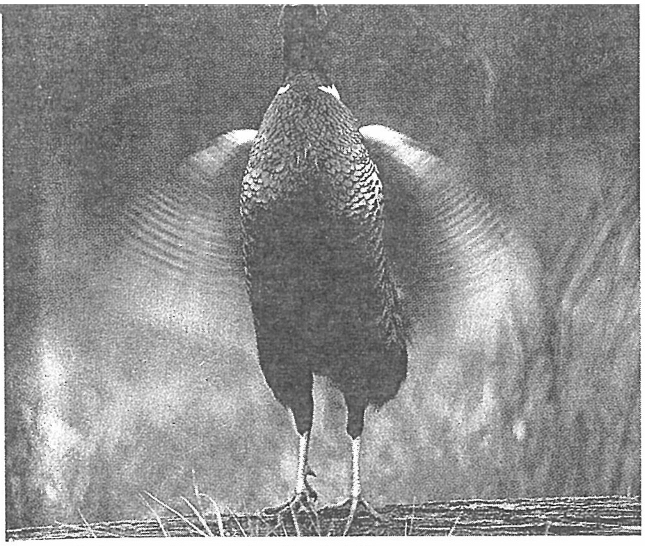


A ring-necked pheasant in a display of territoriality.

52

Animal Behavior

OUTLINE

- I. Ways of looking at animal behavior
- II. Classical ethology and innate behaviors
  - A. Communication in bees
  - B. Fixed action patterns in vertebrates
  - C. Other functions of innate, stereotyped behavior
  - D. Human ethology
- III. Behavior genetics
  - A. The causes of behavior—nature vs. nurture
  - B. Heritability
- IV. Learning
  - A. Habituation
  - B. Sensitization
  - C. Associative learning
    - 1. Classical conditioning
    - 2. Operant conditioning
  - D. Latent learning
  - E. Insight learning
  - F. Imprinting
- V. Behavioral ecology
- VI. Migration
- VII. Social behavior
  - A. Communication
    - 1. Modes of communication
  - B. Dominance hierarchies
  - C. Territoriality
  - D. Sexual behavior and reproduction
    - 1. Pair bonds
    - 2. Care of the young
  - E. Play
  - F. Sociobiology

LEARNING OBJECTIVES

After you have read this chapter you should be able to:

1. Explain how a simple behavior, such as urine marking in dogs, can be interpreted from the point of view of (a) classical ethology, (b) learning, (c) behavior genetics, (d) behavioral ecology, and (e) neurobiology.
2. Distinguish between proximate and ultimate factors as causes of animal behavior.
3. Distinguish fixed action patterns from reflexes and volitional behaviors.
4. Cite examples of how displays may have evolved through the ritualization of less complex behaviors.
5. Provide arguments for and against the appropriateness of interpreting human behavior in terms of innate behaviors in animals (e.g., redirected behavior, displacement behavior).
6. Discuss the influence of genetic and learned components on behavior in the same individual and in populations, and explain how the concept of heritability is used in the latter case.
7. Classify learned behaviors you encounter in animals as examples of (a) classical conditioning, (b) operant conditioning, (c) sensitization, (d) habituation, or (e) insight learning.
8. Discuss the adaptive significance of imprinting.
9. Discuss how travel time and handling time vary when animals forage optimally in good and poor habitats.
10. Postulate biological advantages for migration.
11. Present the concept of a dominance hierarchy, giving at least one example, and speculate its possible general adaptive significance and social function.
12. Distinguish between home range and territory, and give three theories about the adaptive significance of territoriality.
13. Discuss the adaptive value of courtship behavior and describe a pair bond.
14. Summarize the emphases of sociobiology.

A familiar canine behavior is urinating on a lamppost. Why do dogs do this? The answer depends on the level of explanation we have in mind. Animal behavior, succinctly defined as "the movements of animals in response to stimuli," deals with several levels of explanation. These levels include the physiological mechanisms that cause the behavior as well as the evolutionary processes that account for its origin and development. In this chapter we will describe the major approaches to the study of animal behavior. We will discuss several observations and experiments that have been useful in defining and organizing this fascinating field of inquiry.

WAYS OF LOOKING AT ANIMAL BEHAVIOR

To an ethologist the question "Why do dogs do this?" might mean "How does this behavior, called *urine marking*, help a dog survive in its natural habitat?" Broadly defined, **ethology** is the comparative study of behavior. Ethology focuses on *innate* (inherited, inborn), species-typical behaviors seen in nature and on how these behaviors adapt animals to their environment. Ethologists also try to piece together the evolutionary history of behaviors, so the question also might mean to them, "Why did dogs evolve urine marking rather than another behavior?" or, "Did urine marking evolve from a pre-existing behavior, and if so, what was that behavior?" They make the reasonable assumption that innate behaviors like this one are just as responsive to natural selection (Chapter 17) as are anatomical features.

Behavior geneticists are concerned with the relationships between genes and behavior. Accordingly, they ask the same fundamental question most geneticists ask about biological characters: What are the manner and ways in which characters are inherited? After establishing how urine marking varies genetically among individual dogs, they might analyze offspring from specific matings to determine the genetic mechanism that best explains the inheritance of this trait.

Experimental or **comparative psychologists,** particularly those working in the tradition of the *behaviorists* (e.g., B. F. Skinner and his colleagues), focus principally on *learned* behaviors, that is, behaviors acquired or modified by previous experiences. Their objective is to predict behavior in animals, sometimes with the goal of controlling particular behaviors under specific circumstances. To this end they determine experimentally the influence of specific variables—such as diet, age, ambient temperature, or the presence of other animals—on behavior. Even inherited behaviors like urine marking can be modified to some extent by environmental variables. For example, a dog, after being punished for marking a particular spot, may lift its leg at that spot but not actually urinate, even when unattended by its owner.

Most experimental psychologists carefully control the laboratory conditions under which they carry out their experiments. Typically, they use domestic or laboratory animals as subjects.

Behavioral ecology focuses on the evolution of adaptive behavior in relation to the environment. This discipline utilizes theories and techniques from both classical ethology and ecology. Whereas classical ethologists usually concentrate on individuals or small groups, behavioral ecologists generally study the dynamics of behaviors in *populations* of animals, paying particular attention to behavioral differences between individuals of the same species (or between populations of different species). A common approach is to quantify the behaviors of individuals in a population and then incorporate the data into a theoretical model to explain how the population is adapted to its environment. In dealing with such theoretical questions, behavioral ecology often relies heavily on mathematical notation.

Neurobiology seeks to explain the mechanisms of behavior in terms of the structure and function of the nervous system. To return to the example of urine marking in dogs, a neurobiologist might begin a study of this behavior by identifying the specific parts of the brain concerned with its motivation, organization, initiation, coordination, and execution; the neurobiologist later might determine the biochemical reactions in these brain parts that accompany the behavior. **Neuroethology** is somewhat narrower in scope than neurobiology; it concentrates on neural mechanisms that underlie species-typical behaviors (as observed in nature), that is, the behaviors traditionally studied by ethologists.

These areas, all dealing with how and why an animal behaves as it does, are generally regarded as subdisciplines of animal behavior; but many of these areas overlap considerably in subject matter and experimental techniques, and most have been defined in more than one way. The term "ethology," in particular, has been variously defined.

Some of the subdisciplines differ more fundamentally than in level of explanation because they ask different *types* of questions (and thus require different types of answers). Questions about evolution are basically historical questions that must be answered with educated guesses about what *might* have occurred during the evolutionary history of an animal. These long-term evolutionary causes of behavior—called **ultimate factors**—should be explainable in terms of experimentally verifiable mechanisms such as genetic change and natural selection. However, the hypothetical account of what occurred is itself not verifiable.

In contrast, questions dealing with neurobiology, behavior genetics, and experimental psychology are concerned with the immediate conditions or mechanisms—the **proximate factors**—that cause particular behaviors. These questions must be answered either with facts that are verifiable experimentally, or with hypotheses that at least in principle are testable.

CLASSICAL ETHOLOGY AND INNATE BEHAVIORS

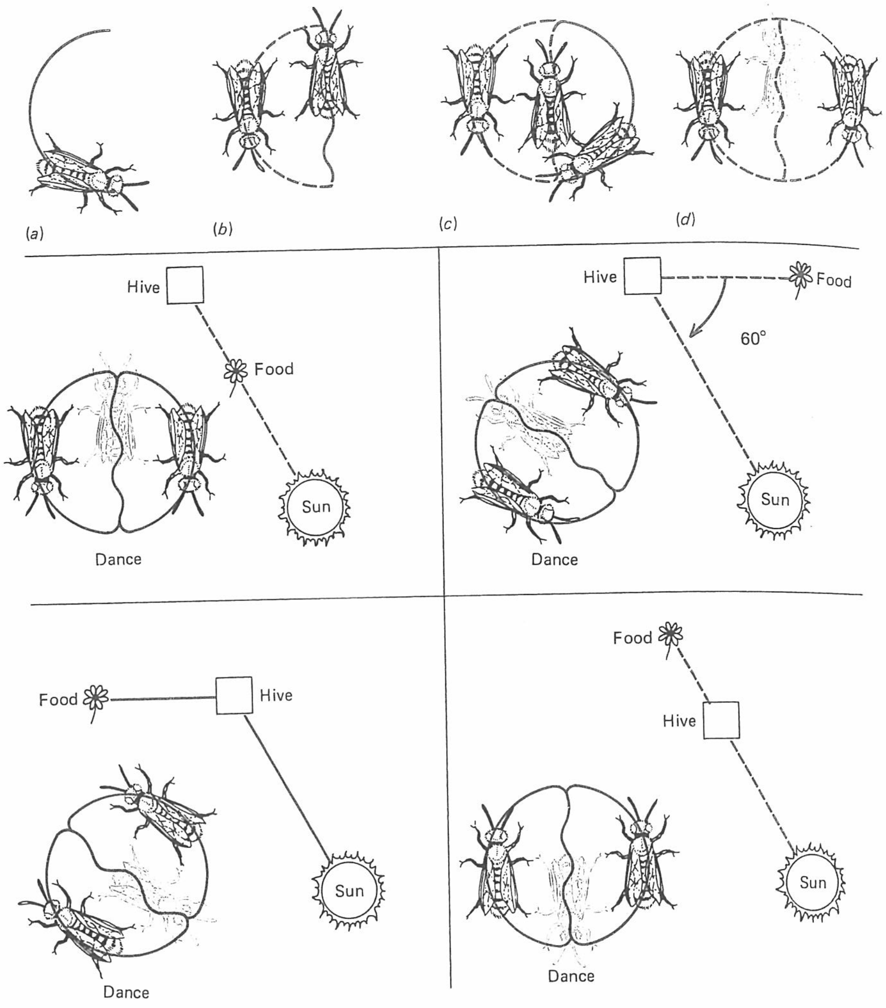
Most of the first important contributions to our understanding of innate behavior were made in the 1930s and 1940s by several European ethologists. Three of these ethologists—Konrad Lorenz, Nikolaas Tinbergen, and Karl von Frisch—received the Nobel Prize in 1973 for their work.

The behaviors that attracted the attention of early ethologists were those that pique the curiosity of many sensitive observers of the behavior of animals in nature. Yet perhaps these extraordinarily creative scientists thought somewhat more deeply about what they saw. Also, they were exceptionally ingenious and careful in designing experiments to test their hypotheses.

Communication in Bees

An innate behavior in invertebrates that was studied extensively by von Frisch and others is the "dance" of honey bees (Figure 52–1). This intricate behavior allows bees to communicate the location of a food source to other bees in the hive. In one species a worker, after locating a distant food source, returns to the hive and performs the dance on a vertical surface of the comb. It moves in a figure 8, the two loops sharing a "straight run." During the straight run the bee waggles its abdomen. These movements communicate the direction and distance of the food source from the hive. They are responses to environmental stimuli that are rather subtle by human standards: gravitational pull and the direction of the sun. The direction of the food source, relative to the sun, is indicated by the angle of

FIGURE 52–1 Dance of the honey bee, indicating direction and distance of a food source in relation to the hive.



the straight run with respect to the axis that is perpendicular to the gravitational force of the earth. The distance of the food source from the hive is indicated by the frequency of the waggles and the speed of the dance.

Other worker bees follow in the dance, then leave the hive and fly the correct direction and distance to the food source. It is usually argued that this behavior is adequately explained by neurophysiological processes in a totally *unaware* insect. However, some scientists have maintained that awareness should not be excluded as a factor in this behavior.

Fixed Action Patterns in Vertebrates

A classic example of innate behavior in vertebrates is *egg-rolling* in waterfowl. When an egg is removed from the nest of an incubating goose and placed a few inches in front of her, she will reach out with her neck and pull the egg back into the nest (Figure 52–2). While perhaps appearing rather insignificant to the casual observer, this behavior suggested a number of important ethological concepts to Lorenz and Tinbergen, who carefully studied its characteristics in the European greylag goose.

After it was confirmed as innate by observing it in inexperienced geese, egg-rolling was analyzed in terms of its behavioral components. It was noted that if, while the goose was rolling the egg back toward the nest, the egg veered off to the side, the goose steered it back toward the nest. This **taxis component**, which steers the behavior relative to the environment, distinguishes egg-rolling from simple reflexes like the knee jerk reflex (Chapter 46). In typical reflexes a muscle contracts involuntarily when part

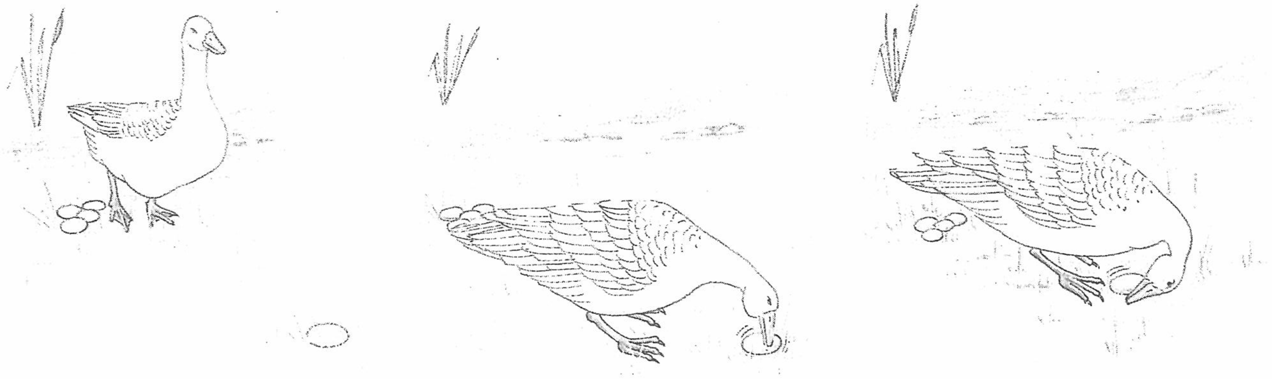


FIGURE 52–2 Egg-rolling behavior in the European grayling goose is termed a fixed action pattern (FAP).

of the body is stimulated, but there is no steering component. In the case of the knee reflex, the lower leg extends in response to a tap on the tendon regardless of what stands in its path.

If egg-rolling is not a reflex, then we may ask whether it is the same sort of behavior a golfer exhibits when he or she reaches out with a golf club to retrieve a ball that has rolled into a ditch. Human behaviors of this type—*volitional behaviors*—are based on conscious choice or decision. Although the mental states of animals are not directly accessible to us, one component of egg-rolling behavior sets it apart from most human volitional behavior. If the egg is snatched away from the goose while she is retrieving it, she continues the retrieving movement *even though there is no longer an egg to retrieve.* Thus, once begun, the behavior is relatively independent of the external stimulus that initiated it. This characteristic is certainly not typical of human volitional behavior, although it superficially resembles certain compulsive behaviors in humans.

Lorenz named this type of behavior—which seems to be neither a simple reflex nor a volitional behavior—a **fixed action pattern (FAP).** Although the behavior is not "fixed" in a literal sense, this term emphasizes that it is more or less invariable (suggesting a strong genetic component). Table 52–1 compares some of the characteristics of reflexes, FAPs, and volitional behaviors. Thus FAPs, while being invariable like reflexes, more closely resemble volitional behaviors because of their steering mechanism. However, FAPs differ from volitional behavior because they continue after the eliciting stimulus is no longer present.

Any stimulus that elicits a FAP—such as the egg in egg-rolling behavior or the red-colored "belly" in the attack behavior of the stickleback fish (Figure 52–3)—is called a **sign stimulus.** For example, a goose will retrieve a wooden egg in the same way as a real egg, so the wooden egg is also by definition a sign stimulus. Yet only the real egg is the "natural" sign stimulus, that is, the one that evolved with the behavior. The special term **releaser** was originally applied only to the latter category of sign stimuli.

Curiously, "artificial" sign stimuli, such as wooden eggs, are sometimes more powerful than releasers. Certain birds (Figure 52–4), when given a choice, will choose a large wooden egg in preference to their own normal-sized eggs. In this case the stimulus has been called a **super sign stimulus.**

Table 52–1 COMPARISON OF REFLEX, FAP, AND VOLITIONAL BEHAVIORS

Reflex	*FAP*	*Volitional Behavior*
Invariable	Invariable	Variable
No steering	Steering	Steering
N/A	Independent of external stimuli once started	Dependent on external stimuli for continued expression

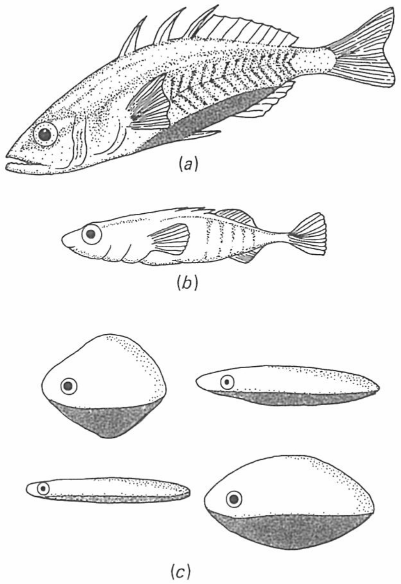


FIGURE 52–3 A sign stimulus is a particular feature that triggers a FAP. A male stickleback fish (*a*) will not attack a realistic model of another male stickleback if it lacks a red belly (*b*), but it will attack another model, however unrealistic, that has a red "belly" (*c*). Therefore, it is the specific red sign stimulus, rather than recognition based on a combination of features, that triggers the aggressive behavior.

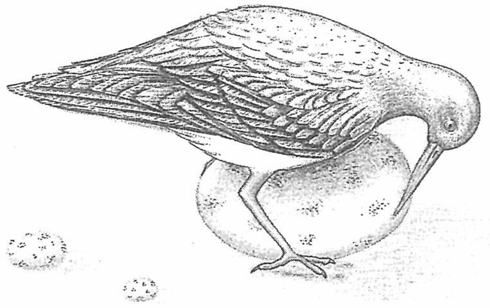


FIGURE 52–4 Sometimes birds such as this oystercatcher choose an artificial egg to incubate rather than their own if the artificial egg is larger. Stimuli of this type are known as super sign stimuli.

In one well-known ethological model, sign stimuli are detected in the central nervous system by special sensory mechanisms called **innate releasing mechanisms (IRMs).** Each IRM is specific to a particular sign stimulus; thus oval-shaped eggs, whether real or artificial, are detected by a specific IRM for this shape. The IRM then sets into motion the FAP, in this case, egg-rolling.

Another well-known example of how releasers and FAPs interact is feeding behavior in gulls. A red spot on the bill of certain gulls is a releaser for begging behavior in nestlings. When the parent gull approaches the nest, with or without food, the IRM in the young gull detects (by means of visual stimuli) the spot on the parent's bill and sets into motion a FAP, specifically, the begging response. Even a red spot painted on a piece of cardboard elicits this begging response. Likewise, the open mouth of a nestling is the releaser for feeding behavior in the parent. In many species the stimulus for feeding behavior may not be species-specific; parent birds will feed young hatched from eggs deposited in their nest by other species (Figure 52–5).

Other Functions of Innate, Stereotyped Behavior

Since many FAPs were seen to function in more than one way, one of the earlier goals of ethologists was to explain how a behavior came to take on other functions. In the example of urine marking in dogs, the original function of lifting a hind leg and urinating was of course to void urine. The additional or "secondary" function, which presumably evolved from the first, was to mark a territory. Other examples of multiple functions of FAPs are known.

FIGURE 52–5 The stimulus for feeding behavior is not always species-specific, as evidenced by this yellow warbler that is feeding a young cowbird. The female cowbird does not build a nest, but rather deposits her eggs in nests of other species.

When an animal's interests are in conflict, it may *redirect* its behavior toward an inappropriate object. For example, when a male bird confronts an opponent and cannot decide whether to fight or run, he may peck furiously at the ground. When fear and aggression are balanced, an adult dog may snap at a puppy rather than confront another adult male. Fighting behavior is redirected toward a less threatening object, rather than directed toward the aggressor. In such **redirected behavior,** an innate, stereotyped behavior originally designed to defend against an aggressor, serves an additional function. Perhaps it releases tension.

Whereas redirected behavior may seem appropriate considering the possible outcome of direct confrontation, animals sometimes perform behaviors that are inappropriate or irrelevant to the situation. When fear and aggression are balanced, gorillas may nibble on a leaf, birds may preen, and wolves may chew on a branch (Figure 52–6). Irrelevant behavior stemming from a conflict situation is known as **displacement activity.** Redirected behavior and displacement activity are assumed to be adaptive, but just how they help animals survive is not known.

FIGURE 52–6 Displacement activity. When two forms of behavior (such as fighting or fleeing) are equally appropriate, an animal may engage in some completely irrelevant behavior, as with this gray timberwolf chewing on a branch.

The concept of **ritualization** was introduced to describe how certain innate behaviors evolved into signals so that they function in communication. For example, in certain gulls a FAP for feeding involves tugging at an object, such as a carcass lying on the beach. During their courtship display these same gulls tug violently at patches of grass, indicating that the FAP has acquired a second function, namely, communication. Tugging at the grass has become incorporated into the courtship display and under these circumstances is said to be a ritualized form of the feeding behavior.

When behavior patterns are changed through ritualization, they frequently become more stereotyped in form. Tugging at grass as an element of a courtship display is less variable than tugging at a carcass during feeding. Ritualized behavior patterns also tend to vary less in intensity, and the displaying animal sometimes "freezes" into a posture by not completing the movement (e.g., it may grab some grass and momentarily remain motionless). These modifications make the ritualized behavior less ambiguous and increase its effectiveness in communication.

Human Ethology

Not unexpectedly, some animal behaviorists are interested in applying ethological methods to the study of presumed innate human behaviors. It was probably inevitable that this approach to human behavior, called **human ethology,** would be controversial, because until recently most influential psychologists maintained that the only valid approach to understanding human behavior was to study learned behaviors. Even the very existence of innate, stereotyped human behaviors has been a topic of vigorous debate. Yet because certain behaviors like fighting, smiling, and dancing are so strikingly similar in widely separate and diverse cultures, many persons are convinced that there is a strong genetic component in at least some human behaviors.

Also, certain behaviors in humans are quite similar in appearance to behaviors that are accepted as innate in animals. These similarities are particularly apparent to animal trainers and pet owners who have an intimate knowledge of animals. On the other hand, it is not clear how to interpret these similarities. When we strike the tabletop with our fist instead of hitting a person who angers us, are we displaying redirected behavior like the scolded dog that bites the nearby puppy? When we chew gum or smoke a cigarette while being reprimanded by a supervisor, are we exhibiting displacement behavior like the turkey that eats when threatened (Figure 52–7)?

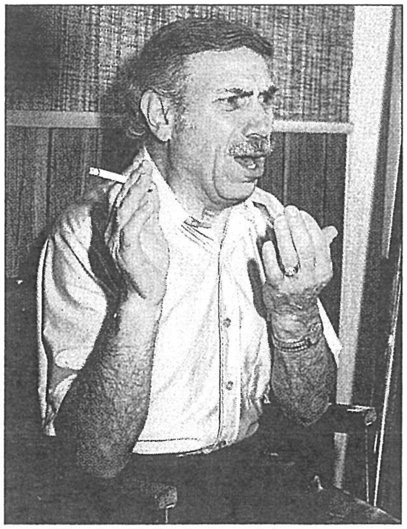


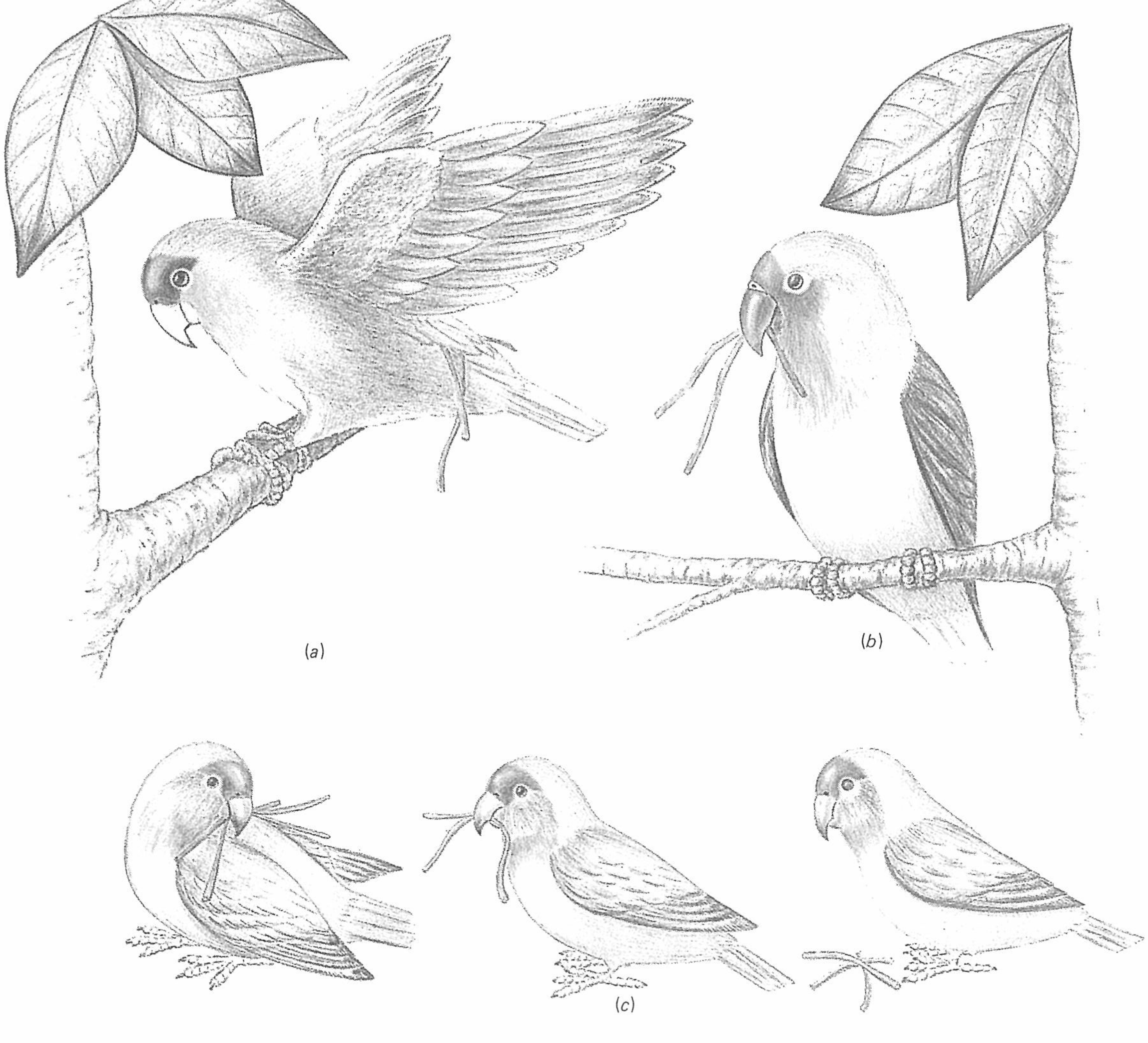
FIGURE 52–7 Displacement behaviors are behaviors that appear irrelevant or inappropriate to the situation. Some ethologists suggest that humans exhibit displacement behaviors, such as eating or smoking under stressful situations. Such interpretations of human behavior are controversial.

BEHAVIOR GENETICS

We can see the influence of genes on behavior when we observe stereotyped behaviors in young animals before they are exposed to learning situations. Further evidence for a genetic basis of behavior comes from studies of inbred strains of animals that have been bred for differences in fighting tendencies, maze running, timidity, preference for alcohol, or other traits. In a famous study begun in 1925, a heterogeneous population of mice was bred selectively on the basis of scores in a T-maze. "Bright" individuals were bred with each other, as were "dull" individuals, until two strains were obtained that had contrasting abilities to score in the maze. These two strains were maintained for 15 years, during which a number of characteristics of innate behaviors were identified. An important observation was that "brights" did not perform better on *all* learning tasks; their ability was relatively task-specific.

Animals that show a particular behavior in different forms are also of interest to behavior geneticists. One species of lovebird *(Agapornis)* carries nesting material to the nest by tucking it under its rump feathers (Figure 52–8); another species carries the material in its bill. Hybrids appear confused and at first unsuccessfully try to carry material both ways. They eventually carry the material in their bills, but may take up to three years to perfect this behavior, while traces of the tucking behavior persist indefinitely.

FIGURE 52–8 Evidence for the inheritance of behavior may be seen in lovebirds. (*a*) The peach-faced lovebird (*Agapornis roseicollis*) carries nesting material to the nest by tucking it under its rump feathers. (*b*) Fischer's lovebird (*A. fischeri*) carries it in its bill. (*c*) Hybrids appear confused and try to carry material both ways.



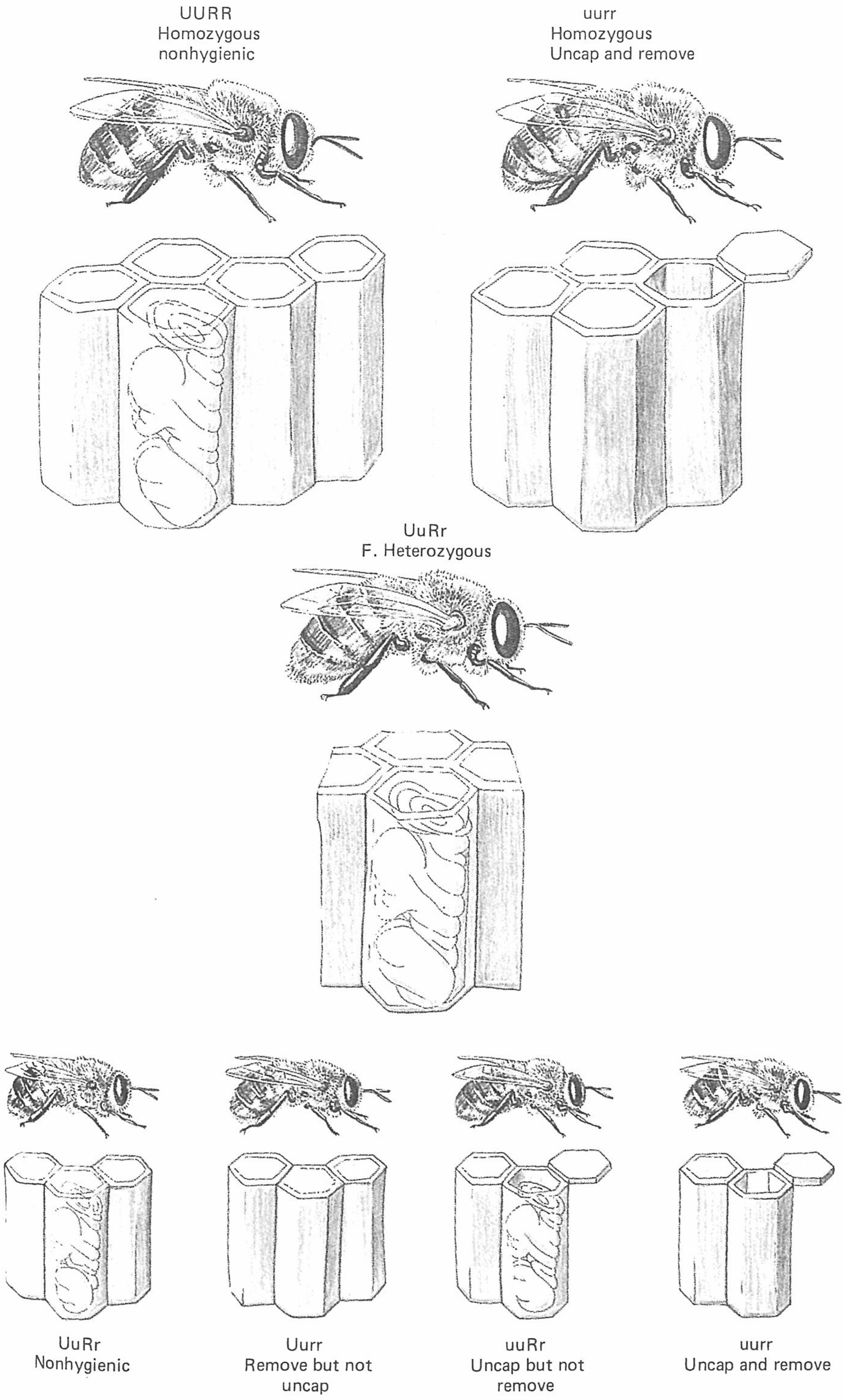


FIGURE 52–9 Bees uncap and remove dead larvae only if they have the correct genotype. See the text for explanation.

One of the goals of behavior genetics is to relate specific behaviors to specific genes or groups of genes. Studies of bees have been especially instructive in this regard (Figure 52–9). Larvae that are killed by a bacterial disease, American foulbrood, are removed from the brood cells by worker bees, but to do this the bees must first uncap the cells. Whether the worker bees succeed in removing the dead larvae in this way depends on their genotype (Chapter 10).

Both the allele for uncapping and the allele for removal are recessive. Thus, if a bee has the genotype *uu,* it will uncap the cell; if it has the genotype *rr,* it will remove the larva from the cell; and *uu rr* individuals will both uncap the cell and remove the larva. On the other hand, if a bee has the *U* allele, either as *UU* or *Uu*, it will not uncap the cell. It will, however, remove larvae from cells that were uncapped by other bees provided it is homozygous for the recessive allele (i.e., *UU rr* or *Uu rr*). The converse is true for bees having the *R* allele either as *RR* or *Rr*: they will uncap a cell if they are also *uu*, but after doing so they will not remove the larvae from the cells.

Individuals that are *UU RR*, *UU Rr*, *Uu RR*, and *Uu Rr* are not homozygous recessive for either of the alleles. Therefore, they will neither uncap cells nor remove larvae from cells already uncapped. This is a clear example of how behavior in invertebrates is inherited in a Mendelian fashion.

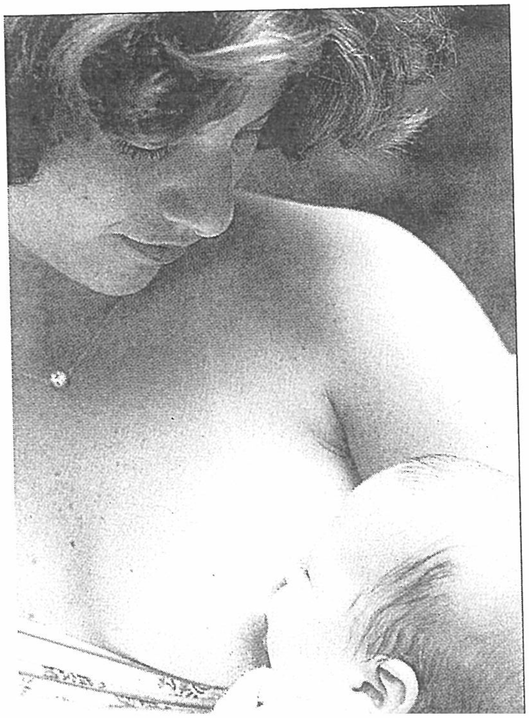
The Causes of Behavior—Nature vs. Nurture

Most students of animal behavior now take it for granted that behaviors are the product of both genetic and environmental factors, the latter including learning (covered in more detail later). Yet it is not clear how best to describe the relationship between the genetic and environmental factors that determine a behavior—a controversy historically described as "nature (genes) vs. nurture (environment)." Several contrasting ways to deal with the issue are possible.

One way is to visualize a behavior, such as feeding behavior in chickens, as an entity that is in some way made up of a genetic "component" and an environmental "component." Suppose, for example, a recently hatched and untrained chick feeds by pecking at grain on the average of twice a second. This feeding behavior is regarded as basically innate, and we might attribute almost all of it to the genetic component. We might even say that essentially 100% of the behavior is innate, meaning that DNA has directed embryonic development to produce chicks that peck twice a second when presented with possible food items.

Suppose that we add a learned component to this innate feeding behavior by appropriately rewarding or punishing the chick so that it pecks only once instead of twice per second. This new feeding behavior is now no longer "100% genetic," since it now has both a genetic component and a learned component. Yet does it make sense to say that the relative contribution of the genetic component has dropped from 100% to a lesser percentage? That is, does the relative influence of the genetic component to the behavior diminish as the influence of the learned component increases, so that together their contributions always add up to 100%? In another example, is it appropriate to say that feeding behavior in a newborn human infant (Figure 52–10) is *mostly* (more than 50%) innate, but that the relative contribution of the genetic component to this behavior becomes less as the baby is trained to eat in a particular way?

FIGURE 52–10 Nature vs. nurture. What is the best way to view the interaction between the genetic and learned components of this infant's feeding behavior as it grows older and is trained to eat in an adult manner?



One disadvantage of using "components" as a metaphor to represent the causes of a particular behavior is that it may tempt us to visualize components of behaviors in the same way we visualize components of physical structures. It might make sense to say that as potter's clay dries the percentage of the water "component" drops and the percentage of the solid "component" (dry clay) rises, so that at any moment the contributions made by each of these components add up to 100%. However, the genetic and learned components of a behavior do not add up in this way to make the whole. We cannot say that the DNA's contribution to feeding behavior in chicks becomes less because exposure to a training regime (learning) has altered the brain to produce a slower feeding behavior.

Another way in which an animal's genetic makeup (its "blueprint") influences its behavior is by predisposing it to learn one behavior rather than another. Animal trainers find it easier to teach animals behaviors that resemble their innate, species-specific behaviors. It is easier to teach a dog to retrieve a stick than to stalk, crouch, and pounce like a cat. Likewise, innate human tendencies may predispose us to learn certain ways of behaving when we seek a mate, care for a child, or defend ourselves against an attacker. The existence of genetic predispositions to learn certain behaviors may partly explain some of the cultural similarities in geographically separated human populations. These societies may have independently learned to behave in similar ways because they shared genes that made learning certain behaviors more probable than others.

Heritability

The preceding discussion deals with the nature-nurture issue with respect to *individual animals.* (Which part of the feeding behavior in the individual chick is due to genetics and which part to learning?) Another way to deal with the genetic and environmental influences on behavior is to concentrate on *populations* rather than individuals. This can be done by expressing the genetic and environmental components of a behavior in terms of **heritability:** a measure that compares the amount of phenotypic variability that is due strictly to the variation in genes with the total amount of phenotypic variability in the population. Expressed differently, heritability is the proportion of the total phenotypic variation that is caused by genetic differences among members of a population. It is a property of the population rather than of the trait *per se.* One therefore speaks of heritability in a population *with respect* to a trait.

Consider the training of cutting horses. These horses are bred and trained to enter a group of calves and efficiently separate, with minimal instructions from the rider, a particular calf for branding (or some other purpose). All horses cannot be trained to do this in the same length of time because they vary genetically in trainability with respect to this behavior. The phenotypic variation in trainability (V_T) for a population of horses can be visualized as a "bell-shaped" or normal distribution curve (Figure 52–11) of their training times. Part of V_T is due to genetic differences, V_g, among individual horses, since all horses would not be expected to be genetically identical with respect to their ability to learn how to cut calves. Part of the variance also reflects environmental factors, V_e, such as the health of the horse, its social interactions with its owner, the way it is trained, and all other factors that influence how its genetic potential is realized. Thus,

$$V_T = V_g + V_e$$

LEARNING

A simple definition of learning is "a change in behavior due to experience." Even behaviors that appear entirely innate are influenced by experience. A newly hatched chick innately pecks at small objects on the ground (Figure 52–12), but after it picks up and eats the first edible object, it is more successful in subsequent feeding attempts. Thus, learning has altered the expression of the FAP for feeding from the very beginning.

In many instances, stereotyped behaviors such as FAPs have advantages over learned behaviors. By being "hard-wired," FAPs permit an animal—in particular a young one—to respond to situations more quickly and with less chance of error; and since FAPs are innate they do not require an investment of time for their development. We would expect that, all else being equal, young animals equipped with an innate begging response will have a greater probability of surviving than animals that must learn how to take food from their parents.

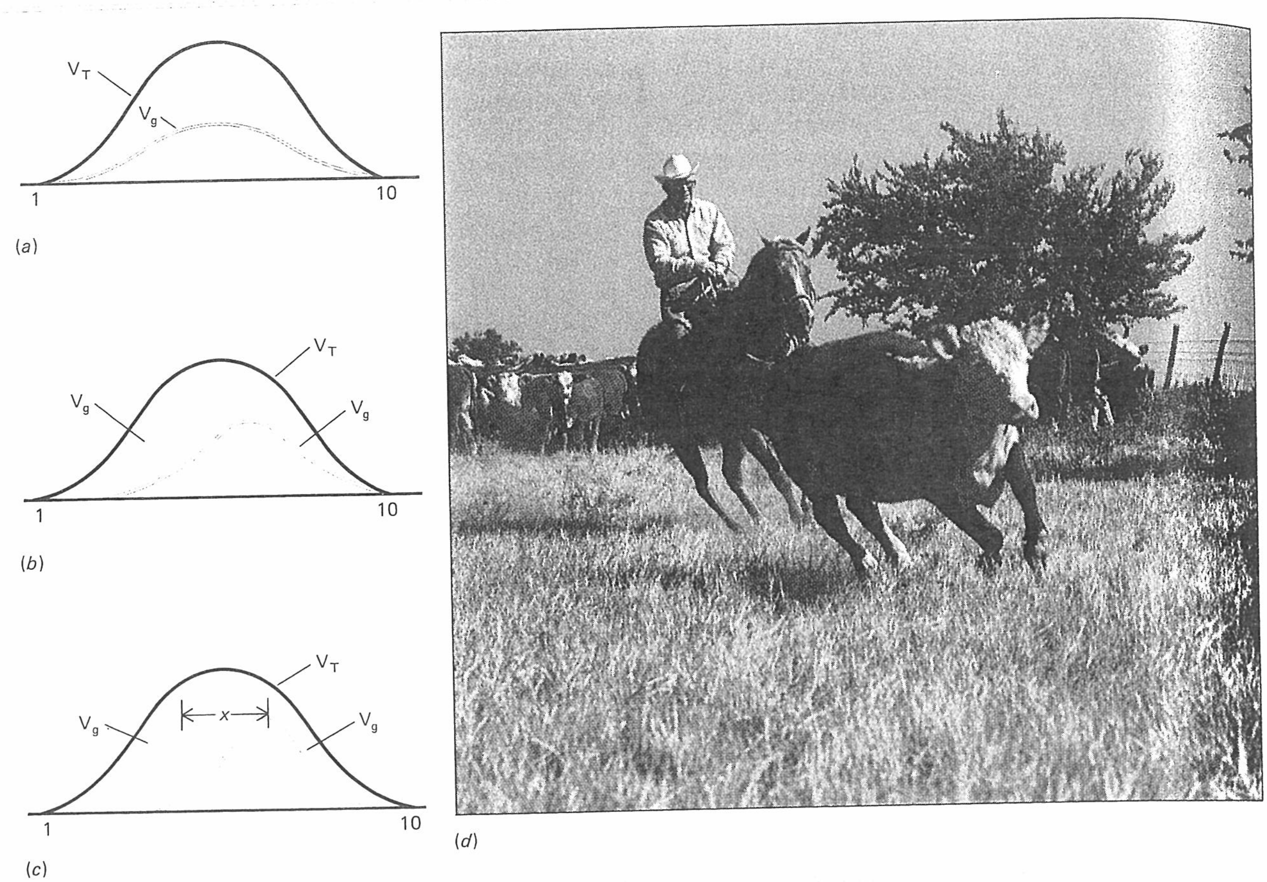


FIGURE 52–11 Curves showing the relationship between phenotypic variation (V_T) and genetic variation (V_g) with respect to trainability in two groups of horses, group A (yellow curve) and group B (blue curve). The two groups were formed from a population of twins, one member of each pair assigned to A and the other to B. Height of curve indicates number of horses; horizontal axis indicates length of time required for training (on scale of 1 to 10). If the ability to learn were entirely genetic (*a*), then V_g for both groups, as well as their average learning times, would be the same (blue and yellow superimposed to make green). In this case it would be better to breed for trainability rather than to spend effort developing new training methods. In contrast, if the genetic contribution to learning were small (*c*), then less emphasis should be placed on selective breeding and more on developing good training methods. In this case, even though the genetic variances for group A (V_g yellow) and group B (V_g blue) are the same (A and B are genetically identical), the mean times for learning (x) are different. The curves in (*b*) represent an intermediate situation in which both a strong breeding program and a continued effort to improve training methods be recommended. (*d*) A cutting horse in action.

FIGURE 52–12 Feeding behavior in a newly hatched chick is innate, but chicks feed more successfully after they have practiced a few times, indicating that even basic innate behaviors are modified by learning.

In other cases, however, the capacity to learn an appropriate response to a situation is more adaptive, because learned responses can be shaped to conform to the changing environment most animals experience. It probably would have been impossible for higher mammals like ourselves to evolve a large enough repertoire of stereotyped behaviors to prepare us for the numerous contingencies we face during our lifetime.

Psychologists have proposed a number of classifications of learning, one of which recognizes the following categories: (a) habituation, (b) sensitization, (c) associative learning (classical conditioning and operant conditioning), (d) latent learning, (e) imprinting, and (f) insight learning.

Habituation

In **habituation** an animal's unlearned response to constant or repeated stimulation wanes, and this waning is not due to sensory adaptation. The background noise in a room commands our attention at first, but soon we habituate to it (we "tune it out" or "get used to it"). A young pigeon

FIGURE 52–13 In the form of learning known as habituation, an animal's unlearned response to constant or repeated stimulation wanes, as in the case of these pigeons, which are unperturbed by the presence of humans.

landing in a new park to feed might initially respond to people by moving away from them, but soon its fright response diminishes to the point that it feeds quite comfortably among the heavy foot traffic (Figure 52–13). In both of these examples we are dealing with *nonassociative learning processes.* The term nonassociative is used because, unlike the classical and operant conditioning explained later in this section, an association is not made between two stimuli. The term learning is appropriate because the behavior of the animal (its response to the stimulus) changes as a result of what it experiences.

Habituation occurs in invertebrates as well. If a snail is placed on a wooden platform, it will move along the platform until the wood is tapped, at which time it will withdraw into its shell. After several seconds it will emerge and continue moving along the platform. Each time this process is repeated the snail emerges more quickly from its shell after the tapping has ceased. Soon it does not withdraw into its shell at all because it has become habituated to the stimulus.

Although the terms "habituation" and "sensory adaptation" are not always interpreted consistently (and have even been used synonymously), habituation is used here to refer to a process that is presumed to take place in more central parts of the nervous system than the sensory organs. An experiment with turkeys illustrates this point. Turkey cocks respond to a variety of sounds by gobbling. When a turkey was presented with an electronically produced sound that had a specific frequency, it responded at first with its gobbling response. When the same sound was repeated at regular intervals, the turkey responded less and less until its gobbling response was no different than it was in the absence of any sound.

At this point in the experiment the pitch and interval of the sound were kept the same but the volume was lowered. The turkey responded by immediately resuming its gobbling response. If the initial waning of the response had been due to sensory adaptation, we would not have expected a reduced stimulus to elicit a response when the initial stimulus was ineffective. Likewise, we can eliminate fatigue as a factor in this example of habituation.

Sensitization

Habituation can be adaptive because it eliminates unnecessary responses to a stimulus (such as a "harmless" noise like an airplane flying over). This conserves time and energy for more important behaviors. In contrast, in **sensitization** there is an increased probability that an animal will respond to a stimulus that has been presented to it (or even to another stimulus). For example, a cat, after being treed several times by dogs, might arch its back and hiss when approached by a puppy that it normally ignores.

Associative Learning

In **associative learning,** an animal's behavior changes because of an association it makes between two stimuli. There are two types of associative learning: classical conditioning and operant (instrumental) conditioning.

Classical Conditioning

In **classical conditioning,** a normal response to a stimulus becomes associated with a new stimulus, which then is also capable of eliciting the response. The eminent Russian physiologist Ivan Pavlov studied this type of learning by carefully measuring saliva secretion when dogs were presented food. The food in this case is the normal or **unconditioned stimulus** (UCS) and the act of salivating is the **unconditioned response** (UCR). When a neutral stimulus such as a ringing bell is presented to the dog prior to the food, the dog makes an association between the neutral stimulus (called the **conditioned stimulus,** or CS) and the food (UCS). After the UCS and CS are paired for a sufficient number of times, the salivating response becomes a **conditioned response** (CR). The dog now salivates when the CS is presented. The CR may vary slightly from the UCR, but it is basically the same (in this case, both are salivation).

Each time the conditioned stimulus (the bell) is followed by the unconditioned stimulus (the food), the conditioned response (salivation) is *reinforced,* and for this reason the UCS is referred to as a **reinforcer.** The CS must always precede the UCS because, once a relationship between the two is established, the CS serves as a signal that the UCS will occur. The dog now salivates in response to the bell and thus has learned to give an old response to a new stimulus.

Because of their historical import, Pavlov's experiments with dogs are frequently cited as a paradigm (example or model) for classical conditioning. Another example is an aquarium fish that learns to swim to the surface for food (CR) when the glass is tapped (CS). The UCS is the odor (or sight) of the food and the UCR is the fish's response to this odor or sight (i.e., swimming to the surface). Thus tapping and odor (or sight) have been linked by classical conditioning. No doubt classical conditioning of this sort occurs commonly among vertebrates. As soon as a fishing vessel enters the harbor, gulls resting on the dock become excited and begin flying around, as they have associated the shrimp boat (CS) with the presence of offal (UCS). The UCR in this case is their normal response to the presence of food. Because the UCS and CS have been paired, their response to the presence of the fishing vessel is the CR.

In both sensitization and classical conditioning, an animal's response to a stimulus depends on another stimulus, but in classical conditioning the associated stimulus is specific: the fish swims to the surface of the aquarium in response to a stimulus specifically associated with food. In contrast, after being repeatedly fed, a sensitized fish may approach *any* stimulus, even nonfood objects that only remotely resemble food.

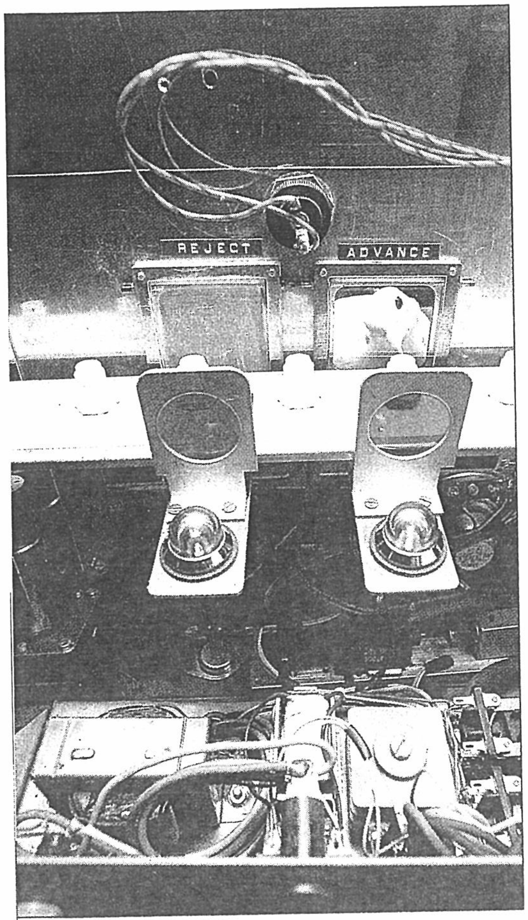


FIGURE 52–14 To demonstrate operant conditioning, an animal is placed in a chamber that contains a button which, when pressed, releases food into the chamber. The animal makes an association between pressing the button and receiving the food; thereafter, every time it presses the button, this behavior is reinforced with food.

Operant Conditioning

In **operant (instrumental) conditioning,** a type of learning extensively studied in the United States by B.F. Skinner and his colleagues, the sequence of events is contingent (i.e., dependent) upon the behavior of the animal. The animal is rewarded or punished after performing a behavior it discovers by chance. (For this reason, this type of learning has also been called "trial and error learning.") In a typical experiment, an animal moves about in a cage (Figure 52–14) and eventually presses a button, without knowing beforehand that pressing the button will release food into the

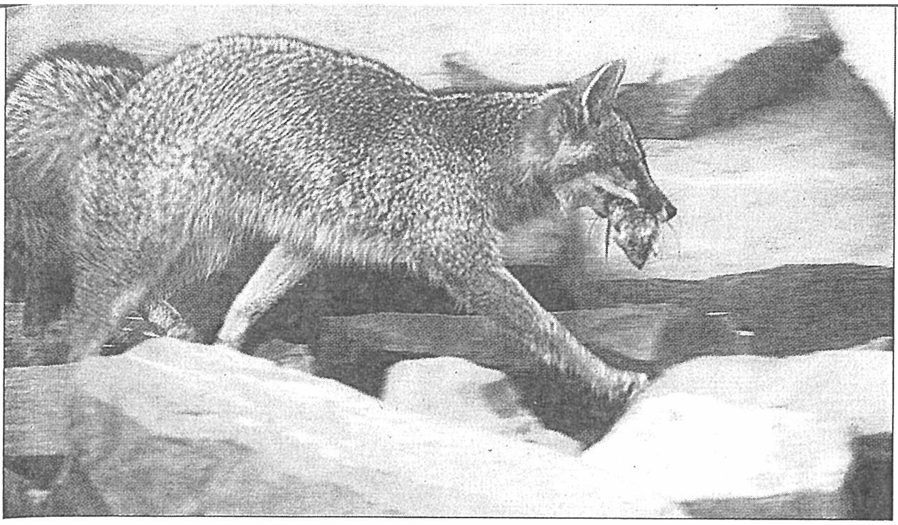


FIGURE 52–15 Operant conditioning may occur in nature when predators, such as this gray fox, discover an area where prey is plentiful. They make an association between visiting that area and capturing prey (the reward).

cage. The animal makes an association between the button and the food (the reward). Thereafter, whenever it presses the button, this behavior (pressing the button) is reinforced with the food.

In classical conditioning the reinforcer is the UCS, because this is the stimulus that actually reinforces the learned behavior (the CR). In operant conditioning, the reinforcer is the reward (e.g., the food) that follows when the animal behaves in a certain way (e.g., pressing the button).

Examples of operant conditioning in nature are not difficult to imagine. A fox randomly searches the forest for prey and chances upon two areas: one where rodents are plentiful and easily caught and another where vicious dogs always drive off intruders like foxes (Figure 52–15). Very quickly the fox learns to frequent the area with the rodents and to avoid the dogs, just as experimental animals learn to press certain buttons and not others.

There are many examples of operant conditioning in invertebrates. Larval grain beetles can learn mazes, and, rather interestingly, this learning survives through metamorphosis into the adult stage. Cockroaches can be conditioned to avoid shock, even when their heads have been removed. This form of learning (passive avoidance) can be demonstrated by delivering an electric shock to the leg when the roach lowers its leg into a saline solution. Roaches that have been shocked lower their leg into the solution fewer times than do controls.

In both classical and instrumental conditioning the learned response must be periodically reinforced or it will not persist. In fact, periodic reinforcement is more effective than continuous reinforcement in maintaining an operant response. If the response is insufficiently reinforced, it diminishes. This is known as **extinction.**

Latent Learning

In **latent learning,** sometimes called "exploratory learning," an animal stores information about its environment that later can influence its behavior. Rats permitted to explore a maze without any apparent reward nonetheless store certain information about the maze (Figure 52–16). When later they are trained to run the maze for a reward (food), they learn to do this more quickly than rats not previously exposed to the maze. Obviously some type of learning occurred when the rats explored the maze. If, as has been suggested, latent learning is a variant of operant conditioning, the rat must have been rewarded in some way for learning some of the maze's features while it was exploring the maze. Perhaps the learning that accompanies exploration is reinforced by the reduced anxiety that comes with becoming familiar with one's surroundings; or maybe the mere process of observing and remembering features about one's surroundings, because of a "natural" curiosity, is a sufficient reinforcer.

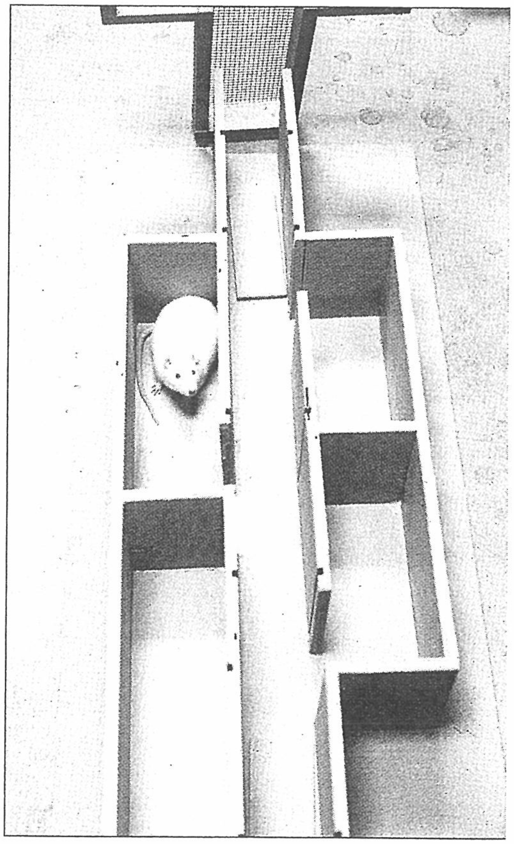


FIGURE 52–16 Rats that have previously been placed in a maze learn more quickly to escape the maze for a reward than do rats placed in the maze for the first time. Therefore, the first group must have "learned" the maze, even though it is not clear what the reward was. This type of learning is known as latent learning.

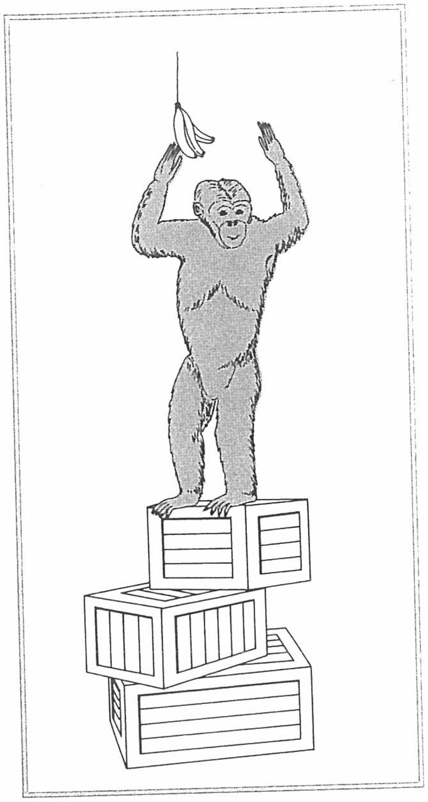


FIGURE 52–17 Insight learning, and in this case, simple tool use. Confronted with the problem of reaching food hanging from the ceiling, the chimpanzee stacks boxes until it can climb and reach the food. Many other examples of apparent insight are known from the behavior of these animals.

Insight Learning

Insight learning is perhaps the most difficult type of learning to demonstrate conclusively in animals, even though we take it for granted in ourselves. Insight learning is the intuitive ("insightful") solution to a problem that has not been previously attempted. One criterion for insight is what has been called the "aha experience" (one "sees the light!"). An animal may be familiar with the separate parts of a problem that are necessary for its solution; but it solves a problem through insight only when it recognizes the relationships, causes and effects of a particular contingency or occurrence. If it is capable of doing this, it is capable of solving problems it has never encountered before.

More than seventy years ago the psychologist Wolfgang Köhler offered evidence for reasoning (or insight) in chimpanzees. He observed that they obtained bananas suspended from the ceiling and out of reach by first stacking boxes to make a platform (Figure 52–17). They then climbed on top of this structure to reach the bananas.

Even this impressive performance may not demonstrate conclusively that animals reason. Critics point out that all of the manipulations observed in these chimps—stacking and climbing on boxes, striking objects with sticks, etc.—are part of the repertoire of play behaviors in chimps. They may have climbed on the stacked boxes while playing. In other words, we may not have to use insight learning to explain their success, since they may not have seen obtaining the banana as a problem to be solved at all! Although there are other observations of primate behavior that suggest insight learning in animals, the issue has not been settled.

Imprinting

Imprinting is a very specialized type of learning. A young waterfowl, such as a gosling, forms a learned attachment to its mother during the first few days of its life. This behavior, known as imprinting, is adaptive since it insures that the gosling will follow its mother at this critical time of its life (Figure 52–18). Its chances of surviving increase because of the mother's protection. Imprinting does not occur in birds that remain helpless in the nest until they mature and are ready to leave. An ability to imprint earlier would serve no useful function.

Imprinting differs from most types of learning in that it normally can occur only at a specific time during an animal's life. This **critical period** is usually shortly after hatching (about 12 hours), and it generally lasts for

FIGURE 52–18 Imprinting. When young, these geese formed an attachment to a human being that has remained firm into their maturity.

just a few days. At this time a young bird will imprint on an adult of its own species if given a choice. In the absence of an adult bird it will imprint on any moving object, including a person. It has been shown experimentally that birds imprint more firmly on nonliving structures if these structures have moving parts and sound-producing devices. Also, birds imprint more firmly on an object if they must crawl over obstacles in their path in order to follow it.

Imprinting shares some features with song learning in some birds. Many young birds learn to sing their own species' song correctly only if they hear it at a critical period during their life. Some scientists have suggested that children learn languages more easily than adults because they are in a critical period for language acquisition comparable to the critical period for song learning in birds.

BEHAVIORAL ECOLOGY

Natural selection tends to produce animals that are maximally efficient at propagating their genes, and this is accomplished by making the best choices in mate selection, territory defense, and foraging. A topic that currently interests a number of behavioral ecologists is **optimal foraging,** which is theoretically the most efficient way for an animal to obtain food.

Optimal foraging may be illustrated by the following example, which is fictitious for the sake of simplicity. Suppose there exists a monkey that eats only one species of fruit and that this fruit is contained in a husk that is either soft, leathery, or hard. It takes 1 minute to remove a soft husk, 5 minutes to remove a leathery husk, and 10 minutes to remove a hard husk. If the forest contains equal numbers of hard-husked, leathery-husked, and soft-husked fruits, if these three forms are randomly distributed, and if a monkey moves randomly and eats every fruit it encounters, then at the end of a foraging bout it should have eaten about the same number of each husk form.

But is it necessarily the best use of the monkey's time and energy to eat all three husk types? Since removing hard husks takes so long, perhaps it is more efficient to pass up these fruits and eat only the soft-husked and leathery-husked fruits. Or maybe the best procedure is to eat only the soft-husked fruits.

These three possible ways of feeding are examples of **feeding strategies.** There are two other feeding strategies: select only the hard-husked fruits, or select the hard-husked fruits and the leathery-husked fruits and pass up the soft-husked fruits. These two strategies are clearly less efficient ways to forage, since they require a greater expenditure of time and energy for the same amount of food. The term **strategy** used in this context does not imply planning as it does in human behavior, but refers to the way an animal locates, procures, and handles food.

Assuming that once husked, all three forms can be eaten in the same brief time, we may ask which of the following strategies is most adaptive, that is, which one permits the monkey to forage optimally:

Strategy I: select the soft-husked fruits whenever encountered and pass up the other two kinds
Strategy II: select the soft-husked and leathery-husked fruits whenever encountered, and pass up the hard-husked fruits
Strategy III: select all three kinds whenever encountered

Strategy I has its trade-offs. Since only every third fruit is soft-husked, the monkey must travel three times as far to get the same number of fruits

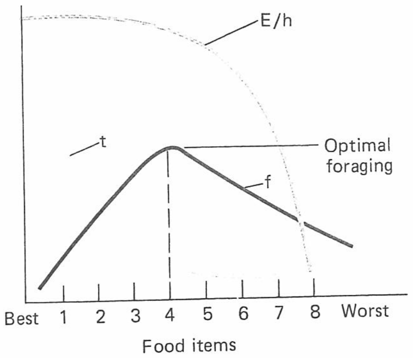


FIGURE 52–19 Graph illustrating optimal foraging, based on food intake (expressed as energy, *E*). In any habitat there is a tradeoff between travel time (*t*) and handling time (*h*). Handling time is graphed here as *E/h*. Once *h* and *t* are determined, the optimal feeding strategy can be calculated. Numbers on the horizontal axis refer to feeding strategies concerning eight species of food items, arranged from best to worst. Number 1 refers to selection of only the best food item, number 2 to selection of the best food item plus the second best food item, number 3 to selection of the three best food items, and so forth. In this hypothetical case, an animal that forages optimally (as indicated by the peak of the red curve) would select the four best food items. In better habitats the peak is to the left of 4; in poorer habitats, it is to the right of 4.

it will get if it selects leathery-husked and hard-husked fruits as well. Maybe it would be worth traveling farther if it meant spending less time husking, but of course that would depend on *how much* farther.

What do we need to know in order to select the best foraging strategy? Obviously we need to know how long it takes to get from one fruit tree to the next, and this depends on the density of the fruit trees. If the density of fruit trees is so low that it takes an hour to get from one fruit tree to the next, then common sense would tell us not to pass up a hard-husked fruit just because it takes 10 minutes to husk. On the other hand, if the fruit trees are so dense that it takes only 2 minutes to get to the next tree, then we would certainly pass up all the hard-husked forms and perhaps would even consider passing up both the hard-husked and leathery-husked forms. After all, the next soft-husked fruit is only 6 minutes away, and it takes almost that long just to husk a hard-husked fruit.

This relationship between travel time, handling time, and net food intake can be expressed graphically (Figure 52–19). This graph, based on eight rather than three food items, indicates eight possible feeding strategies. Assuming that the caloric value (expressed as *E*, for energy) of all items are equal, the best item would be the one that requires the least handling time, the worst would be the item that requires the most handling time, and all others would be ranked accordingly.

The numbers on the horizontal axis do not refer to the specific items, but rather to feeding strategies. The number "1" refers to the strategy in which the animal selects only the best item, the one requiring the shortest handling time (*h*) per unit of food and hence the highest ratio of energy to handling time (*E/h*). Yet by being so selective, the animal has a large traveling time (*t*), since it has chosen to pass up the other seven items. In the feeding strategy indicated by "2," the animal selects the best item plus the second best item, thereby decreasing traveling time but increasing handling time (and consequently decreasing *E/h*). As the animal includes more and more unfavorable food items in its diet, travel time decreases while handling time increases. Thus, the animal spends the least amount of time traveling if it selects all eight food items, but by adding more unfavorable items to its diet to reduce travel time, it must also spend more time handling the items.

In good habitats, where good food items are abundant and the animal does not have to travel far to obtain these items, the optimal feeding strategy would tend toward the left of graph (strategy 1, 2, or 3, depending on how good the habitat is). In contrast, in poor habitats, where it takes longer to find the best food items, the optimal strategy would be to select more items, even though doing so requires more handling time.

How do these theoretical considerations apply to the actual behavior of animals? By measuring travel time, handling time, and eating time and relating these values to the theoretical values calculated for optimal foraging, one can test the hypothesis that a particular animal does, in fact, forage optimally. If the actual values do not fit the theoretical values, it may mean that all relevant variables have not been accounted for. The monkey may choose to forage very inefficiently (in terms of consuming a certain number of calories each day) by selecting only hard-husked fruits; but it may do this because it prefers the taste of hard-husked fruits, or because they contain a critical nutrient that is absent in the other two forms. Thus, other hypotheses concerning foraging behavior may come to mind.

If the monkey indeed was observed foraging optimally, according to predicted values, it may have learned to do so through trial and error (operant conditioning), that is, by randomly trying all three strategies and selecting the one that it associated with the fewest hunger pains at the end of the day!

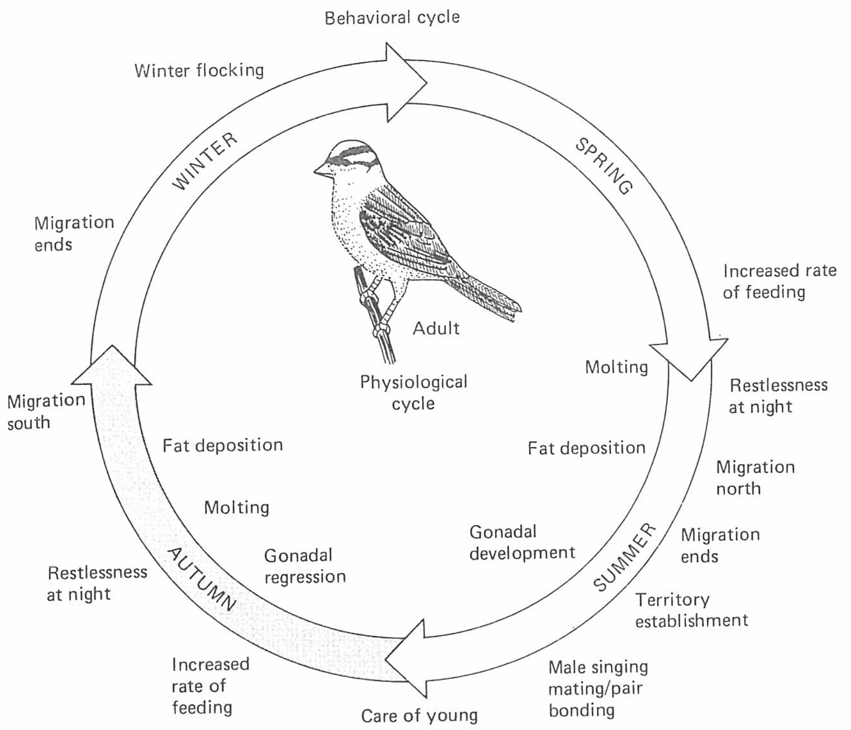


FIGURE 52–20 Seasonal changes in the physiology and behavior of the white-crowned sparrow. This coordinated sequence of events is based on a one-year "biological clock."

MIGRATION

Animal **migration** includes two separate but related phenomena that depend on separate physiological mechanisms: (1) the stimulus to migrate; and (2) **orientation** and **navigation.**

In many birds, environmental conditions such as temperature, rainfall, length of day, and food availability are so closely linked in time to migration that it is tempting to regard these factors as the "causes" of migration. It is now thought that the stimulus to migrate in most birds is just one event in a coordinated sequence of events that includes reproduction, molting, and accumulation of fat prior to migration (Figure 52–20). These events are seen as responses to an innate circannual rhythm (an endogenous rhythm of approximately one year in duration). The circannual rhythm is based on a "biological clock" that has about a one-year cycle. This clock can be "reset" during the year by external factors, somewhat like a conventional clock that can be reset throughout the day. The environmental stimuli that reset the clock at the beginning of the migratory season could be a change in photoperiod, a drop in temperature, or some other cue. The same environmental stimuli could reset the clock at the beginning of the reproductive season.

Navigation is the ability of an animal in unfamiliar surroundings to find its goal without relying on landmarks with which it is familiar. Many invertebrates, including mollusks and arthropods, as well as representatives from virtually every vertebrate class have exhibited this ability. It has been demonstrated experimentally that birds can orient by responding to environmental cues such as the position of the sun and stars and the earth's magnetic field. When migratory birds are placed in circular cages equipped with electronically monitored perches, they more frequently fly to perches in the south side of the cage during autumn. One might speculate that they are trying to escape in the direction they normally take during migration at that time of year. They do this on nights with clear skies but not on cloudy nights. When the cages are placed in a planetarium and the night sky is rotated 180 degrees, the birds orient toward the north, indicating that in some way they use the configuration of the stars as directional cues.

The biological mechanisms underlying the response of animals to the earth's magnetic field are especially perplexing. However, the discovery of numerous submicroscopic iron-containing (magnetite) objects in the brains of homing pigeons is encouraging. These particles might in some way enable birds to detect the earth's magnetic field.

SOCIAL BEHAVIOR

Social behavior involves adaptive interactions among animals, especially among members of the same species. In assessing the extent of social behavior characteristic of a given species, ethologists consider the number of animals that form a group, the portion of the life cycle that the group remains together, the amount of time and energy devoted to social behavior, the structure of the group, communication among group members, formation of families, and the nature of interactions. Many of the behaviors already discussed in this chapter, including urine marking in dogs, are aspects of social behavior.

Communication

The ability to communicate is an essential ingredient of social behavior, for only by exchanging mutually recognizable signals can one animal influence the behavior of another (Figure 52–21). **Communication** occurs when an animal performs an act that changes the behavior of another organism. Communication may facilitate finding food, as in the elaborate dances of the bees. It may hold a group together, warn a group of danger, indicate social status, solicit or indicate willingness to provide care, identify members of the same species, or indicate sexual maturity.

Modes of Communication

Animal communication differs significantly from most human communication in that it is not symbolic. As you read, information is conveyed to your mind by words; yet the words themselves are not the information. They stand for it. The relationship between the word "cat" and the animal itself is a learned one; a person who could read only Japanese would not recognize it. This is not to say that **signals** in some sense are not employed by animals. In a way, all releasers are signals. However, releasers are not necessarily learned, whereas true symbols are.

Although in humans some body communication is culturally determined learned behavior, a large part of it (such as smiling) is truly universal and appears to be physiologically determined. The pupil of the human eye dilates in certain emotional situations, such as sexual interest or excitement. Without realizing it, people respond to such subtle cues. In experiments, a photograph of a woman's face with the pupils retouched to appear greatly dilated was far more attractive to male subjects than one in which they were shown as pinpoints.

Signals are often transmitted involuntarily as an accompaniment of the physiological state of the organism. Information about an animal's emotional or mental state may be transmitted even if no other members of the species are nearby. For example, a bird automatically gives an alarm call when it sights a predator. Certainly there are times when human beings would rather not communicate their true feelings—yet there may be instances in which we do not really have any choice, as with pupil dilation.

FIGURE 52–21 A male hylid frog of Costa Rica calling to locate a mate.

And who has not blushed at a time when he would have given almost anything not to have done so?

Do animals ever employ symbols, or are animal signals totally restricted to the equivalent of gasps of alarm? The matter is controversial. Many ethologists think that even dogs do not respond to spoken language as we do, but deduce the behavior we command from an astute reading of human facial expression, vocal intonation, and bodily attitude. On the other hand, chimpanzees have been taught to speak a very few words meaningfully, and to a limited extent can use sign language appropriately. Whether apes employ symbolic language in nature is unlikely, although the potential seems to exist.

The singing of birds is an obvious example of auditory communication, serving to announce the presence of a territorial male. Some animals communicate by scent rather than sound. Antelopes rub the secretions of facial glands on conspicuous objects in their vicinity (Figure 52–22). Dogs mark territory by frequent urination. Certain fish, the gymnotids, use electric pulses for navigation and communication, including territorial threat, in a fashion similar to bird vocalization. As E.O. Wilson has said, "The fish, in effect, sing electrical songs." Who would have guessed it?

FIGURE 52–22 Pronghorn antelope marking territory by applying scent from its facial glands on any convenient object.

Displays are visual signals that include movements, postures, and facial expressions. The comparative study of facial expressions reveals how they function to help an individual increase, decrease, or maintain a certain distance from members of the same species. For example, the variety of facial expressions observed in members of the dog family (Canidae) turns out to be unexpectedly large (Table 52–2). Also, related species tend to have similar facial expressions. Table 52–2 shows that foxes, which in general have more felinelike displays than other canids, differ from coyotes, wolves, and dogs in lacking the agonistic baring of teeth (vertical contraction of lips) expression.

A greater range of facial expressions is possible when constituents of displays are superimposed. The successive shifts in intensity of fear/submission and aggression in the coyote are indicated in Figure 52–23, where the position of the ears in 7 is combined with the configuration of the mouth in 3 to produce 9.

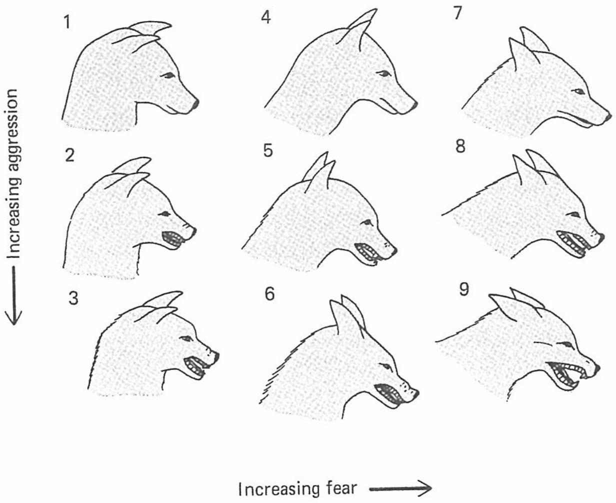
Table 52–2 **COMPONENTS OF FACIAL EXPRESSIONS RELATED TO BEHAVIOR IN CANIDS**

Components of Expressions Associated with Decrease of Social Distance and Submission	*R*	*A*	*G*	*C*	*W*	*D*
Head lowered and neck extended horizontally (crouch)	+	+	+	+	+	+
Ears flattened and turned down to sides	+	+	+	+	+	+
Submissive "grin" (horizontal retraction of lips)	+	+	±	+	+	+
"Play face"	+	+	±	+	+	+
Licking (cut off)	−	−	−	+	+	+
Licking (social greeting)	±	±	±	+	+	+
Licking (intention)	−	−	−	+	+	+
Nibbling	−	−	±	±	+	+
Jaw wrestling (play)	−	±	±	+	+	±
Whining and whimpering	−	−	±	+	+	+
Looking away	±	±	±	+	+	+

Components of Expressions Associated with Increase of Social Distance and Aggression	*R*	*A*	*G*	*C*	*W*	*D*
Head high and neck arched	+	±	+	+	+	+
Gape*	+	+	+	±	−	−
Growl	±	+	+	+	+	+
Bark	±	±	±	±	±	+
Agonistic "pucker" (horizontal contraction of lips)	+	+	+	+	+	+
Agonistic baring of teeth (vertical contraction of lips)	−	−	−	+	+	+
Snapping of teeth	−	−	−	±	+	+
Ears erect and forward	+	+	+	+	+	+
Direct stare	+	+	+	+	+	+
Eyes large	+	+	+	+	+	+
Ears flattened and turned back	+	+	+	+	+	+

R = red fox A = Arctic fox G = grey fox C = coyote W = wolf D = dog
+ denotes frequent expression
± denotes infrequent expression
− denotes expression not observed
*Occasional spitting in red fox.
Source: Adapted from Fox, 1971a.

FIGURE 52–23 Shifts in intensity for fear/submission (1, 4, 7) and aggression (1, 2, 3) in dogs. Facial expressions may be combined or superimposed, as in the case of 9, which is a combination of 3 and 7.



Pheromones are chemical signals that convey information between members of the same species. Pheromone communication has been discovered in nearly all organisms studied including unicellular organisms and plants. Most pheromones act as releasers eliciting a very specific, immediate, but transitory type of behavior. Others act as primers triggering hormonal activity that may result in slow but long-lasting responses.

An advantage of pheromone communication is that little energy must be expended to synthesize these distinctive, but simple, organic compounds. Conspecific individuals (those of the same species) have receptors that combine with the pheromone. Pheromones have the advantage of lasting for several hours or longer, and they are an effective way of communicating even in the dark. Major disadvantages of pheromone communication are slow transmission and limited information content. Some animals compensate for the latter by secreting a variety of pheromones with different meanings.

Pheromones are important in attracting the opposite sex and in sex recognition in many species. Many female insects produce pheromones that attract males of the appropriate species. We have taken advantage of some sex attractant pheromones to help control such pests as gypsy moths by luring the males to traps baited with synthetic analogs of the female pheromone.

Dominance Hierarchies

Many years ago it was observed that chickens living together in a pen squabble among themselves by chasing and pecking each other until they establish a rank order, or **dominance hierarchy,** among themselves. The individual at the top of this dominance hierarchy dominates all other individuals. In some species the dominance hierarchy is said to be linear, with the dominant individual being represented by a letter such as *A*. In a linear hierarchy, *A* dominates over the next highest ranking individual *B*, as well as over all others in the group; *B* dominates over C and all others beneath C, and so forth. However, rank order in some groups is not linear, with *A* dominating over *B*, *B* over *C*, and C over *A*. In larger groups there are even more complex hierarchies.

Conflicts that reinforce rank order may occur when individuals compete for food in the trough. Dominant individuals win most but not necessarily all of their encounters with subordinate individuals. In many vertebrates fighting rarely occurs once rank has been established because individuals quickly learn which members of the group are above them in rank (Figure 52–24). When the dominance hierarchy of a group of animals is studied in depth, questions such as the following come to mind.

1. Which physical characteristics influence an individual's rank in the hierarchy?
2. Does an individual's past history influence its rank in the hierarchy?
3. Does the rank of an individual's parents influence that individual's position in the hierarchy?
4. Are contests between individuals more frequent at certain levels in the hierarchy?
5. Is there a correlation between the rank of an individual and its reproductive success?

In general, dominance hierarchies have been interpreted as adaptive because they make it unnecessary to expend energy for continually competing with group members for food resources.

FIGURE 52–24 Social animals use many signals to convey messages relating to social dominance. In the case of baboons, one signal serves two functions. Females turn their buttocks toward males to signify readiness to mate. Subordinate males use the same gesture to assure dominant males that they do not intend to challenge the higher-ranking animals. Here a subordinate male presents to a more dominant one. The dominant male in turn reassures the subordinate with a peaceful pat on the back.

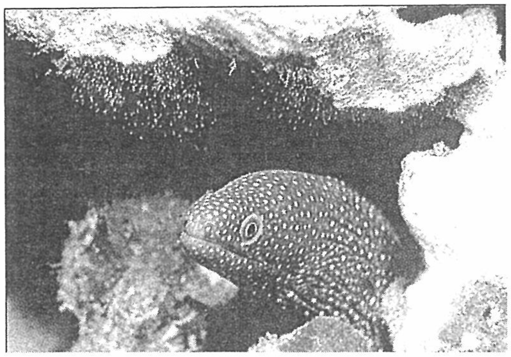
Territoriality

Virtually all animals, and even some plants, maintain a minimum personal distance from their neighbors, as one can observe in the even spacing among the members of a flock of birds resting on a telephone line. Most animals have a geographical area that they seldom or never leave. Such an area is called a **home range** (Figure 52–25). Since the animal has the opportunity to become familiar with everything in that range, it has an advantage over both its predators and its prey in negotiating cover and finding food. Some, but not all, animals defend a portion of the home range against other individuals of the same species and even against individuals of other species. Such a defended area is called a **territory.** The tendency to defend such a territory is known as **territoriality.**

Territoriality is easily studied in birds. Typically, the male chooses a territory at the beginning of the breeding season. This behavior results from high concentrations of sex hormones in the blood. The males of adjacent territories fight until territorial boundaries become fixed. Generally, the dominance of a cock varies directly with his nearness to the center of his territory. Thus, close to "home" he is a lion. When invading some other bird's territory, he is likely to be a lamb. The interplay of dominance values among territorial cocks eventually produces a neutral line at which neither is dominant. That line is the territorial boundary. Bird songs announce the existence of a territory and often serve as a substitute for violence. Furthermore, they announce to eligible females that a propertied male resides in the territory. Typically, male birds take up a conspicuous station, sing, and sometimes display striking patterns of coloration to their neighbors and rivals (Figure 52–26).

Territoriality among animals may be adaptive in that it tends to reduce conflict, control population growth, and ensure the most efficient use of environmental resources by encouraging dispersion and spacing organisms more or less evenly throughout a habitat. Usually, territorial behavior is related to the specific life-style of the organism that displays it, and to whatever aspect of its ecology is most critical to its reproductive success. For instance, sea birds may range over hundreds of square miles of open water but exhibit territorial behavior that is restricted to nesting sites on a rock or island, their resource that is in the shortest supply and for which competition is keenest.

FIGURE 52–25 A coral reef has many secluded areas in which a territorial animal can establish a home range. Among the most territorial of coral reef fishes is the moray eel, pictured here, which will attack any animal (including a human diver) that comes too close to its shelter.



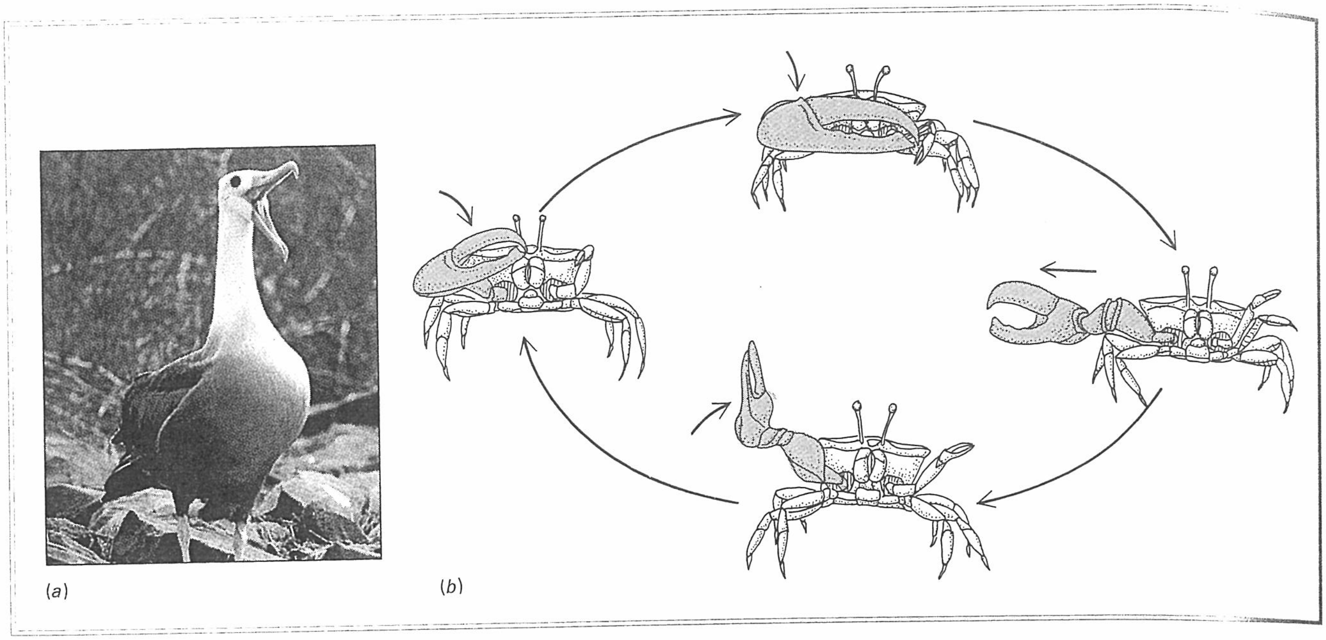


FIGURE 52–26 Courtship displays. (*a*) A male waved albatross from the Galapagos Islands. (*b*) Courtship signals by male fiddler crabs are specific to each species. This particular sequence of the motion of the large right claw is characteristic of the species *Uca lactae*.

Sexual Behavior and Reproduction

The minimum social contact, and for some species of animals (for example, many species of spiders) the only social contact, is the sex act. Fertilization and perhaps the rearing of young are some animals' only forms of social behavior (Figure 52–27). Let us consider the sex act as a basic example of social behavior, for the elements to which it can be reduced are also the least common denominators of most social behavior.

Like other social relationships, the sex act is adaptive in that it promotes the welfare of the species. It requires *cooperation*, the *temporary suppression of aggressive behavior*, and a *system of communication*. Among some jumping spiders, for example, mating is preceded by a ritual courtship on the part of the male, the effect of which is to produce temporary paralysis in the female. While she is thus enthralled, the male inseminates her. Should she recover before he makes his escape, he becomes the main course at his own wedding feast. Whether he appreciates the opportunity or not, he is thus able to make the ultimate in material contributions to the eggs the female will presently produce. She would otherwise have to bear the metabolic burden of their production all by herself.

Since an individual that reproduces perpetuates its genes, it is not surprising that natural selection has favored mechanisms, including behavior, that promote successful reproduction. To fertilize as many females as possible, the males often compete intensely with one another. Sexual competition among males of the same species often has contributed to the evolution of large male size, brilliant breeding colors, ornaments, antlers, and other features that give a male an advantage in establishing dominance among his peers and attracting females.

Since the female usually chooses the mate, selection has favored those male characteristics that make a male most attractive. Selection has also favored those female attributes that enable her to determine that the male is worthy of her investment. Success of a male in dominance encounters with other males indicates his fitness to the female. Although the female of some species accepts the first male that attempts to court her, in other species the female tests the males by provoking encounters. Female baboons and chimpanzees in estrus have enlarged, brilliantly colored genital

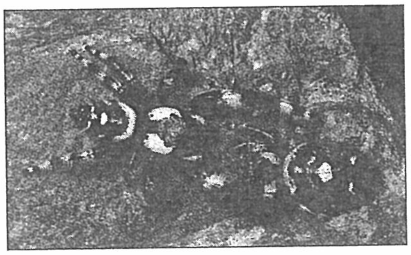


FIGURE 52–27 Male and female jumping spiders, *Phidippus audax*, in the courtship behavior that precedes mating. The male performs an elaborate dance that inhibits the female's natural aggression toward him, allowing him to get close enough to inseminate her.

swellings that attract all males and incite competition among them (Figure 52–28).

The victorious male courts the female. An important function of courtship is to ensure that the male is a member of the same species, but it also provides the female further opportunity to evaluate the quality of the male. Courtship may also be necessary as a signal to trigger nest building or ovulation. Courtship rituals may be long and complex. The first display of the male releases a counter behavior of a conspecific female. This, in turn, releases additional male behavior, and so on until the pair are ready for copulation. Certain male spiders make an offering of food to the female during courtship. This inhibits any aggressive tendencies that the female may have on being approached and also provides the female with some of the food needed for egg production.

Sexual selection has also led to strategies whereby a successful male protects an inseminated female from copulation with other males. After copulation a male damselfly continues to grasp and fly with the female until she has deposited her eggs. A successful drone honeybee discharges much of his genital apparatus into the virgin queen's genital passages, thereby blocking them against insemination by another male.

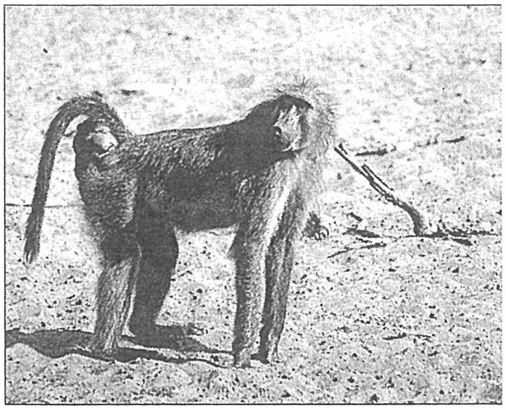


FIGURE 52–28 This female baboon signals periodic sexual readiness with her bright red posterior.

Pair Bonds

A **pair bond** is a stable relationship between animals of the opposite sex that ensures cooperative behavior in mating and the rearing of the young (Figure 52–29). In some species a newly arrived female is initially treated as a rival male. Then, through the use of instinctive appeasement postures and gestures by both male and female, the initial hostility is dissipated and mating takes place. Such sexual appeasement behavior may be very elaborate and gives rise to mating dances in some birds.

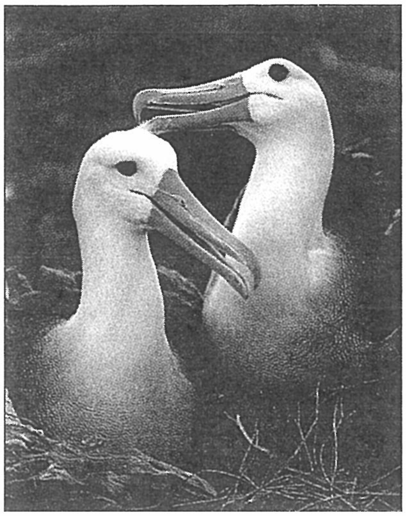
The releaser mechanisms involved in the establishment and maintenance of the pair bond are often remarkably detailed. A male flicker possesses a black, mustache-like marking under the beak. This is lacking in the female. If a "happily married" female flicker is captured and such a mustache is painted on her, her mate will vigorously attack her as if she were a rival male. He will accept her again if it is removed. Such cues enable courtship rituals to function as behavioral genetic isolating mechanisms among species.

Care of the Young

Care of the young is an additional component of successful reproduction in many species, and it, too, requires a parental investment (Figure 52–30). The benefit of parental care is the increased likelihood of the survival of the offspring, but the cost is a reduction in the number of offspring that can be produced. Because of the time spent carrying the developing embryo, the female has more to lose than the male if the young do not develop. Thus, females are more likely to brood eggs and young than males, and usually the females invest more in parental care.

Investing time and effort in care of the young is usually less advantageous to a male, for time spent in parenting is time lost in inseminating other females. Even worse, it may not be certain who fathered the offspring. Raising some other male's offspring is a definite genetic disadvantage. In some situations, however, it may be to the male's advantage to help rear his own young, or those of a genetic relative. Receptive females may be scarce. And gathering sufficient food may require more effort than one parent can provide. In some habitats the young may need protection against predators.

FIGURE 52–29 A pair of nesting albatrosses. In many species pair bonds are maintained by grooming or other displays of attraction.



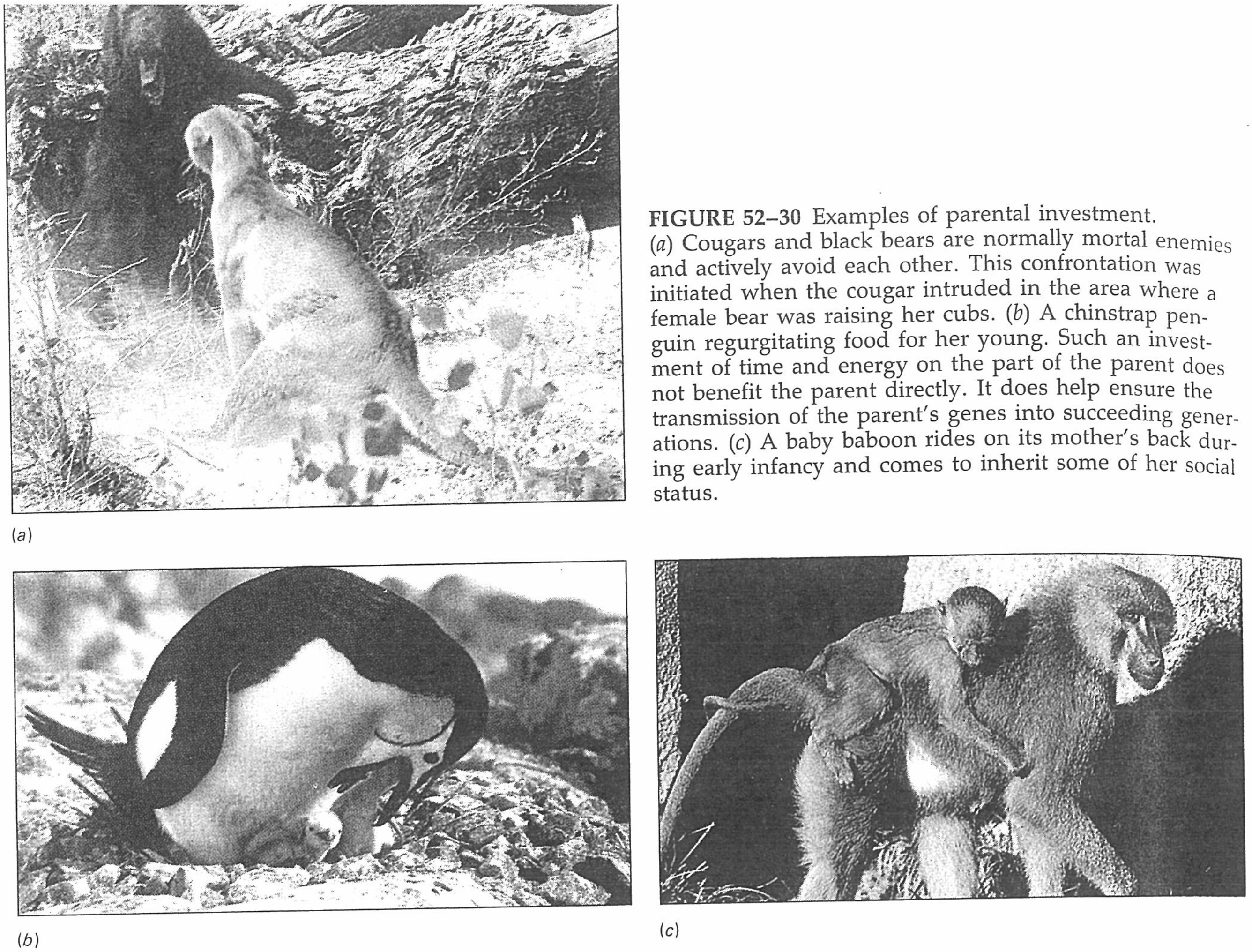


FIGURE 52–30 Examples of parental investment. (*a*) Cougars and black bears are normally mortal enemies and actively avoid each other. This confrontation was initiated when the cougar intruded in the area where a female bear was raising her cubs. (*b*) A chinstrap penguin regurgitating food for her young. Such an investment of time and energy on the part of the parent does not benefit the parent directly. It does help ensure the transmission of the parent's genes into succeeding generations. (*c*) A baby baboon rides on its mother's back during early infancy and comes to inherit some of her social status.

Play

Play is an important aspect of the development of behavior in many species, especially young mammals. It serves as a means of practicing adult patterns of behavior and perfecting means of escape, prey killing, and even sexual conduct. In true play the behavior may not be actually consummated. Thus a kitten pounces upon a dead leaf but of course does not kill it, even though the kitten administers a typical carnivore neck bite. When playing with a littermate, the same kitten may practice the disemboweling stroke with its hind claws (Figure 52–31), but the littermate is not intentionally injured in the process.

Sociobiology

Sociobiology is the school of ethology that focuses on the evolution of social behavior through natural selection. Like many biologists of the past (including Darwin), Edward O. Wilson and other sociobiologists emphasize the animal roots of human behavior, but they have attempted to inform their discipline with population genetics, with particular emphasis on the effect of kin selection (Chapter 18) on patterns of inheritance.

For the sociobiologist, the organism and its adaptations—including its behavior—are ways its genes have of making more copies of themselves. The cells and tissues of the body support the functions of the reproductive system. The reproductive system's job is the transmission of genetic information to succeeding generations.

There are unique pitfalls in attempting to reconstruct the evolution of behavior, since behavior rarely leaves an explicit fossil record. Addition-

FIGURE 52–31 Young lions playing in southern Africa. Play is behavior that is not consummated and often serves as a means of practicing behavior that will be used in earnest in later life, possibly in hunting, fighting for territory, or competing for mates.

ally, by applying human social terms to behavior in animals that may be only superficially similar, we create the perhaps entirely false impression that it is the *same* behavior. It is an easy step from that to the assumption that the causes and utility of these behaviors are the same as those of corresponding human behavior. Consider, for instance, the question of whether humans are territorial. We do tend to preserve space between us as individuals, to defend our homes, and as groups to defend larger, political areas. However, do these behaviors have the same genetic and adaptive value in humans as in animals? And is human territoriality homologous with that of other animals, or is it merely analogous?

Also, problems of objectivity can exist. Any assumptions we may have about our own territoriality can cause us to look at the behavior of animals as a mirror of our own. Among closely related species of primates, social organization and the degree of territoriality and aggressive behavior vary widely. Which of these species should we choose as models for studying human behavior?

Most of the controversy that has been triggered by sociobiology seems related to its possible ethical implications. Sociobiology is often taken as denying that human behavior is flexible enough to permit substantial improvements in the quality of our social lives. Yet sociobiologists do not disagree with their critics that human behavior is flexible. The debate therefore seems to rest on the *degree* to which human behavior is genetic and the *extent* to which it can be modified.

As sociobiologists acknowledge, people through culture possess the ability to change their way of life far more profoundly in a few years than a hive of bees or a troop of baboons could accomplish in hundreds of generations of genetic evolution. This ability is indeed genetically determined, and that is a very great gift. How we use it and what we accomplish with it is not a gift but a responsibility upon which our own well-being and the well-being of other species depend.

SUMMARY

I. Animal behavior, or the movements of animals in response to stimuli, may be studied from the points of view of several subdisciplines.
   A. Classical ethology focuses primarily on the characteristics, adaptive value, and evolutionary history of innate, species-typical behaviors.
   B. Behavior genetics is concerned with how behavioral traits are inherited.
   C. Comparative psychology typically deals with learned behavior and how it can be predicted under specified conditions.
   D. Behavioral ecology studies behavior in relation to ecological variables.
   E. Neurobiology seeks to explain behavioral mechanisms in anatomical and physiological terms.

II. The questions that animal behaviorists ask usually fall into one of two categories:
   A. Questions concerned with long-term evolutionary causes of behavior, called ultimate factors.
   B. Questions concerned with immediate conditions or mechanisms, called proximate factors.

III. Central to much of classical ethology is the fixed action pattern (FAP), an innate, stereotyped response to a stimulus (a sign stimulus, or releaser) that has a taxis component and that continues after the stimulus has ceased.
   A. Sign stimuli are detected in the central nervous system by special sensory mechanisms known as innate releasing mechanisms, each of which is specific to a particular sign stimulus.