receptor for vasopressin, they fail to form pair-bonds after mating.
- The vasopressin receptor gene of prairie voles is highly expressed in the brain, whereas that of meadow voles is not.

- To test whether the amount of the vasopressin receptor present in the brain regulates the post-mating behavior of voles, researchers inserted the vasopressin receptor gene from prairie voles into male meadow voles.
- These meadow voles developed brains with higher levels of the vasopressin receptor and also showed monogamous mating behaviors.
- Although many genes influence pair-bond formation and parenting among voles, the level of the vasopressin receptor alone determines which behavioral pattern develops.

Concept 51.4 Selection for individual survival and reproductive success can explain most behaviors.

- The genetic components of behavior evolve through natural selection, favoring traits that enhance survival and reproductive success in a population.
- Behavior can affect fitness through influences on foraging and mate choice.

Genetic variation contributes to the evolution of foraging behavior.

- Foraging includes not only eating but also any mechanism that an animal uses to recognize, search for, and capture food items.
- Variation in a single locus called *forager (for)* dictates the food-search behavior of the larvae of the fruit fly, *D. melanogaster*.
  - Larvae carrying the for^R or "Rover" allele travel nearly twice as far while feeding as larvae with the for^s or "sitter" allele.
  - Molecular analysis revealed that an enzyme encoded by the forager locus is more active in for^R than in for^s larvae.
  - The type of enzyme encoded typically helps bring signals from the cell surface to the nucleus.
- Changes in the processing of environmental information can substantially alter behavior.
- Both the for^R and for^s alleles are present in natural populations, so what circumstances favor one allele over the other?
- To study this question, flies were kept for many generations at high and low population densities.
  - Larvae maintained for many generations at a low density foraged over shorter distances than larvae kept at high density.
  - Genetic tests indicated that the for^s allele increased in frequency in the low-density populations, whereas the for^R allele increased in frequency in the high-density group.
- At low population densities, short-distance foraging yields sufficient food, whereas long-distance foraging results in unnecessary energy expenditure.
- In contrast, under crowded conditions, long-distance foraging enables larvae to move beyond areas of food depletion.
- Thus, an interpretable evolutionary change in behavior was seen in the laboratory populations.

Costs and benefits of diverse foraging strategies can be analyzed.

- **Optimal foraging theory** views foraging behavior as a compromise between the benefits of nutrition and the costs of obtaining food, such as the energy expenditure and risk of predation while foraging.

- Natural selection should favor foraging behavior that minimizes the costs of foraging and maximizes the benefits.
- An optimal foraging model was applied to the feeding behavior of the Northwestern crow *(Corvus caurinus)*.
- Crows search tide pools for snails called whelks, flying up and dropping whelks onto the rocks to break their shells.
    - If the drop is successful, the crow eats the snail's soft body.
    - If the drop is not successful, the crow flies higher and tries again.
- What determines how high the crow flies?
    - The higher the crow flies, the greater the force with which the whelk strikes the rocks, increasing the chance the shell will break. Flying higher, however, consumes more energy.
- Researchers suggested that the average drop height reflects a trade-off between the cost of flying higher and the benefit of more frequent success.
    - To test this hypothesis, researchers dropped whelks from different heights and noted the number of drops required to break a shell.
    - For each height, researchers calculated the average number of drops and the average *total flight height*, the drop height times the average number of drops.
    - A drop height of about 5 m is optimal, breaking the shells with the lowest total flight height.
    - The actual average flight height for crows in their whelk-eating behavior is 5.2 m, very close to the prediction based on an optimal trade-off between energy gained (food) versus energy expended.
- The close agreement between the predicted and actual flight heights indicates that the foraging model may reflect the selective forces that shaped the evolution of this behavior.
    - It is possible that the average flight height actually minimizes the average *time* necessary to break open a whelk.
    - Further experiments are needed to distinguish between these hypotheses.
- Risk of predation is one of the most significant potential costs to a forager.
- Mule deer *(Odocoileus hemionus)* are preyed on by mountain lions throughout their range in the mountains of western North America.
- Researchers studied mule deer populations in Idaho to determine whether they forage in a way that reduces their risk of falling prey to mountain lions.
    - The researchers found that food available to mule deer was fairly uniform across the potential foraging area, while the risk of predation varied greatly.
    - Mountain lions killed most mule deer at forest edges; few were killed in open areas and forest interiors.
- How does mule deer feeding behavior respond to the differences in feeding risk?
- Mule deer feed predominantly in open areas, avoiding forest edges and forest interiors.
- Mule deer foraging behavior thus reflects the large variation in predation risk and not the smaller variation in food availability.

Mating systems and extent of parental care vary greatly.

- Mating behavior, which includes seeking and attracting mates, choosing among potential mates, and competing for mates, is the product of a form of natural selection called *sexual selection*.

- How mating behavior enhances reproductive success varies, depending on the species' mating system.
- The mating relationship between males and females varies a great deal from species to species.
  - In many species, mating is **promiscuous**, with no strong pair-bonds or lasting relationships.
  - In species in which the mates remain together for a longer period, the relationship may be **monogamous** (one male mating with one female) or **polygamous** (one individual mating with several partners).
  - Polygamous relationships may involve a single male and many females **(polygyny)** or a single female and many males **(polyandry).**
- Among monogamous species, males and females are often morphologically similar and difficult to distinguish based on external characteristics.
- Polygynous species are generally dimorphic, with males being larger and more showy.
- In polyandrous species, females are more ornamented and larger than males.
- The needs of young are an important factor constraining the evolution of mating systems.
- Parental investment refers to the time and resources expended for raising offspring.
- Most newly hatched birds cannot care for themselves and require a large, continuous food supply that a single parent cannot provide.
  - In such cases, a male will have more successful offspring if he helps his partner to rear their chicks than if he goes off to seek more mates. This is why most birds are monogamous.
- Birds with young that can feed and care for themselves from birth, such as pheasant and quail, have less need for parents to stay together.
  - Males of these species can maximize their reproductive success by seeking other mates, and polygyny is relatively common in such birds.
- In mammals, the lactating female is often the only food source for the young.
  - Males provide no parental care in most mammal species.
  - In some mammals, males protect many females and their young.
- Certainty of paternity can influence mating systems and parental care.
  - If the male is unsure that offspring are his, his parental investment is likely to be lower.
  - Females can be sure that they contributed to an offspring when they give birth or lay eggs.
  - Males do not have that assurance in species with internal fertilization because the acts of mating and birth are separated over time.
- Males in many species with internal fertilization engage in behaviors that increase their certainty of paternity, including guarding females, removing sperm from the female's reproductive tract before copulation, and introducing large numbers of sperm to displace the sperm of other males.
- Certainty of paternity is much higher in species that engage in external fertilization, when egg laying and mating occur together.
- This finding may explain why parental care in aquatic invertebrates, fishes, and amphibians, when it occurs, is as likely to be by males as females.
  - Male parental care occurs in only 7% of fish and amphibian families with internal fertilization, but in 69% of families with external fertilization.
- The expression *certainty of paternity* does not imply conscious awareness of paternity by the father: Parental behavior is correlated with certainty of paternity because this link has been reinforced over generations by natural selection.

Sexual selection is a form of natural selection.

- Sexual dimorphism within a species results from sexual selection, a form of natural selection in which differences in reproductive success among individuals are a consequence of differences in mating success.
- Sexual selection can take the form of *intersexual selection*, in which members of one sex choose mates on the basis of particular characteristics of the other sex, such as courtship songs, or *intrasexual selection*, which involves competition among members of one sex for mates.
- Mate preferences by females may play a central role in the evolution of male behavior and anatomy through intersexual selection, as in the courtship behavior of stalk-eyed flies.
  - Males have elongated eyestalks, which they display to females during courtship.
  - Females prefer to mate with males that have relatively long eyestalks.
- How is this preference adaptive for females?
  - Males with long eyestalks may be demonstrating superior genetic quality to females.
  - In general, ornaments such as long eyestalks and brightly colored feathers correlate with a male's health and vitality.
- A female that chooses a healthy male increases the chance that her offspring will be healthy.
- Imprinting by young female zebra finches influences their adult choice of mates.
  - Male and female zebra finches lack a feather crest on the head.
  - Researchers taped a 2.5-cm-long red feather to the heads of either or both zebra finch parents before the young chicks opened their eyes.
  - Control zebra finches were reared by unadorned parents.
  - When the chicks matured, they were given a choice of ornamented or non-ornamented mates.
  - Males showed no preference, but females reared by ornamented fathers or parents preferred ornamented mates.
- These results suggest that females imprint on their fathers and that mate choice by female zebra finches has played a key role in the evolution of ornamentation in male zebra finches.
- Males compete with each other by (often ritualized) **agonistic behaviors** that determine which competitors gain access to resources.
  - The outcome of such contests may be determined by strength or size.
- In some species, more than one mating behavior or morphology can result in successful reproduction.
- In such cases, sexual selection has led to the evolution of alternative male strategies.

Game theory can model behavioral strategies.

- **Game theory** evaluates alternative strategies in situations where the outcome depends on each individual's strategies and also on the strategies of other individuals.
- Researchers used game theory to analyze the mating behavior of the side-blotched lizard *(Uta stansburiana).*
- Male lizards have three genetically controlled colors: orange throats, blue throats, and yellow throats.
- Each throat color is associated with a different pattern of behavior.
  - Orange-throat males are the most aggressive and defend large territories with many females.

- Blue-throat males are also aggressive but defend smaller territories with fewer females.
- Yellow-throat males are nonterritorial and use "sneaky" tactics to mimic females and sneak copulations.

- Within a population, the frequency of the three types of males varies from year to year.
- Modeling showed that the relative success of different males varies with the abundance of other types of males, an example of frequency-dependent selection.
  - When blue-throat males are abundant, they can defend their few females from the sneaky yellow-throat males. However, they cannot defend their territories against the aggressive orange-throat males.
  - Orange-throat males take over large territories but cannot defend large numbers of females against the sneaky yellow-throat males.
  - Yellow-throat males then increase in numbers but are defeated by the blue-throat males.
- Game theory provides a way to think about complex evolutionary problems in which relative performance, not absolute performance, is the key to understanding the evolution of behavior.
- The relative performance of one phenotype compared with others is a measure of Darwinian fitness.

Concept 51.5 Inclusive fitness can account for the evolution of altruistic social behavior.

- Most social behaviors are selfish, benefiting the individual at the expense of competitors.
- Behaviors that maximize an individual's survival and reproductive success are favored by selection, regardless of their effect on other individuals.
- How do we account for "unselfish" behaviors that help others?

Altruistic behaviors may evolve by increasing inclusive fitness.

- **Altruism** is behavior that decreases individual fitness but increases the fitness of other individuals in the population.
- Belding's ground squirrel lives in some mountainous regions of the western United States. It is vulnerable to predators such as coyotes and hawks.
- If a squirrel sees a predator approach, it often gives a high-pitched alarm call, which alerts unaware individuals. The alerted squirrels then retreat to their burrows.
- This conspicuous alarm behavior calls attention to the caller, who has a greater risk of being killed.
- In honeybees, workers are sterile but labor on behalf of a single fertile queen.
  - Workers will sacrifice themselves to sting intruders in defense of the hive.
- Naked mole rats *(Heterocephalus glaber)* are highly social rodents that live in underground chambers and tunnels in Africa.
  - These rodents are almost hairless and nearly blind and live in colonies of 75–250 individuals.
  - Each colony has only one reproducing female, the queen, who mates with one to three males, called kings.
  - The rest of the colony is made up of nonreproductive females and males that forage for underground roots and tubers and care for the kings, queen, and new offspring.

- How can a naked mole rat (or a worker bee or a Belding's ground squirrel) enhance its fitness by helping other members of the population?
- How is altruistic behavior maintained by evolution if it does not enhance the survival and reproductive success of the self-sacrificing individuals?
- Selection for altruistic behavior is most apparent in the acts of parents sacrificing for their offspring.
- When parents sacrifice their own well-being to produce and aid offspring, this increases the fitness of the parents because it maximizes their genetic representation in the population.
- Individuals sometimes help others who are not their offspring, however.
- Biologist William Hamilton proposed that an animal could increase its genetic representation in the next generation by "altruistically" helping close relatives other than its own offspring.
- **Inclusive fitness** is defined as the total effect an individual has on proliferating its own genes by reproducing *and* by helping close relatives produce offspring.
- Hamilton proposed a quantitative measure for predicting when natural selection should favor altruistic acts.
- There are three conditions under which altruistic acts will be favored by natural selection.
  1. The benefit to the recipient is B, the average number of *extra* offspring that the beneficiary of an altruistic act produces.
  2. The cost to the altruist is C, a measure of how many *fewer* offspring the altruist produces.
  3. The **coefficient of relatedness** is r, the fraction of genes that, on average, are shared.
- **Hamilton's rule** states that natural selection favors altruism when the benefit to the recipient multiplied by the coefficient of relatedness exceeds the cost to the altruist—in other words, when $rB > C$.
- Natural selection that favors altruistic behavior by enhancing the reproductive success of relatives is called **kin selection**.
  - The more closely related two individuals are, the greater the value of altruism.
  - Siblings have an r of 0.5, but between an aunt and her niece, $r = 0.25$ (¼), and between first cousins, $r = 0.125$ (⅛).
  - As the degree of relatedness decreases, the rB term in the Hamilton inequality decreases.
- If kin selection explains altruism, then the examples of unselfish behavior we observe among diverse animal species should involve close relatives.
  - Female Belding's ground squirrels settle close to their site of birth, whereas males settle at distant sites. Since nearly all alarm calls are given by females, they are most likely aiding close relatives.
  - In the case of worker bees, who are all sterile, anything they do to help the entire hive benefits the only permanent member who is reproductively active—the queen, who is their mother.
  - In the case of naked mole rats, DNA analyses have shown that all the individuals in a colony are closely related.
    - Genetically, the queen appears to be a sibling, daughter, or mother of the kings, and the nonreproductive rats are the queen's direct descendants or her siblings.
    - When a nonreproductive individual enhances a queen's or king's chances of reproducing, it increases the chances that genes identical to its own will be passed to the next generation.

Animals may exchange aid in a pattern of reciprocal altruism.

- Some animals behave altruistically toward others who are not close relatives.
- Such behavior can be adaptive if the aided individual can be counted on to return the favor in the future.
- This exchange of aid is called **reciprocal altruism** and is commonly used to explain altruism between unrelated humans.
- Reciprocal altruism is limited to species with stable social groups in which individuals have many opportunities to exchange aid and where there are negative social consequences for those who "cheat" and refuse to return favors to those who have helped them in the past.
- Because cheating may provide a large benefit to cheaters, researchers have questioned how reciprocal altruism can arise.
- Game theory provides a possible answer in the form of a behavioral strategy called *tit for tat*, in which one individual treats another in the same way it was treated the last time they met.
  - Individuals are always altruistic, or cooperative, on the first encounter and remain so as long as their altruism is reciprocated.
  - When its altruism is not reciprocated, an individual will retaliate immediately but then return to cooperative behavior as soon as the other individual becomes cooperative.
- Tit-for-tat strategy has been used to explain the few apparently reciprocal altruistic interactions observed in animals—ranging from blood sharing between nonrelated vampire bats to social grooming in primates.

Animals learn by observing others.

- **Social learning** is learning through observing others.
- Social learning forms the roots of **culture**, which can be defined as a system of information transfer through social learning or teaching that influences the behavior of individuals in a population.
- Cultural transfer of information has the potential to alter behavioral phenotypes and influence the fitness of individuals.
  - Culturally based changes in the phenotype occur on much shorter time scales than changes resulting from natural selection.

In many species, mate choice is strongly influenced by social learning.

- Social learning is not restricted to humans. **Mate-choice copying**, a behavior in which individuals in a population copy the mate choices of others, has been studied in the guppy *Poecilia reticulata*.
- When a female guppy chooses between males with no other females present, the female selects males with a high percentage of orange coloration.
- If a female sees another female (or artificial model female) engaging in courtship with a male that has relatively little orange, however, she copies the preference of the other female and selects a male with relatively little orange coloration.
- Mate-choice behavior typically does not change when the difference in coloration is very large.
  - Below a certain threshold of difference in mate color, mate-choice copying by female guppies masks genetically controlled female preference for orange males.
- What is the advantage of mate-choice copying for females?

- A female that mates with males that are attractive to other females increases the probability that her male offspring will also be attractive and have high reproductive success.

Vervet monkeys provide a case study of the social learning of alarm calls.

- Studies of vervet monkeys *(Cercopithecus aethiops)* in Amboseli National Park, Kenya, showed that the performance of a behavior can improve through learning.
- Vervet monkeys produce a complex set of distinct alarm calls that warn of leopards, eagles, or snakes, all of which prey on the small vervets.
- Vervets react to each alarm differently, depending on the threat.
    - They run up a tree on hearing the alarm for a leopard, look up on hearing the alarm for an eagle, and look down on hearing the alarm for a snake.
- Infant vervets give alarm calls, but in an undiscriminating way. For example, they call "eagle" for any bird. With age, they improve their accuracy.
- Vervets learn how to give the right call by observing other members of the group and by receiving social confirmation for accurate calls.

Sociobiology places social behavior in an evolutionary context.

- Human culture is related to evolutionary theory in the discipline of **sociobiology**, whose main premise is that certain behavioral characteristics exist because they are expressions of genes that have been perpetuated by natural selection.
- In his seminal 1975 book, *Sociobiology: The New Synthesis*, E. O. Wilson speculated about the evolutionary basis of certain kinds of social behavior in nonhuman animals, but he also included human culture, sparking a heated debate.
- The spectrum of possible human social behaviors may be influenced by our genetic makeup, but that is very different from saying that genes are rigid determinants of behavior.
- This distinction is at the core of the debate about evolutionary perspectives on human behavior.
    - Evolutionary explanations of human behavior do not reduce us to robots stamped out of rigid genetic molds.
    - Just as individuals vary extensively in anatomy, so we should expect variations in behavior.
- Because of our capacity for learning, human behavior is probably more plastic than the behavior of any other animal.
- Over our recent evolutionary history, we have built up a diversity of structured societies with governments, laws, religions, and cultural values that define acceptable and unacceptable behavior, even when unacceptable behavior might enhance an individual's Darwinian fitness.
- In human behavior, as in other animals, genes and environmental factors build on each other.
- What is unique about our species? Perhaps our social and cultural institutions are our only uniquely human feature.