Chapter 51  Behavioral Ecology

Lecture Outline

Overview: Studying Behavior

- Humans have studied animal behavior for as long as we have lived on Earth.
- As hunter and hunted, knowledge of animal behavior was essential to human behavior.
- The modern scientific discipline of behavioral ecology studies how behavior develops, evolves, and contributes to survival and reproductive success.

Concept 51.1 Behavioral ecologists distinguish between proximate and ultimate causes of behavior

- Scientific questions that can be posed about any behavior can be divided into two classes: those that focus on the immediate stimulus and mechanism for the behavior and those that explore how the behavior contributes to survival and reproduction.
- What is behavior?
  - Behavioral traits are an important part of an animal’s phenotype.
  - Many behaviors result from an animal’s muscular activity, such as a predator chasing a prey.
    - In some behaviors, muscular activity is less obvious, as in bird song.
  - Some nonmuscular activities are also behaviors, as when an animal secretes a pheromone to attract a member of the opposite sex.
  - Learning is also a behavioral process.
- Put simply, behavior is everything an animal does and how it does it.
- Proximate questions are mechanistic, concerned with the environmental stimuli that trigger a behavior, as well as the genetic, physiological, and anatomical mechanisms underlying a behavioral act.
  - Proximate questions are referred to as “how?” questions.
- Ultimate questions address the evolutionary significance of a behavior and why natural selection favors this behavior.
  - Ultimate questions are referred to as “why?” questions.
- Red-crowned cranes breed in spring and early summer.
A proximate question about the timing of breeding by this species might ask, “How does day length influence breeding by red-crowned cranes?”

- A reasonable hypothesis for the proximate cause of this behavior 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 hypothesis might be that red-crowned cranes reproduce in spring and early summer because that is when breeding is most productive.
  - At that time of year, parent birds can find an ample supply of food for rapidly growing offspring, providing an advantage in reproductive success compared to birds that breed in other seasons.

These two levels of causation are related.

- Proximate mechanisms produce behaviors that evolved because they increase fitness in some way.
- For example, increased day length has little adaptive significance for red-crowned cranes, but because it corresponds to seasonal conditions that increase reproductive success, such as the availability of food for feeding young birds, breeding when days are long is a proximate mechanism that has evolved in cranes.

Classical ethology presaged an evolutionary approach to behavioral biology.

- In the mid-20th century, a number of pioneering behavioral biologists developed the discipline of ethology, the scientific study of animal behavior.

- In 1963, Niko Tinbergen suggested four questions that must be answered to fully understand any behavior.
  1. What is the mechanistic basis of the behavior, including chemical, anatomical, and physiological mechanisms?
  2. How does development of the animal, from zygote to mature individual, influence the behavior?
  3. What is the evolutionary history of the behavior?
  4. How does the behavior contribute to survival and reproduction (fitness)?

- Tinbergen’s list includes both proximate and ultimate questions.
  - The first two, which concern mechanism and development, are proximate questions, while the second two are ultimate, or evolutionary, questions.

- 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.
  ○ In the red-spined stickleback, the male 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.
• A proximate explanation for this aggressive behavior is that the red belly of the intruding male acts as a sign stimulus that releases aggression in a male stickleback.
• An ultimate explanation is that by chasing away other male sticklebacks, a male decreases the chance that eggs laid in his nesting territory will be fertilized by another male.
• **Imprinting** is a type of behavior that includes learning and innate components and is generally irreversible.
  ○ Imprinting has a sensitive period, a limited phase in an animal's behavior that is the only time that certain behaviors can be learned.
• An example of imprinting is young geese following their mother.
  ○ In species that provide parental care, parent-offspring bonding is a critical time in the life cycle.
    ▪ During the period of bonding, the young imprint on their parent and learn the basic behavior of the species, while the parent learns to recognize its offspring.
  ○ Among gulls, the sensitive period for parental bonding on young lasts one or two days.
    ▪ If bonding does not occur, the parent will not initiate care of the infant, leading to certain death of the offspring and decreasing the parent's reproductive success.
• How do young gulls know on whom—or what—to imprint?
  ○ The tendency to respond is innate in birds.
  ○ The world provides the imprinting stimulus, and young gulls respond to and identify with the first object they encounter that has certain key characteristics.
    ▪ In greylag geese, the key stimulus is movement of the object away from the young.
• A proximate explanation for young geese following and imprinting on their mother is that during an early, critical developmental stage, the young geese observe their mother moving away from them and calling.
• An ultimate explanation is that, on average, geese that follow and imprint on their mother receive more care and learn
necessary skills, and thus have a greater chance of surviving, than those that do not follow.

- Early study of imprinting and fixed action patterns helped make the distinction between proximate and ultimate causes of behavior.
  - They also helped to establish a strong tradition of experimental approaches in behavioral ecology.

**Concept 51.2 Many behaviors have a strong genetic component**

**Behavior results from both genes and environmental factors.**

- Behavioral traits, like other aspects of a phenotype, are the result of complex interactions between genetic and environmental factors.
- In biology, the nature-versus-nurture issue is not about whether genes or environment influence behavior, but about how both are involved.
  - All behaviors are affected by both genes and environment.
- Behavior can be viewed in terms of the norm of reaction.
  - We can measure the behavioral phenotypes for a particular genotype that develop in a range of environments.
  - In some cases, the behavior is variable, depending on environmental experience.
  - In other cases, nearly all individuals in the population exhibit identical behavior, despite internal and external environmental differences during development and throughout life.
    - Behavior that is developmentally fixed is called innate behavior.
    - Such behaviors are under strong genetic influence.
    - The range of environmental differences among individuals does not appear to alter innate behavior.

**Many animal movements are under substantial genetic influence.**

- A kinesis is a simple change in activity or turning rate in response to a stimulus.
  - For example, sowbugs are more active in dry areas and less active in humid areas.
  - This increases the chance that they will leave a dry area and encounter a moist area.
- A taxis is an automatic, oriented movement toward or away from a stimulus.
For example, many stream fishes exhibit positive rheotaxis, automatically swimming or orienting themselves in an upstream direction (toward the current).

This keeps them from being swept away and keeps them facing in the direction in which food is coming.

- Ornithologists have found that many features of migratory behavior in birds are genetically programmed.
  - Migration is the regular movement of animals over relatively long distances.

- One of the best-studied migratory birds is the blackcap (Sylvia atricapilla), a small warbler that ranges from the Cape Verde Islands off the coast of West Africa to northern Europe.

- Migratory behaviors of blackcaps vary greatly among populations.
  - During the migration season, captive migratory blackcaps hop restlessly about their cages all night or rapidly flap their wings while sitting on a perch.

- Peter Berthold studied the genetic basis of this behavior, known as "migratory restlessness," in several populations of blackcaps.

- In one study, the researchers crossed migratory blackcaps with nonmigratory ones and subjected their offspring to environments simulating one location or the other.
  - Forty percent of offspring raised in both conditions showed migratory restlessness, leading Berthold to conclude that migration is under genetic control and follows a polygenic inheritance pattern.

*Animal communication is an essential component of interactions between individuals.*

- Much of the social interaction between animals involves transmitting information through specialized behaviors called signals.
  - In behavioral ecology, a signal is a behavior that causes a change in another animal's behavior.

- The transmission, reception, and response to signals constitute animal communication.

- Some features of animal communication are under strong genetic control, although the environment makes a significant contribution to all communication systems.

- Many signals are efficient in energy costs.
  - For example, a territorial fish erects its fins when aggressively approaching an intruder.
  - It takes less energy to erect fins that to attack an invading fish.
• Animals communicate using visual, auditory, chemical, tactile, and electrical signals.
• The type of signal is closely related to an animal’s lifestyle and environment.
  ◦ For example, nocturnal species use olfactory and auditory signals.
  ◦ Birds are diurnal and have a poor olfactory sense.
    ▪ They communicate primarily by visual and auditory signals.
  ◦ Humans are more attentive to the colors and songs of birds than the rich olfactory signals of many other animals because of our own senses.
• Many animals secrete chemical substances called pheromones.
  ◦ These chemicals are especially common in mammals and insects and often relate to reproductive behaviors.
  ◦ In honeybees, pheromones produced by the queens and her daughters (workers) maintain the hive’s very complex social order.
    ▪ Male drones are attracted to the queen’s pheromone when they are outside the hive.
  ◦ Pheromones can also function in nonreproductive behavior.
    ▪ When a minnow is injured, an alarm substance is released from glands in the fish’s skin, inducing a fright response among other fish in the area.
      * They become more vigilant and group in tightly packed schools.
    ◦ Pheromones are effective at very low concentrations.
• The songs of most birds are at least partly learned.
• In contrast, in many species of insect, mating rituals include characteristic songs that are under direct genetic control.
• In Drosophila, males produce a song by wing vibration.
  ◦ A variety of evidence suggests that song structure in Drosophila is controlled genetically and is under strong selective pressure.
    ▪ Females can recognize the songs of males of their own species.
    ▪ Males raised in isolation produce a characteristic song with no exposure to other singing males.
    ▪ The male song shows little variation among individuals.
• Some insect species are morphologically identical and can be identified only through courtship songs or behaviors.
  ◦ For example, morphologically identical green lacewings were once thought to belong to a single species.
However, studies of their courtship songs revealed the presence of at least 15 different species, each with a different song.

Hybrid offspring sing songs that contain elements of the songs of both parental species, leading researchers to conclude that the songs are genetically controlled.

**Prairie vole mating and parental behaviors are under strong genetic influence.**

- Mating and parental behavior by male prairie voles (*Microtus ochrogaster*) are under strong genetic control.
- Prairie voles and a few other vole species are monogamous, a social trait found in only 3% of mammalian species.
  - Male prairie voles help their mates care for young, a relatively uncommon trait among male mammals.
  - Male prairie voles form a strong pair-bond with a single female after they mate, engaging in grooming and huddling behaviors.
  - Mated males are intensely aggressive to strange males or females, while remaining nonaggressive to their mate and pups.
- Research by Thomas Insel at Emory University suggests that arginine-vasopressin (AVP), a nine-amino-acid neurotransmitter released in mating, mediates both pair-bond formation and aggression in male prairie voles.
- In the CNS, AVP binds to a receptor called the V₁a receptor.
  - The researcher found significant differences in the distribution of V₁a receptors between the brains of monogamous prairie voles and related promiscuous montane voles.
- Insel inserted the prairie vole V₁a receptor gene into laboratory mice.
  - The mice developed the same distribution of V₁a receptors as the prairie voles and also showed many of the mating behaviors of the voles.
- Thus, a single gene appears to mediate much of the complex mating and parental behavior of the prairie vole.

**Concept 51.3 Environment, interacting with an animal’s genetic makeup, influences the development of behaviors**

- Environmental factors modify many behaviors.
- Diet plays an important role in mate selection by *Drosophila mojavensis*, which mates and lays its eggs in rotting cactus tissues.
• Two populations of this fruit fly species use different species of cactus for their eggs.

• Flies from each population were raised on artificial media in the lab.
  ◦ Females would mate only with males from their own population.
  ◦ The food eaten by male flies as larvae strongly influenced mate selection by female flies.
    ▪ The proximate cause in the female mate choices was in the exoskeletons of the flies, assessed by the sense of taste in female flies.
    ▪ When males from the other population were “perfumed” with hydrocarbons extracted from males of the same population, they were accepted by female flies.

• The California mouse (*Peromyscus californicus*) is monogamous.
  ◦ Like male prairie voles, male California mice are highly aggressive to other mice and provide considerable parental care.
    ▪ Unlike prairie voles, even unmated California mice are aggressive.

• Researchers placed newborn California mice in the nests of white-footed mice (and vice versa).
  ◦ White-footed mice are not monogamous and provide little parental care.

• This cross-fostering changed the behavior of both species.
  ◦ Cross-fostered California mice provided less parental care and were less aggressive toward intruders when they grew up and reared their own young.
    ▪ Their brains had reduced levels of AVP, compared with California mice raised by their own parents.
  ◦ White-footed mice reared by California mice were more aggressive as parents than those raised by their own parents.

• One of the most powerful ways that environmental conditions can influence behavior is through learning, the modification of behavior based on specific experiences.

• Learned behaviors can be very simple, such as imprinting, or highly complex.

• Habituation involves a loss of responsiveness to unimportant stimuli or stimuli that do not provide appropriate feedback.
  ◦ For example, some animals stop responding to warning signals if signals are not followed by a predator attack (the “cry wolf” effect).
  ◦ In terms of ultimate causation, habituation may increase fitness by allowing an animal’s nervous system to focus on
meaningful stimuli, rather than wasting time on irrelevant stimuli.

The fitness of an organism may be enhanced by the capacity for spatial learning.

- Every natural environment shows spatial variation.
- As a consequence, it may be advantageous for animals to modify their behavior based on experience with the spatial structure of their environment, including the locations of nest sites, hazards, food, and prospective mates.
  - The fitness of an animal may be enhanced by the capacity for spatial learning.
- Niko Tinbergen found that digger wasps found their nest entrances by using landmarks, or location indicators, in their environment.
  - Landmarks must be stable within the time frame of the activity.
  - Because some environments are more stable than others, animals may use different kinds of information for spatial learning in different environments.
    - Sticklebacks from a river learned a maze by learning a pattern of movements.
    - Sticklebacks from a more stable pond environment used a combination of movements and landmarks to learn the maze.
      * The degree of environmental variability influences the spatial learning strategies of animals.
  - Some animals form cognitive maps, internal codes of spatial relationships of objects in their environment.
    - It is difficult to distinguish experimentally between the use of landmarks and the development of a true cognitive map.
      * Researchers have obtained good evidence that corvids (a bird family including ravens, crows, and jays) use cognitive maps.
      * Many corvids store food in caches and retrieve it later.
      * Pinyon jays may store nuts in as many as a thousand widely dispersed caches, keeping track of location and food quality (based on time since the food was stored).
    - Birds can learn that caches are halfway between two landmarks.

Many animals can learn to associate one stimulus with another.

- Associative learning is the ability of animals to learn to associate one stimulus with another.
• For example, a mouse may have an unpleasant experience with a colorful, poisonous caterpillar and learn to avoid all caterpillars with that coloration.

• **Classical conditioning** is a type of associative learning.
  • Researchers trained *Drosophila melanogaster* to avoid air carrying a particular scent by coupling exposure to the odor with an electrical shock.
  • *Drosophila* has a surprising capacity for learning.

• **Associative learning** may play an important role in helping animals to avoid predators.
  • Zebra fish, an Asian minnow, and pike, an American predatory fish, do not occur together in the wild.
  • Researchers exposed zebra fish in an experimental group to an influx of 20 mL of water containing an alarm substance and then, 5 minutes later, to 20 mL of water with pike odor.
  • Zebra fish had no innate negative reaction to pike odor, but learned to associate pike odor with the alarm substance.
  • The zebra fish were conditioned to associate pike odor with the alarm substance.

• **Operant conditioning** is also called trial-and-error learning.

• An animal learns to associate one of its own behaviors with a reward or a punishment.
  • An example is the mouse eating the poisonous caterpillar and learning to avoid such caterpillars in the future.

**The study of cognition connects behavior with nervous system function.**

• The term *cognition* is variously defined.
  • In a narrow sense, it is synonymous with consciousness or awareness.
  • In a broad sense, animal *cognition* is the ability of an animal’s nervous system to perceive, store, process, and use information gathered by sensory receptors.

• The study of animal cognition, called *cognitive ethology*, examines the connection between an animal’s nervous system and its behavior.

• One area of research investigates how an animal’s brain represents physical objects in the environment.

• Cognitive ethologists have discovered that many animals, including insects, categorize objects in their environment as “same” or “different.”

• Primates, dolphins, and corvids (crow, ravens, and jays) are capable of novel problem-solving behavior.
  • Individual animals may show great individual variation in the way they attempt to solve a problem.
• Many animals solve problems by observing the behavior of other individuals.
  ○ Chimpanzees learn to solve problems by copying the behavior of other chimpanzees.

Varying degrees of genetic and environmental factors contribute to the learning of complex behavior.
• Considerable research on the development of songs by birds has revealed varying degrees of genetic and environmental influence on the learning of complex behavior.
• In some species, learning plays only a small part in the development of song.
  ○ For instance, New World flycatchers that are reared away from adults of their own species will sing the song characteristic of their own species without ever having heard it.
• Some songbirds have a sensitive period for developing their songs.
  ○ Individual white-crowned sparrows reared in silence perform abnormal songs, but if recordings of the proper songs are played early in the life of the bird, normal songs develop.
  ○ Although the young bird does not sing during the sensitive period, it memorizes the song of its own species by listening to other white-crowned sparrows sing.
  ○ During the sensitive period, white-crowned sparrows fledging seem to be stimulated more by songs of their own species than songs of other species, chirping more in response.
  ○ The young birds learn the songs, but the learning appears to be bounded by genetically controlled preferences.
• The sensitive period in a white-crowned sparrow's learning of his song is followed by a second learning phase, when the juvenile bird sings some tentative notes that researchers call a subsong.
  ○ The juvenile bird hears its own song and compares it with the song that it memorized in the sensitive period.
  ○ Once they match, the bird sings that song for the rest of his life.
• Canaries may learn new song "syllables" each year, adding to their song during a yearly plastic song stage.
Concept 51.4 Behavioral traits can evolve by natural selection

- Because of the influence of genes on behavior, natural selection can result in the evolution of behavioral traits in populations.

Behavior varies in natural populations.

- Behavioral differences between closely related species are common.
  - Males of different *Drosophila* species sing different courtship songs.
  - Species of voles differ in paternal care.

- Although less obvious, significant differences in behavior can be found within animal species.

- When behavioral variation within a species corresponds to variation in environmental conditions, it may be evidence of past evolution.

- One of the best-known examples of genetically based variation in behavior within a species is prey selection by the garter snake *Thamnophis elegans*.
  - Coastal garter snakes feed on salamanders, frogs, and toads, but mainly on slugs.
  - Inland snakes eat frogs, leeches, and fish, but not slugs.

- Stevan Arnold investigated this variation.
  - He offered slugs to snakes from both populations, but only coastal snakes readily accepted the slugs.
  - He tested newborn snakes born in the laboratory and found that 73% of young snakes from coastal mothers attacked slugs they were offered.
    - Only 35% of naïve snakes from inland mothers attacked the slugs.

- Arnold proposed that when inland snakes colonized coastal environments 10,000 years ago, a small fraction of the population had the ability to recognize slugs by chemoreception.
  - 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.

- The funnel web spider *Agelenopsis aperta* lives in riparian zones and the surrounding arid environment in the western United States.
  - The spider’s web is a silken sheet ending in a hidden funnel, where the spider sits and watches for food while foraging.
  - When prey strikes the web, the spider runs out across the web to make its capture.
Riechert and her colleagues found a striking contrast in the behavior of spiders in riparian forests and those in arid habitats.
- In arid, food-poor habitats, *A. aperta* is more aggressive to potential prey and to other spiders in defense of its web, and it returns to foraging more quickly following disturbance.

Hedrick and Riechert reared spiders in the lab and found that the differences in aggressiveness between desert and riparian spiders are genetic.
- Highly productive riparian sites are rich in prey for spiders, but the density of bird predators is also high.
- The timid behavior of *A. aperta* in riparian habitats was selected for by predation risk.

**Experiments provide evidence for behavioral evolution.**

Researchers are carrying out experiments on organisms with short life spans, looking for evidence of evolution in laboratory populations.

Marla Sokolowski studied a polymorphism in a gene for foraging in *Drosophila melanogaster*.

The gene is called *for*, and it has two alleles.
- One allele, *for*R, results in a “rover” phenotype in which the fly larva moves more than usual.
- The other allele, *for*S, results in a “sitter” phenotype in which the fly larva moves less than usual.

Sokolowski reared *Drosophila* at high and low population densities for 74 generations.
- The *for*S allele increased in low-density populations, while *for*R increased in high-density populations.
- At low densities, short-distance foraging yielded sufficient food.
- At high densities, long-distance foraging helped the larvae to move beyond areas of food depletion.

Peter Berthold and his colleagues captured 20 male and 20 female blackcaps wintering in Britain and transported them to southwest Germany.
- The birds were caged in glass-covered funnel cages lined with carbon paper.
- As the birds moved around the funnels, the marks they made on the paper showed the direction they were trying to migrate.
  - The migratory orientation of wintering adult birds captured in Britain was similar to their laboratory-reared offspring.
- Young birds originally from Germany had a very different migratory orientation.
- This study indicates a genetic basis for migratory orientation of the young birds.
- Has the behavior evolved over time?
  - Berthold’s study suggests that the change in migratory behavior of the blackcaps is recent and rapid, having taken place over the past 50 years.
  - Before 1960, there were no westward-migrating blackcaps in Germany.
  - By the 1990s, westward migrants made up 7–11% of the blackcap populations of Germany.
  - Berthold suggested that westward migrants benefited from their new behavior, due to the milder winter climate and greater abundance of bird feeders in Britain.

**Concept 51.5 Natural selection favors behaviors that increase survival and reproductive success**

- The genetic components of behavior evolve through natural selection favoring traits that enhance survival and reproductive success in a population.
- Two of the most direct ways that behavior can affect fitness are through influences on foraging and mate choice.
- Foraging includes not only eating, but also any mechanisms that an animal uses to recognize, search for, and capture food items.
- **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.
- Behavioral ecologists apply cost-benefit analysis to study the proximate and ultimate causes of diverse foraging strategies.
- Reta Zach of the University of British Columbia carried out a cost-benefit analysis of feeding behavior in crows.
  - Crows search the tide pools of Mandarte Island, B.C., for snails called whelks.
  - A crow flies up and drops the whelk onto the rocks to break its shell.
  - If the drop is successful, the crow eats the snail’s soft body.
  - If it is not successful, the crow flies higher and tries again.
- Zach predicted—and found—that crows would, on average, fly to a height that would provide the most food relative to the total amount of energy required to break the whelk shells.

- Bluegill sunfish feed on small crustaceans called *Daphnia*, selecting larger individuals that supply the most energy per unit time.
  - Smaller individuals will be selected if larger prey are too far away.

- Optimal foraging theory predicts that the proportion of small to large prey captured will vary with prey density.
  - At high densities, it is efficient for bluegill sunfish to feed only on large crustaceans.
  - At low densities, bluegill sunfish should exhibit little size selectivity because all prey are needed to meet energy requirements.

- In experiments, young bluegill sunfish forage efficiently but not as close to optimum as older individuals.
  - Perhaps younger fish do not judge size and distance as accurately because their vision is not yet completely developed.
  - Learning may also improve the foraging efficiency of bluegill sunfish as they age.

- Risk of predation is one of the most significant potential costs to a forager.

- Mule deer are preyed on by mountain lions throughout their range.
  - Researchers studied mule deer populations in Idaho to determine if 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.
    - Risk of predation varied greatly, however.
    - 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.
  - When deer are at the forest edge, they spend significantly more time scanning their surroundings than when they are in other areas.

- 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.
The mating relationship between males and females varies greatly from species to species.
- In many species, mating is promiscuous, with no strong pair-bond or lasting relationships.
- In species where 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 so much alike morphologically that they are impossible to distinguish based on external characteristics.
- Polygynous species are generally dimorphic, with males being larger and more showy.
- In polyandrous species, females are 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 the raising of 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.

In mammals, the lactating female is often the only food source for the young, and males play no role in caring for them in most mammal species.
- In some mammal species, males protect many females and their young.

Certainty of paternity can influence mating systems and parental care.
- If the male is unsure if offspring are 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 because the acts of mating and birth are separated over time.
  - Males in many species with internal fertilization engage in behaviors that appear to 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 when egg laying and mating occur together, in external fertilization.
  - 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 and in 69% of families with external fertilization.
  - The expression certainty of paternity does not imply conscious awareness of paternity by the father.

**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.
- Witte and Sawka experimented to see whether imprinting by young zebra finches on their parents influenced their choice of mates when they matured.
  - They taped a red feather to the heads of both parents, male parent only, or female parent only, 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 unornamented mate finches.
  - Males showed no preference, but females reared by ornamented fathers 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 evolution of ornamentation in male zebra finches.
- Courtship behaviors of stalk-eyed flies are fascinating.
Males have elongated eyestalks, which they display to females during courtship.
- Females prefer to mate with males with relatively long eyestalks.
- How is this preference adaptive for females?
  - Researchers have correlated certain genetic disorders in male flies with an inability to develop long eyestalks.
  - Males with long eyestalks may be demonstrating their 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.

- 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 can result in successful reproduction.
  - In such cases, intrasexual selection has led to the evolution of alternative male mating behavior and morphology.

- Alternative male mating behaviors have been documented in the marine intertidal isopod Paracerceis sculpta, which lives in sponges in the Gulf of California.

- This species includes three genetically distinct male types—alpha, beta, and gamma.
  - Large alpha males defend harems of females within intertidal sponges, largely against other alpha males.
  - Beta males mimic female morphology and behavior and gain access to guarded harems.
  - Tiny gamma males invade and live within large harems.

- The mating success of each type of isopod depends on the relative density of males and females in the sponges.
  - The alpha males sire the majority of young when defending a single female.
  - If more than one female is present, beta males father 60% of the offspring.
  - The reproductive rate of gamma males increases linearly with harem size.

- Overall, all three types of males have approximately equal mating success, and variation among males in this species is sustained by natural selection.
**Game theory can model behavioral strategies.**

- Game theory evaluates alternative strategies in situations where the outcome depends on each individual's strategies and the strategies of other individuals.
- Barry Sinervo and Curt Lively used game theory to account for the existence of three different male phenotypes in populations of side-blotched lizards (*Uta stansburiana*).
- Males have three genetically controlled colors: orange throats, blue throats, and yellow throats.
  - 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.
- 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.
  - 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.
  - The cycle continues.

**Concept 51.6 The concept of inclusive fitness can account for most altruistic social behavior**

- Most social behaviors are selfish, meaning that they benefit the individual at the expense of others, especially competitors.
- Behavior that maximizes an individual's survival and reproductive success is favored by selection, regardless of its effect on other individuals.
- How do we account for behaviors that help others?
  - **Altruism** is defined as behavior that appears to decrease individual fitness but increases the fitness of others.
- Belding's ground squirrel lives in some mountainous regions of the western United States.
  - The squirrel 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 are highly social rodents that live in underground chambers and tunnels in Africa.
  - These rodents are 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 consists of nonreproductive females and males who forage for underground roots and tubers and care for the kings, queen, and young rats.

- How can a naked mole rat (or a honeybee or a ground squirrel) enhance its fitness by helping other members of the population?
  - How is altruistic behavior maintained by evolution?
  - If related individuals help each other, they are, in effect, helping keep their own genes in the population.

**Inclusive fitness** is defined as the effect an individual has on proliferating its own genes by reproducing *and* by helping relatives raise offspring.

- William Hamilton proposed a quantitative measure for predicting when natural selection should favor altruistic acts.
  - Hamilton's rule states the conditions under which altruistic acts will be favored by natural selection.

- The three key variables are as follows:
  1. The benefit to the recipient is $B$.
  2. The cost to the altruist is $C$.
  3. The **coefficient of relatedness** is $r$, which equals the probability that a particular gene present in one individual will also be inherited from a common parent or ancestor in a second individual.

- The rule is as follows:
  - $rB > C$
  - The more closely related two individuals are, the greater the value of altruism.

**Kin selection** is the mechanism of inclusive fitness, where individuals help relatives raise young.
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 would be negative social consequences for those who “cheat” and refuse to return favors to those who have helped them in the past.

However, because cheating may provide a large benefit to cheaters, behavioral ecologists have questioned how reciprocal altruism could arise.

To answer this question, behavioral ecologists have turned to game theory.
  - Axelrod and Hamilton found that reciprocal altruism can evolve and persist in a population where individuals adopt a behavioral strategy called **tit for tat**.
  - In this strategy, an individual treats another individual the same way it was treated the last time they met.
  - Individuals are always altruistic, or cooperative, on the first encounter, and will remain so as long as their altruism is reciprocated.
    - When it is not, they will retaliate immediately but will return to cooperative behavior as soon as the other individual becomes cooperative.

**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.
    - Cultural transfer of information has the potential to alter behavioral phenotypes and influence the fitness of individuals.

Social learning is not restricted to humans.

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

**Mate choice copying**, a behavior in which individuals in a population copy the mate choices of others, has been extensively studied in the guppy *Poecilia reticulata*.

Female guppies prefer to mate with males having a high percentage of orange coloration.
- However, if a female sees another female engaging in courtship with a male with relatively little orange, she will choose a male with little orange herself.
  - Below a certain threshold of difference in mate color, mate choice copying by female guppies can mask genetically controlled female preference for orange males.

- What is the advantage for females?
  - A female that mates with males that are attractive to other females may increase the probability that her male offspring will also be attractive and have high reproductive success.

- In their studies of vervet monkeys in Amboseli National Park, Kenya, Dorothy Cheny and Richard Seyfarth found that performance of a behavior can improve through learning.

- Vervet monkeys (*Cercopithecus aethiops*) produce a complex set of alarm calls.
  - Distinct alarm calls warn of leopards, eagles, or snakes, all of which prey on the small vervets.
  - Vervets react to each alarm differently, depending on the threat.
  - 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 variation in behavior.
• Because of our capacity for learning, human behavior is probably more plastic than that of any other animal.

• Over our recent evolutionary history, we have built up a diversity of structured societies with governments, laws, 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 it is our social and cultural institutions that provide us with the only uniquely human feature.