Principles of

Animal Behavior

Contents in Brief

1 Principles of Animal Behavior

I grew up in the heart of New York City. One animal that my family and I encountered on a fairly regular basis was the American cockroach (*Periplaneta americana*) (Figure 1.1). Much to my mother's chagrin, we seemed locked in a never-ending battle with this creature—a battle that we usually lost. And we probably lost because cockroaches have been subject to this sort of problem—other organisms trying to kill them—for tens of millions of years. As a result, they have evolved an exquisite set of antipredator behaviors, which have had the side effect of making them a thorn in the side of modern apartment dwellers.

As a very young boy, I had, of course, never heard of the **scientific method**—which the *Oxford English Dictionary* defines as "scientific observation, measurement, and experiment, and the formulation, testing, and modification of hypotheses." Nevertheless, I was able to draw some inferences and formulate some hypotheses about cockroach behavior by watching my mother put out the roach traps. First, it seemed to me that roaches liked to spend their time in dark places, and second, it appeared that most roaches agreed on what was a good place for roaches to be, as we kept putting the traps out in the same place. These two thoughts on cockroach behavior could easily be developed into the following hypotheses: (1) cockroaches will choose dark places over light places, and (2) roaches will return to the same places over and over, rather than moving randomly through their environment. Of course, as a child, I didn't formally sit down and generate these

hypotheses, and I surely didn't run the controlled experiments that a scientist studying animal behavior would run to test these ideas, but I was nonetheless dabbling with scientific hypotheses in **ethology**—the study of animal behavior.

Many people think like ethologists: from my mother, who understood roach behavior, to the farmer who has detailed knowledge about pigs, cows, chickens, and other domesticated farm animals. The girl who works to train her dog, and the outdoorsman who, on his camping vacation, searches for some animals and tries to avoid others, also think like ethologists. Indeed, humans have always thought and acted like ethologists. If our hunter-gatherer ancestors had not thought like ethologists, and hadn't, for example, understood the prey they were trying to catch, as well as the behavior of the predators that were trying to catch them, we wouldn't be here today.

The study of animal behavior appears to have been so important that the earliest cave paintings tended to depict animals. Early cave drawings might have focused on any number of things, but apparently understanding something about the other life forms surrounding our ancestors was fundamental enough that they chose animals as the subjects for the earliest art. This focus on animals, and their behaviors, continued as humans began developing other types of art. Artifacts from 4,000-year-old Minoan cultures suggest an advanced understanding of some aspects of animal behavior: for example, a golden pendant from a Cretan cemetery that depicts two wasps transferring food to one another (Figure 1.2). Masseti hypothesizes that this kind of knowledge of insect food-sharing behavior could only have come from people who observed and studied the details of wasp life (Masseti, 2000). A similar sort of argument has been made regarding a Minoan wall painting of "white antelopes." This painting likely depicts gazelles in the early stages of an aggressive interaction (Figure 1.3), and it is the sort of art that is associated with an in-depth knowledge of the subject in question (Voultsiadou and Tatolas, 2005).

Spanning the millennia between ancient Cretan civilization and the present, thousands of amateur and professional naturalists have made some

FIGURE 1.1. **American cockroach.** The American cockroach, often thought of as a pest in households around the world. *(Photo credit: © Thomas Won)*

FIGURE 1.2. **Art captures animal behavior.** This pendant from the Chrysolakkos funeral complex in Crete suggests that some members of this ancient culture had a detailed knowledge of wasp behavior. *(From Gianni Dagli Orti/The Art Archive at Art Resource, NY)*

contribution to the study of animal behavior. These contributions have enabled ethologists to draw on a rich trove of information that has greatly expanded our understanding of animal behavior (Figure 1.4). Aristotle's work on animals, for example, though 2,500 years old, is a treasure chest of ethological tidbits. Indeed, with Aristotle's books *Physics* and *Natural History of Animals*, the field of natural history was born. In these and other works, Aristotle distinguished among 500 species of birds, mammals, and fish, and he wrote entire tracts on the behavior of animals.

In many ways, a course in animal behavior is where all the other biology and psychology classes that you have sat through up to this point in your academic career come together. Evolution, learning, genetics, molecular biology, development, neurobiology, and endocrinology congeal into one grand subject— animal behavior. The field of ethology is integrative in the true sense of the word, in that it combines the insights of biologists, psychologists, anthropologists, and even mathematicians and economists.

Types of Questions and Levels of Analysis

Ethologists have asked questions about almost every conceivable aspect of animal behavior—feeding, mating, fighting, and so on. At a broad level, ethologists pose four distinct *types of questions*, which Niko Tinbergen outlined in a classic paper entitled "On the Aims and Methods of Ethology" (N. Tinbergen, 1963; Bateson and Laland, 2013; Taborsky, 2014; Burkhardt, 2014; Dawkins, 2014; Strassmann, 2014; Lefebvre, 2015). These questions center on:

- Mechanism—What stimuli elicit behavior? What sort of neurobiological and hormonal changes occur in response to, or in anticipation of, such stimuli?
- Development—How does behavior change with the ontogeny, or development, of an organism? How does developmental variation affect behavior later in life?
- Survival value—How does behavior affect survival and reproduction?
- Evolutionary history—How does behavior vary as a result of the evolutionary history, or **phylogeny**? When did a behavior first appear in the evolutionary history of the species under study?
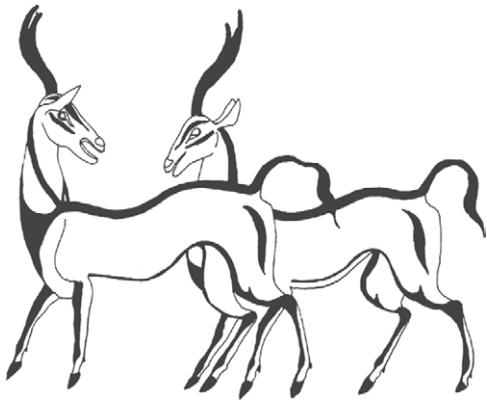
FIGURE 1.3. **Minoan wall paintings of "white antelopes."** The drawing may depict a "lateral intimidation" during an aggressive encounter between the animals. *(From Masseti. Courtesy Ministry of Culture, Hellenic Republic)*

FIGURE 1.4. **Images from a cave.** A drawing of a herd of antelope found on the walls of a cave at Dunhuang, China. *(Photo credit: © Jean Clottes)*

Thousands of studies have been undertaken on each of these four types of questions. Tinbergen's four questions can be captured in two different kinds of analyses—proximate analysis and ultimate analysis (Alcock and Sherman, 1994; Dewsbury, 1992, 1994; Hailman, 1982; Hogan, 1994; J. Huxley, 1942; Mayr, 1961; Orians, 1962; Reeve and Sherman, 1993; Haig, 2013). **Proximate analysis** focuses on *immediate causes*, whereas **ultimate analysis** centers on *evolutionary forces* that have shaped a trait over time. As such, proximate analysis incorporates Tinbergen's first two types of questions, and ultimate analysis covers the latter two types (Figure 1.5). We could ask, for example: Why do some bird chicks peck at red stimuli but not stimuli of other colors? Does red trigger a set of neuronal responses that are not triggered otherwise? If so, exactly which neurons and when? These are questions about proximate causation. An analysis at the ultimate level, on the other hand, would ask: What selective forces in the birds' evolutionary past would have favored individuals that had responses to red stimuli? Was the color red associated with a particular food source? Do other closely related bird species show similar responses to red stimuli?

Every chapter of this book examines animal behavior from both proximate and ultimate perspectives.

What Is Behavior?

What do ethologists mean by the word *behavior*? It turns out that this is not a trivial question, and it is one that ethologists have grappled with for some time. Early on, ethologists like Tinbergen defined behavior as "the total movements made by the intact animal," but that definition seems far too general, incorporating almost everything an animal does. But if a definition proposed by Tinbergen—who shared a Nobel Prize as a founder of the study of animal behavior—doesn't work, how can a satisfactory definition be achieved?

One solution is to survey ethologists to get a discipline-wide view of the way the term *behavior* is employed. In a review paper on definitions of behavior, Daniel Levitis and his colleagues surveyed 174 members of three professional societies that focus on behavior to try to understand what researchers mean when they used the term *behavior* (Levitis et al., 2009). What they found was much variation among ethologists on how behavior should be defined. Based on their survey results, Levitis and his colleagues argued that many of the definitions that ethologists use can be captured by a few published, but quite dated, definitions already in the literature. These include Tinbergen's 1952 definition of behavior, as well as the following:

- "Externally visible activity of an animal, in which a coordinated pattern of sensory, motor and associated neural activity responds to changing external or internal conditions" (Beck et al., 1981).
- "A response to external and internal stimuli, following integration of sensory, neural, endocrine, and effector components. Behavior has a genetic basis, hence is subject to natural selection, and it
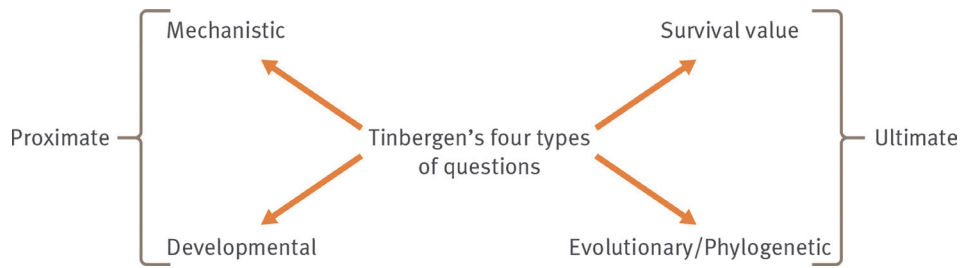
FIGURE 1.5. **Tinbergen's four types of questions.** A diagrammatic representation of the four different types of questions asked by ethologists. Two of these types of questions are proximate and two are ultimate.

commonly can be modified through experience" (Starr and Taggart, 1992).

- "Observable activity of an organism; anything an organism does that involves action and/or response to stimulation" (R. Wallace et al., 1991).
- "Behavior can be defined as the way an organism responds to stimulation" (D. Davis, 1966).
- "What an animal does" (Raven and Johnson, 1989).
- "All observable or otherwise measurable muscular and secretory responses (or lack thereof in some cases) and related phenomena such as changes in blood flow and surface pigments in response to changes in an animal's internal and external environment" (Grier and Burk, 1992).
- "Behavior is defined as the expression of the activity of the nervous system" (Hogan, 2015).

Each of these definitions has its pluses and minuses. If "behavior has a genetic basis," as it certainly does in many instances, does that mean that we should exclude all actions that have not been studied from a genetic perspective when we speak of behavior? Surely not. For any of the definitions above we could pose equally strong challenges. That said, I needed to adopt a consistent definition of behavior in this book, and I will use one that is a slight modification of a suggestion by Levitis and his colleagues—namely, that behavior is the coordinated responses of whole living organisms to internal and/or external stimuli. This definition is appropriate for a number of reasons (all of which are admittedly somewhat subjective): (1) it seems to capture what most modern ethologists and behavioral ecologists mean when they use the term behavior, (2) it works fairly well for the behaviors covered in detail in chapters 6–17 of this book, and (3) it makes an important distinction between organism and organ. What this third point means is that, as Levitis and his colleagues note, sweating in response to increasing body temperature is not generally thought of as a behavior per se. But when an animal moves to

the shade in response to heat and its own sweating, most ethologists would agree that this is a behavioral response.

Three Foundations

Incredible tales and fascinating natural history make a textbook on animal behavior different from a textbook on organic chemistry or molecular genetics. What links animal behavior to all scientific endeavors, however, is a structured system for developing and testing falsifiable hypotheses and a bedrock set of foundations on which such hypotheses can be built. Throughout this book, the force of natural selection, the ability of animals to learn, and the power of transmitting learned information to others (cultural transmission) will serve as the foundations upon which we build our approach to ethology.

In his classic, *On the Origin of Species*—widely regarded as the most important biology book ever written—Charles Darwin laid out general arguments for how evolutionary change has shaped the diversity of life and how the primary engine of that change is a process that he dubbed **natural selection** (Darwin, 1859). In a nutshell, Darwin argued that any trait that could be transmitted across generations (i.e., is heritable) and provided an animal with some sort of reproductive advantage over others in its population would be favored by natural selection. Natural selection is, then, the process whereby traits that confer the highest relative reproductive success on their bearers increase in frequency over generations.

Whereas natural selection changes the frequency of different behaviors over the course of many generations, **individual learning** can alter the frequency of behaviors displayed within the lifetime of an organism. Animals learn about everything from food and shelter to predators and familial relationships. If we study how learning affects

behavior *within the lifetime* of an organism, we are studying learning from a proximate perspective. If we study how natural selection affects the *ability* of animals to learn, we are approaching learning from an ultimate perspective. Later in this chapter we will examine a study on learning and foraging (feeding) behavior in grasshoppers. When we ask what sort of cues grasshoppers use to learn where to forage, we are addressing learning from a proximate perspective. When we examine how a grasshopper's ability to learn about food sources affects its reproductive success, and how selection might favor such abilities, we are studying learning from an ultimate perspective.

Cultural transmission also affects the type of behavior animals exhibit and the frequency with which behaviors occur. While definitions vary widely across disciplines, this book uses the term *cultural transmission* to mean a transmission system in which animals learn through various forms of **social learning**. Cultural transmission can allow newly acquired traits to spread through populations at a very quick rate, as well as permit the rapid transmission of information across generations. As with individual learning, natural selection can also act on animals' ability to transmit, acquire, and act on culturally transmitted information.

NATURAL SELECTION

Darwin recognized that his theory of natural selection applied to behavioral traits as well as morphological, anatomical, and developmental traits. Indeed, morphological traits are often the physical underpinning for the production of behavior, so morphology and behavior are linked at many levels. More detail about this linkage is provided below and throughout the book, but for the moment, the key point is that Darwin's ideas on evolution, natural selection, and behavior were revolutionary, and ethology today would look very different were it not for the ideas that Darwin set forth in *On the Origin of Species*. A fascinating example involving mating and parasites in Hawaiian crickets illustrates how natural selection operates on animal behavior in the wild.

In the evening on the Hawaiian Islands, male crickets sing to attract their mates. This "singing" results when the male cricket rapidly moves the smooth scraper on the front of one wing against the serrated file on the other wing. Females cue in on male songs, and they typically will not mate with males that do not produce songs. But as with many behavioral traits associated with attracting mates, male singing is not cost free. Just as females are attracted to male song, so too are potentially dangerous parasites (Zuk and Kolluru, 1998).

Marlene Zuk and her colleagues have been studying this trade-off in male song production—between attracting females and attracting parasites—in the field cricket *Teleogryllus oceanicus* (Zuk et al., 2006). These crickets are parasitized by the fly *Ormia ochracea*, who are attracted to singing males. If a fly finds a singing cricket, it lays its eggs on the cricket, and then the fly larvae burrow their way into the cricket and grow. Emergence of the flies from the larvae kills the cricket.

Parasitic flies are found on three of the Hawaiian Islands—Oahu, Hawaii, and Kauai—that are also home to *T. oceanicus*. The flies are most common on the island of Kauai, where 30 percent of the crickets are parasitized. Zuk and her team have been studying the relationship between crickets and parasitic flies since 1991, and over time, they noted what appeared to be a significant decline in the cricket population on Kauai. Over the years, they heard fewer and fewer singing males on this island, and they assumed that the parasitic fly was slowly causing the extinction of *T. oceanicus* on Kauai. Indeed, in 2003 they heard only a single male singing. But when they got down on their hands and knees and searched for crickets, Zuk and her team found *T. oceanicus* in abundance. How could they explain these seemingly contradictory findings?

What Zuk and her team found was that most of the males on Kauai had modified wings that were not capable of producing song (Figure 1.6). The file section of the wings of these Kauai males (called "flatwing males") was significantly reduced compared to that of normal males, and its position on the wings changed, such that song production was no longer possible. These changes were likely the result of mutations of one, or possibly, a few genes associated with wing development and song production. Once such mutations arose, natural selection should strongly favor such flatwing males, that would virtually never be parasitized by very dangerous flies. Or should it?

Flatwing males should have a huge survival advantage, but they might also be at a disadvantage with respect to attracting females that hone in on singing males as potential mates. For flatwing males to be favored by natural selection, they must

FIGURE 1.6. **Natural selection in crickets.** Marlene Zuk and her colleagues have been studying the field cricket *Teleogryllus oceanicus*. Pictured here are (A) a field cricket with normal wings (the arrow points to the file on its outstretched wing); (B) a field cricket with flat wings, in which the file section on the outstretched wing has evolved to a much smaller size and is visible only under a high-powered microscope; and (C) fly larvae in a parasitized cricket. *(Photo credits: Robin Tinghitella; John Rotenberry)*

should be strongly favored by natural selection. And indeed, Zuk and her colleagues suggest that the mutation(s) leading to the loss of song occurred only fifteen to twenty generations ago and has quickly increased in frequency, so that now most males on Kauai are flatwing males (Rotenberry et al., 2015; Rotenberry and Zuk, 2016). Remarkably, on the nearby Hawaiian island of Oahu, Zuk and her team have found an independent, parallel, case of the evolution of flatwing males, and they are currently tracking the success of flatwings on that island (Pascoal et al., 2015). We will delve more deeply in this sort of **convergent evolution** in subsequent chapters.

As a second example of natural selection acting on animal behavior, let's examine how individuals in social groups respond to strangers. For animals that live in stable groups, strangers—unknown individuals from outside your group—represent a threat. Such individuals may compete for scarce resources (including food and mates), disrupt group dynamics that have long been in place, and so on. Because of such costs, ethologists have examined whether animals from group-living species display **xenophobia**—a fear of strangers. In particular, ethologists hypothesize that xenophobia may be especially strong when resources are scarce, since competition for such resources will be intense then, and keeping strangers away may have an especially strong impact on the lifetime reproductive success of group members.

To examine the effect of resource scarcity on the

somehow still secure opportunities to mate. Zuk and her colleagues hypothesized that flatwing males do this by staying near the handful of singing males still on Kauai, and mating with females as they approach singers. This sort of "satellite" male mating behavior has been seen in many *T. oceanicus* populations (Tinghitella et al., 2009). To test their hypothesis, they collected 133 Kauai males—121 of which were flatwings, and 12 of which were singers. They then used "playback" experiments, in which male songs were broadcast over loudspeakers. What they found was that flatwing males were drawn to playbacks more strongly than normal males, suggesting that flatwing males stay near singer males in order to secure chances to mate with females drawn in by the singers. With both a huge survival advantage and the continued ability to obtain matings, flatwing males

evolution of xenophobia, Andrew Spinks and his colleagues examined xenophobia in the common mole rat (*Cryptomys hottentotus*) (Spinks et al., 1998; Figure 1.7). Common mole rats live in South Africa in underground colonies made up of two to fourteen individuals. They are an ideal species in which to examine xenophobia and its possible connection to resource availability for two reasons: First, all populations of common mole rats are "tightly knit" in the sense that each group typically has a single pair of breeders that produce most of the offspring in a colony, which means that most group members are genetic relatives (J. M. Bishop et al., 2004). Second, populations of common mole rats differ in terms of the amount of resources in their environments. Some common mole rat populations live in moderately moist (mesic) environments that present only mild resource limitations, while other populations live in dry (arid) environments and face intense limitations on their resources. Variation in resource availability between arid and mesic populations is largely due to the fact that mesic environments have about four times as much rainfall as arid environments.

Spinks and his colleagues examined whether populations from arid areas were more xenophobic than those from mesic environments, as one might predict based on the discussion above about natural selection, resources, and xenophobia. To do so, they conducted 206 trials in which two mole rats—one from the arid and one from the mesic environment—were placed together, and aggression was recorded. When the pair of individuals were both males or both females, aggression toward such strangers was much more pronounced in the common mole rats from the arid environment, where resources were limited, than it was in the common mole rats from the mesic environment. This result was not a function of individuals from arid populations just being more aggressive in general. Control experiments demonstrated that when two individuals that knew each other from the arid population were tested together, aggression disappeared—it was the identification of a stranger that initiated the aggression. Natural selection has favored stronger xenophobic responses in common mole rats whose resources are more limited.

The ecology of common mole rats is such that some individuals leave their home colony to find a mate. What this means is that some strangers that

FIGURE 1.7. **Common mole rat.** This xenophobic common mole rat (*Cryptomys hottentotus*) is showing an aggressive stance in response to a stranger. *(Photo credit: Chris and Tilde Stuart/ FLPA/Minden Pictures)*

are encountered by members of a social group are potential mates, and perhaps worth tolerating. Natural selection then should not simply favor all xenophobia, but a xenophobia that is sensitive to the sex of the stranger. In trials in which the two individuals tested were a male and a female, Spinks and his colleagues found that while aggression was still observed in the low-resource, arid population, the level of aggression decreased dramatically when compared with aggression in same-sex interactions (Figure 1.8). Natural selection has favored common mole rats that temper their fear of strangers as a function of both where they live and the sex of the strangers.

INDIVIDUAL LEARNING

As chapter 5 explores in much greater detail, individual learning can take many forms. Let's begin our discussion by considering a hypothetical case of learning and mate choice. Suppose that we are studying a species in which female birds mate with numerous males throughout the course of their lifetime and females are able to keep track of how many chicks fledged their nest when they mated with male 1, male 2, male 3, and so forth. If we found that females changed their mating behavior as a result of direct personal experience, preferring to mate with males that fathered the most successful fledglings, such results would suggest that learning had changed the behavior of an animal within the course of its lifetime (Figure 1.9).

The learning example above highlights an important relationship between learning and natural

A male mole rat from an arid environment was more likely to reject a male from his own population than was a male from a mesic environment.

When males were paired with females, more aggression was seen in individuals from the arid environment, but the overall level of aggression was low in these mixed sex pairs.
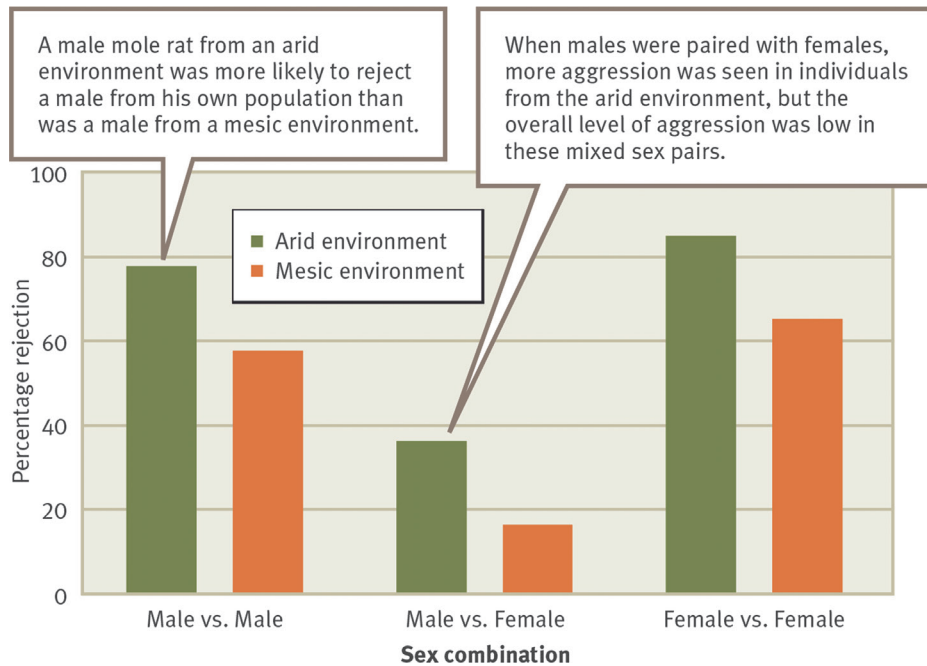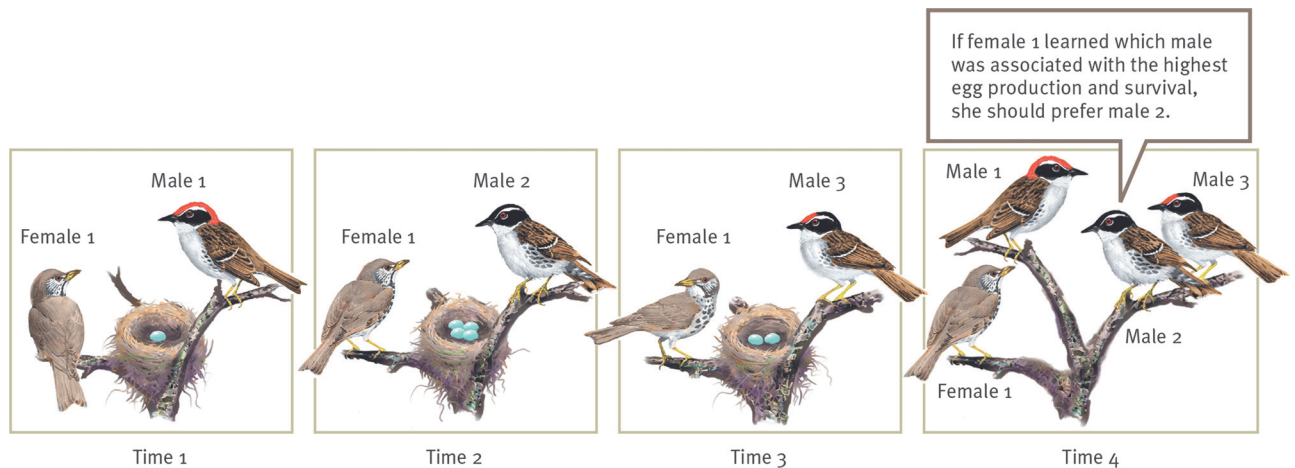
FIGURE 1.8. **Xenophobia in common mole rats.** Spinks and his colleagues found that mole rats from an arid environment (green bars) were more likely to reject a potential partner from their own population than were mole rats from a resource-rich mesic environment (orange bars). *(From Spinks et al., 1998, p. 357)*

FIGURE 1.9. **A role for learning.** Imagine a female that mates with different males over the course of time. Such a female might learn which male is a good mate by keeping track of the number of eggs she laid after mating with each male.

If female 1 learned which male was associated with the highest egg production and survival, she should prefer male 2.

selection. In our example, females changed their preference for mates as a result of prior experience, and so learning affected mating behavior within a generation. But just because the use of a behavior is changing within the course of an individual's lifetime does not mean that natural selection is not occurring. It is certainly possible for natural selection to operate on the *ability* to learn. That is, natural selection might favor the ability to learn which individuals make good mates over, say, the lack of such an ability. If this were the case in the example above, learning would change behaviors within a generation, and natural selection might change the frequency of different learning rules across generations.

Learning and natural selection are tied together

nicely in Reuven Dukas and Elizabeth Bernays's ingenious experiment examining the fitness consequences of learning in insects (Dukas and Bernays, 2000). While learning in insects is well documented, documenting the potential fitness-related benefits of learning has proved to be more difficult (Dukas, 2006). To address the question of learning-related benefits directly, Dukas and Bernays examined the potential fitness-related benefits of learning in the context of feeding behavior in the grasshopper, *Schistocerca americana* (Figure 1.10).

In their experiment, they placed two food dishes in a grasshopper's cage. The food in one dish provided a "balanced diet (b)" that included proteins and carbohydrates—a diet that promotes maximal growth

FIGURE 1.10. **Some components of foraging in grasshoppers are learned.** *Schistocerca americana* grasshoppers learned to associate various cues with food sources. *(Photo credit: American bird grasshopper, © Maria de Bruyn; https:// mybeautifulworldblog.com/)*

rates in *S. americana*. The food in a second dish was labeled a "deficient diet (d)." This diet contained flavoring and protein, but no carbohydrates. Specific odors and colors were associated with each of the two diets. Diets were supplemented with either citral (odor 1) or coumarin (odor 2), and food dishes were placed near either a brown-colored card (color 1) or a green-colored card (color 2). This created an opportunity for the grasshoppers to pair balanced and deficient diets with both odor cues and color cues.

Dukas and Bernays's experiment contained a "learning" treatment and a "random" treatment (Figure 1.11). In the learning treatment, the balanced diet dish was always paired with one specific odor and one specific colored card. Twice a day, a grasshopper was presented with the two food dishes and allowed to choose one from which to feed. For example, grasshopper A might be placed in a cage in which the balanced diet was always paired with the brown color and the odor of coumarin. In principle, grasshopper A could learn that together the cues coumarin and brown color are associated with a food dish that contained the balanced diet. In contrast, in the random treatment, the odor and color cues associated with the balanced diet were randomly assigned. For example, in the morning, grasshopper B might have the balanced diet dish paired with the color green and the odor of coumarin, but in the afternoon, the balanced diet dish might be paired with the color green and the odor of citral, while the next morning the balanced diet dish might be paired with the color brown and the odor of coumarin. In this treatment,

the grasshopper could not learn to pair the balanced diet with specific color and odor cues.

Significant differences between the grasshoppers in the learning and random treatments were uncovered. Grasshoppers in the learning treatment ate a greater proportion of their food from the balanced diet dish than did the grasshoppers in the random treatment (Figure 1.12): they learned to pair diet type with color and odor cues when the situation allowed for such learning. Over the course of the experiment, individuals in both treatments increased the proportion of time they spent feeding on the balanced diet, but grasshoppers in the learning treatment did so more quickly than did those in the random treatment. This difference was most likely due to the fact that grasshoppers in the learning treatment went to the balanced diet dish almost immediately when feeding, while those in the random treatment ended up at the balanced diet dish, but only after much sampling of the deficient diet dish. Perhaps most important of all, the individuals in the learning treatment had a
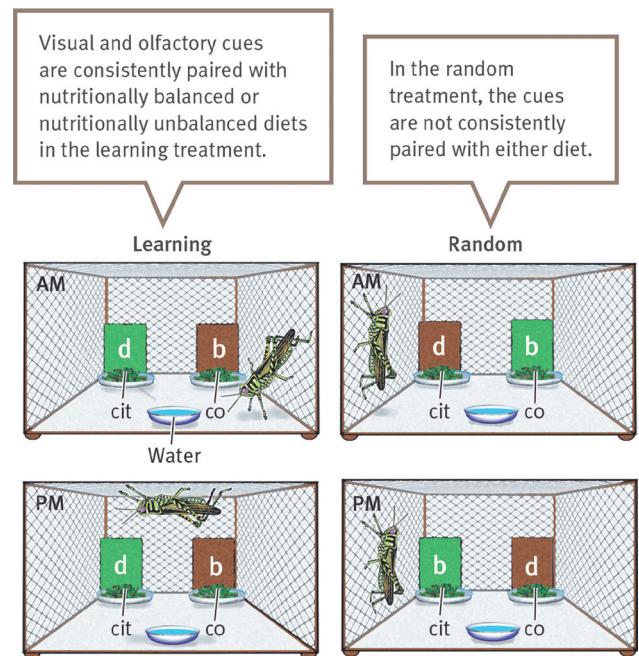

FIGURE 1.11. **Learning, foraging, and fitness in grasshoppers.** A schematic of the set-up showing the learning and random conditions. In the learning condition, the set-up consisted of a water dish in the center of the cage and a nutritionally balanced dish (b) on one side of the cage and a nutritionally deficient dish (d) on the other side of the cage. Each dish was paired with one odor (citral [cit] or coumarin [co]) and one colored card (brown or green). *(Based on Dukas and Bernays, 2000)*
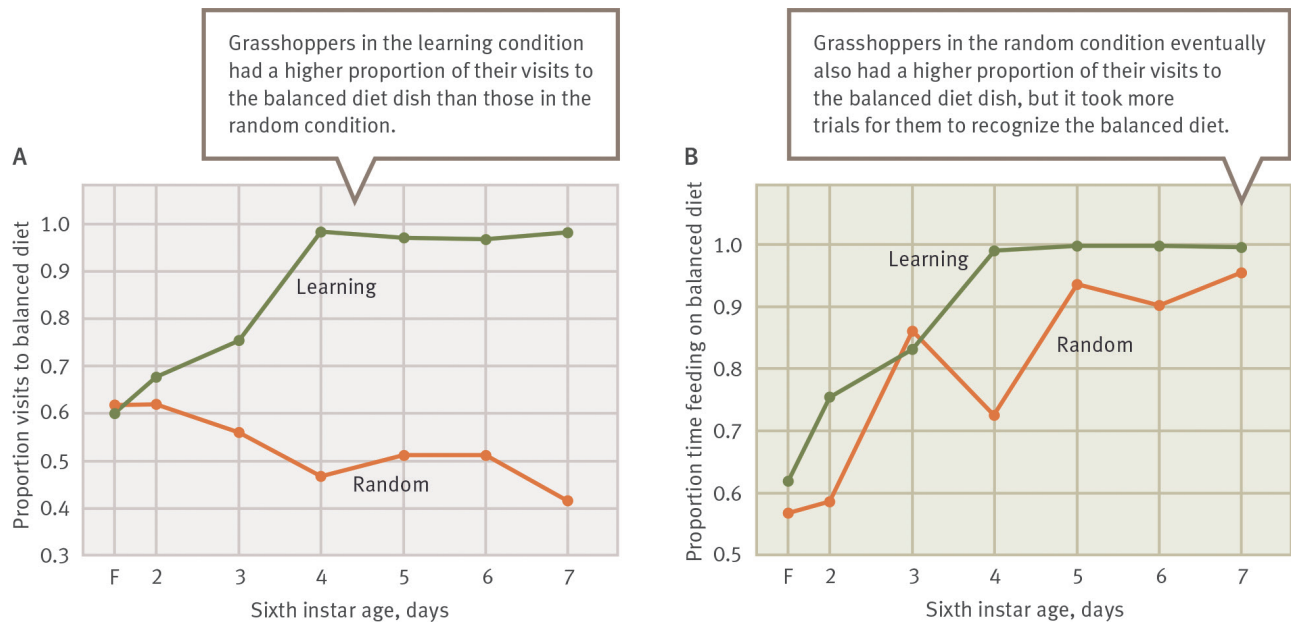
Grasshoppers in the learning condition had a higher proportion of their visits to the balanced diet dish than those in the random condition.

Grasshoppers in the random condition eventually also had a higher proportion of their visits to the balanced diet dish, but it took more trials for them to recognize the balanced diet.

A

Proportion visits to balanced diet

Learning

Random

Sixth instar age, days

B

Proportion time feeding on balanced diet

Learning

Random

Sixth instar age, days

Growth rate, mg/day

Learning   Random

Treatment

FIGURE 1.12. **A balanced diet in grasshoppers.** Grasshoppers in the sixth instar stage of insect development were given a choice between a balanced diet or a deficient diet, and researchers recorded the proportion of visits and feeding times of those in a learning treatment and those in a random treatment. In the learning condition, the food was presented in a way in which grasshoppers could learn to associate colored background cards and odors with balanced and unbalanced diets. In the random condition, food was presented in such a manner that grasshoppers could not make such associations. *(From Dukas and Bernays, 2000)*
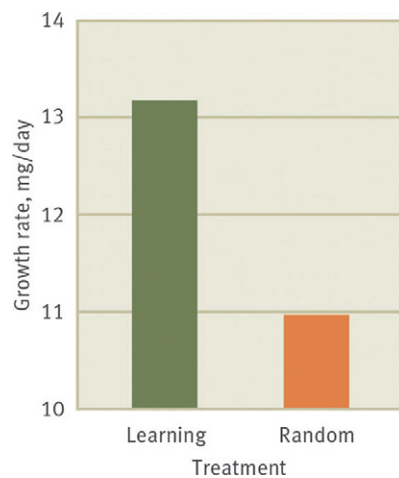
FIGURE 1.13. **Fitness and foraging.** Not only did grasshoppers in the learning condition approach the balanced diet dish more often, but this translated into quicker growth. Growth rate in grasshoppers is positively correlated with egg size and number. *(From Dukas and Bernays, 2000)*

growth rate that was 20 percent higher than that of the grasshoppers in the random treatment (Figure 1.13).

The ability to learn about food in *S. americana* translated into an important fitness gain: a significant increase in growth rate observed in individuals in the learning treatment. This difference in growth rate likely translates into greater reproductive success later in life, as growth rate is positively correlated with the number and size of eggs laid over the course of an individual's life (Atkinson and Begon, 1987; Slansky and Scriber, 1985).

CULTURAL TRANSMISSION

Cultural transmission has received much less attention in the ethological literature than natural selection or individual learning, but work in this area

is growing quickly (Danchin et al., 2004; Galef and Laland, 2005; Galef et al., 2005; Kendal et al., 2005; Mesoudi et al., 2006; Whiten et al., 2012; Laland and Galef, 2009: Mesoudi, 2011; Henrich, 2015).

For an interesting case study illustrating the importance of cultural transmission and social learning in animals, let's examine Jeff Galef's work on foraging behavior in rats. Rats are scavengers and often encounter new foods (Figure 1.14A). This has probably been true for most of the rat's long evolutionary history, but it has been especially true over the last few thousand years, during which time humans and rats have had a close relationship. Scavenging presents a foraging dilemma. A new food source may be an unexpected foraging bounty for rats, but it may be dangerous, either because it

FIGURE 1.14. **Scavenging rats and cultural transmission.** (A) When a rat scavenges in the trash, it may encounter new food items that are dangerous or spoiled and that can lead to illness or even death. (B) Smelling another rat provides olfactory cues about what it has eaten. This transfer of information from one rat to another about safe foods is a form of cultural transmission. *(Photo credits: Paul Hobson/npl/Minden Pictures; Joe Blossom / Alamy Stock Photo)*

contains elements inherently bad for rats, or because rats have no experience with the odor of that food, so they may not be able to tell if some piece of this new food type is fresh or spoiled. One possible way to get information about new food types is through the cultural transmission of information.

Galef began his study of cultural transmission and food preferences in rats by testing what is known as the information-center hypothesis, which posits that foragers may learn critical pieces of information about the location and identity of food by interacting with others that have recently returned from foraging bouts (Figure 1.14B; Ward and Zahavi, 1973). Galef and his colleagues tested this hypothesis in the Norway rat (Galef and Wigmore, 1983). To examine whether cultural transmission via social learning played a role

in rat foraging, rats were divided into two groups—observers and demonstrators (also known as tutors). The critical question that Galef examined was whether observers could learn about a novel, distant food source by interacting with a demonstrator that had recently encountered such a food source.

After the observer and demonstrator had lived together in the same cage for a few days, a demonstrator rat was removed and taken to another experimental room, where it was given one of two novel diets—either rat chow flavored with Hershey's cocoa (eight demonstrators) or rat chow mixed with ground cinnamon (eight demonstrators). The demonstrator was then brought back to its home cage and allowed to interact with the observer for fifteen minutes, at which time the demonstrator was removed from the cage. For the next two days, the observer rat—that had no personal experience with either of the novel foods, and had never *seen* the demonstrator eat anything—was given two food bowls, one with rat chow and cocoa, the other with rat chow and cinnamon. Galef found that through the use of olfactory cues, observer rats were influenced by the food their tutors had eaten, and they were more likely to eat that food (Figure 1.15).
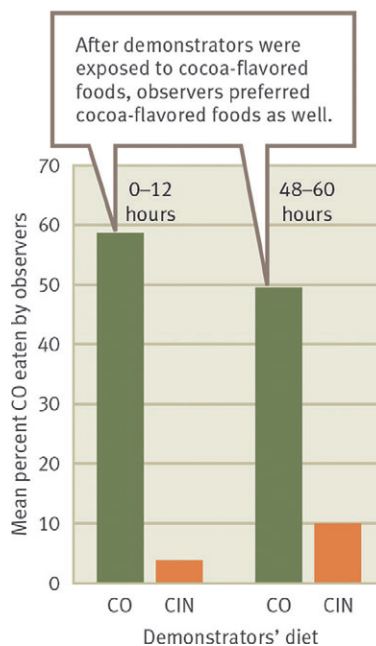

FIGURE 1.15. **Social learning and foraging in rats.** Observer rats had a "tutor" (demonstrator) that was trained to eat rat chow containing either cocoa (CO) or cinnamon (CIN) flavoring. After the observer rats had time to interact with a demonstrator rat, the observer rats were more likely to add their tutor's food preferences to their own. *(From Galef and Wigmore, 1983)*

Panel 1

Panel 2

Panel 3

Demonstrator D eating hot dog.

Pups

Generation 1 observers smell demonstrator.

Observers

Rat pups O_2 smell O_1 rats after O_1 rats have eaten hot dog.

Generation 2 O_2 eating hot dogs.

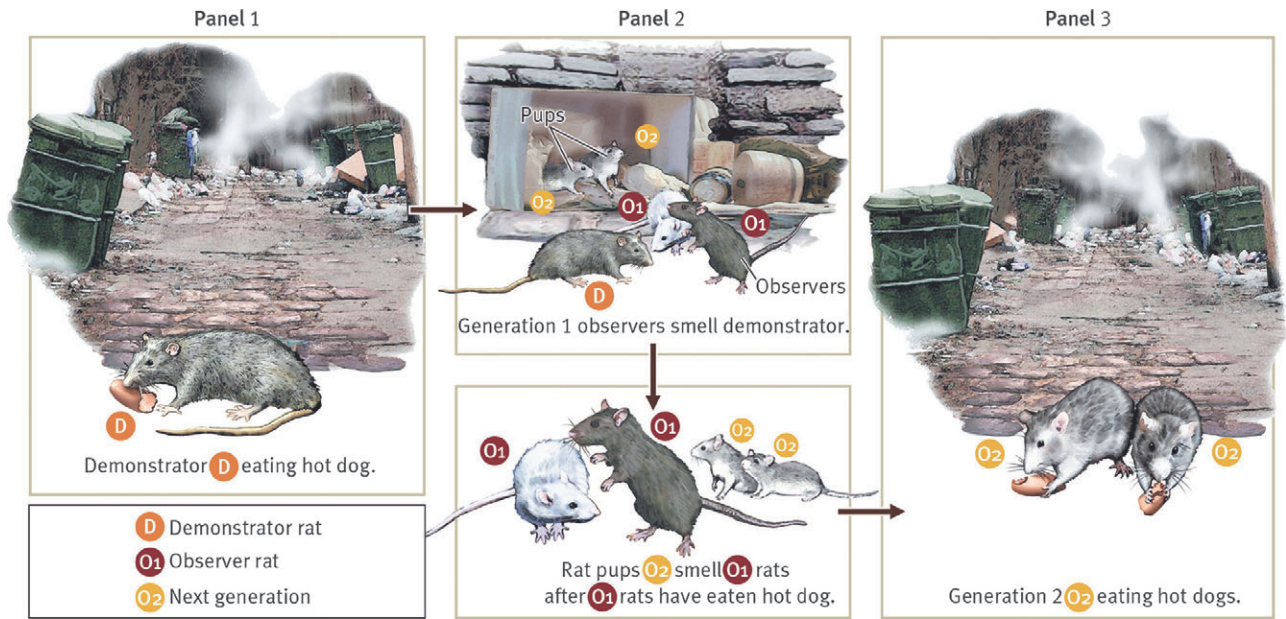D Demonstrator rat
O_1 Observer rat
O_2 Next generation

FIGURE 1.16. **A role for cultural transmission.** In panel 1, a rat eats a new food type (hot dog). When this rat (D for demonstrator rat) returns to its nest (panel 2), observer rats (O_1) smell the rat and then are more likely to add hot dogs to their diet when they encounter such an item. Multigenerational cultural transmission occurs when rats from the next generation (O_2) smell generation O_1 rats after they have eaten hot dogs and subsequently add hot dogs to their own diet (panel 3).

Cultural transmission is more complicated than individual learning. The information acquired via individual learning never makes it across generations. In contrast, with cultural transmission, if a single animal's behavior is copied, it can affect individuals many generations down the road (see chapter 6).

Suppose adult rat A (in generation 1) adopts a novel, formerly uneaten, type of food into its diet after it smelled this food on a nestmate. Now suppose young individuals (generation 2) in the same colony as rat A add this new food to their diet after they smell it on rat A. When individual A dies, the cultural transmission chain it began may still be in force, as the young individuals that copied rat A will still be around: a culturally learned preference in generation 1 may make it to generation 2 (Figure 1.16). If generation 3 individuals learn from generation 2 individuals, then the culturally derived preference will have been transmitted across two generations, and potentially so on down the generations (Mesoudi et al., 2006). Cultural transmission itself, in other words, has both within- and between-generation effects (see chapter 6). Understanding the dynamics of cultural transmission can be very complicated. In addition to the within- and between-generation effects just discussed, if there is variation in the tendency to copy the behavior of others, and that variation is due

to certain types of genetic variation, then natural selection can act on the tendency to use culturally transmitted behavior as well.

Conceptual, Theoretical, and Empirical Approaches

As in all sciences, in ethology, every question can be studied using conceptual, theoretical, and empirical approaches (Dugatkin, 2001a, 2001b; Figure 1.17): the best studies tend to use all three of these approaches to one degree or another. In addition to the focus on natural selection, learning, and cultural transmission, the empirical/theoretical/conceptual axis also plays an important role in almost every chapter of this book.

CONCEPTUAL APPROACHES
Conceptual approaches to ethology involve integrating formerly disparate and unconnected ideas and combining them in new, cohesive ways. Generally speaking, natural history and experimentation play a role in concept generation, but a broad-based concept itself is not usually directly tied to any specific observation or experiment.

Major conceptual advances tend not only to generate new experimental work, but also to reshape
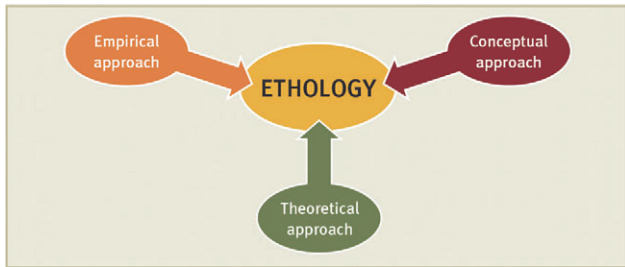
FIGURE 1.17. **Different approaches to ethology.** Ethology can be studied from a conceptual, theoretical, or empirical approach.

the way that a discipline looks at itself. One conceptual breakthrough that has made animal behaviorists rethink the basic way they approach their science is W. D. Hamilton's ideas on **kin selection** (chapter 9). Kin selection expanded the bounds of classic natural selection models by demonstrating that natural selection not only favors behaviors that increase the reproductive success of individuals expressing that behavior, but also favors behaviors that increase the reproductive success of those individuals' close genetic kin (Figure 1.18). Hamilton's work has a strong theoretical component to it as well, but here we will focus on the conceptual nature of this idea.

Hamilton hypothesized that individual 1's fitness is not simply the number of viable offspring it produces (Hamilton, 1964; Figure 1.19). Instead, Hamilton proposed that fitness is composed of two parts: direct fitness and indirect fitness. **Direct fitness** is measured by the number of viable offspring produced, plus any effects that individual 1 might have on the direct descendants of its own offspring: for example, any effect individual 1 might have on the reproductive success of its grand-offspring. **Indirect fitness** effects are measured by the increased reproductive success of individual 1's genetic relatives—not including its offspring and any lineal descendants of offspring—that are *due to individual 1's behavior*. These actions *indirectly* get copies of individual 1's genes into the next generation. An individual's **inclusive fitness** is the sum of its direct and indirect fitness (J. L. Brown, 1980; Hamilton, 1964).

Chapter 9 explores the logic of inclusive fitness in detail, but the kernel of this powerful idea is that, evolutionarily speaking, close genetic relatives are important because of their shared genes—genes inherited from some common ancestor. Imagine for a moment a Mexican jay, a species of birds that has been the subject of much work on inclusive

FIGURE 1.18. **Kin selection and the mother-offspring bond.** In many species, like the vervets shown here, mothers go to extreme lengths to provide for and protect their young offspring. W. D. Hamilton's kin selection ideas provided a conceptual framework for understanding the special relations between close genetic relatives. *(Photo credit: © Vlasenko / Dreamstime)*

fitness (J. L. Brown, 1987). A jay's inclusive fitness is a composite of the number of offspring it has, plus some fraction of the number of offspring it helps a relative raise. Let's say that a jay helps its parents raise an additional brood of two siblings, above and beyond what its mother and father could have raised on their own. Our helper is related to its siblings by a value of 0.5 (see chapter 9 for more on this calculation). By helping its mother (and perhaps father) raise two additional offspring, it has contributed 2×0.5 or the equivalent of 1 offspring to its inclusive fitness. If this is the only help that it gives, our jay's inclusive fitness is calculated by adding its indirect fitness (from helping its parents to raise its siblings) to its direct fitness.
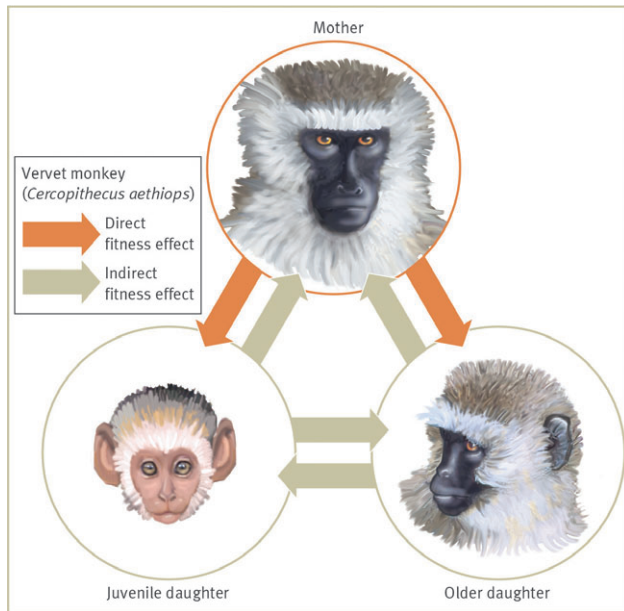
FIGURE 1.19. Two components to fitness. Three vervet monkeys—a mother, her juvenile offspring, and her older female offspring. Mother helping either daughter would be an example of a direct fitness effect. Siblings helping each other, or helping their mother, would represent indirect fitness effects. *(Based on J. L. Brown, 1987)*

Today, one of the first things that ethologists consider when studying social behavior is whether the individuals involved are close genetic kin. This is a direct result of Hamilton's conceptual breakthrough.

THEORETICAL APPROACHES

In the late 1960s and early 1970s, ethologists' understanding of how natural selection operates on animal behavior was greatly advanced with the appearance of sophisticated, usually mathematical, models of the evolution of social behavior in animals and humans. This work is most closely associated with George C. Williams, John Krebs, William D. Hamilton, John Maynard Smith, Robert Trivers, and Richard Alexander. The models that these animal behaviorists developed revolutionized the way that ethologists look at almost every type of behavior they study.

A **theoretical approach** to animal behavior often entails the generation of some sort of mathematical model of the world. During the formative years of modern ethology, much theoretical work focused on animal foraging behaviors (Kamil et al., 1987; Stephens and Krebs, 1986). One foraging-related question of particular interest was "which food items should an animal add to its diet, and under what conditions?"

To tackle this question, a mathematical tool called optimality theory was used (see chapter 11). Optimality theory searches for the best (optimal) solution to a particular problem, given that certain constraints exist in a system.

For example, one might be interested in building a model that examines how animals choose which prey to add to their diet to maximize the amount of energy they take in per unit time foraging. In that case, the amount of daylight could be a constraint (for some foragers), and your mathematical model could include the total amount of time an animal has to search for food (let's label that Ts), the energy (e) provided by a prey type, the time it takes to handle (h) the prey (e.g., to kill and then eat it), and the rate at which prey are encountered (λ). You would then examine how these variables affect foraging decisions made by animals (Figure 1.20). These variables are then built into an algebraic inequality, and solving this inequality produces numerous testable, and often counterintuitive, predictions (see chapter 11). For example, one such model predicts that the decision to add certain prey types into a forager's diet does not depend on how often a predator encounters that prey, but on how often it encounters more preferred prey types.

It is important to realize that theoreticians, including those who work on ethological questions, are not interested in mimicking the natural world in their models, but rather in condensing a difficult, complex topic to its barest ingredients in an attempt to make specific predictions. In that sense, the criticism that a particular theory doesn't match the details of any given system will often be true, but irrelevant. A good theory will whittle away the details of specific systems, but just enough to allow for general predictions that can apply to many systems.

EMPIRICAL APPROACHES

Much of this book is devoted to empirical studies. Empirical work in ethology can take many forms, but essentially it can be boiled down to one of two types—either observational or experimental studies. Both have been, and continue to be, important to the field of animal behavior.

While empirical studies in ethology preceded the work of Karl von Frisch, Niko Tinbergen, and Konrad Lorenz, modern ethological experimentation is often associated with these three Nobel Prize winners,
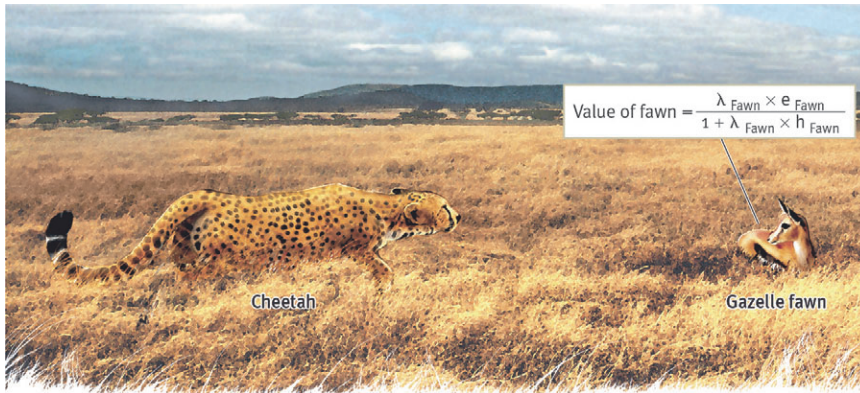
FIGURE 1.20. **Mathematical optimality theory and foraging.** Cheetahs can feed on many different prey items, including a gazelle fawn. Ethologists have constructed mathematical models of foraging that determine which potential prey items should be taken. The value assigned to each prey is a composite of energy value (e), handling time (h), and encounter rate (λ).

$$\text{Value of fawn} = \frac{\lambda_{\text{Fawn}} \times e_{\text{Fawn}}}{1 + \lambda_{\text{Fawn}} \times h_{\text{Fawn}}}$$

each of whom was an extraordinary naturalist who had a fundamental understanding of the creatures with whom he worked and the world in which these creatures lived. They were able to ask fundamentally important questions about animal behavior— questions that could be addressed by a combination of observation and experimentation.

Observational work involves gathering data on what animals do, without attempting to manipulate or control any ethological or environmental variable. For example, I might go out into a marsh and record every action that I see red-winged blackbirds doing from 9 a.m. to 5 p.m. I might record information on foraging behavior, encounters with predators, the feeding of nestlings, and so forth, and be able to piece together how red-winged blackbirds in my study population spend their time. Next, from my observations, I might hypothesize that red-winged blackbirds seem to make fewer foraging bouts when predators are in the vicinity. To empirically examine the relationship between foraging and predation pressure, I might make detailed observations on how much food red-winged blackbirds eat and how many predators I can spot. I could then look for a relationship between these two variables and test the hypothesis that they are correlated.

Let's say that when I graph foraging behavior against predation pressure, I find that they are correlated. Redwings do increase and decrease their foraging behavior as a function of the number of predators in their environment. During periods when lots of predators are around, redwings forage infrequently, but when predators are few and far between, redwings forage significantly more often. What then can I conclude? Is it fair to say that increased predation pressure causes decreased

foraging? No, the data we have so far do not demonstrate causation. I can say that predation and foraging are correlated, but from the existing data, I can't speak to the subject of what caused what— correlation does not equal causation. It might be that some other variable is causing both greater predation pressure and less redwing foraging behavior. For example, it might be that when the temperature rises, redwing predators become more active, but redwings themselves become less active, and so forage less frequently. Increased predation pressure and foraging would still be correlated, but now the former wouldn't be seen as causing the latter; rather, they would both be associated with changes in weather.

In order to examine causality, I must experimentally manipulate the system. I might, for example, experimentally increase the number of redwing predators in area 1, but not in area 2, and see how redwing foraging is affected in these populations (Figure 1.21). I might do so by using trained predators or by simulating increased predation pressure by flying realistic predator models in area 1, but not in area 2. In either case, if redwing foraging behavior decreases in area 1 but not in area 2, I would more confident that increased predation pressure causes decreased foraging in red-winged blackbirds.

Before completing this section on conceptual, theoretical, and empirical perspectives in ethology, we need to address one more question—whether there is any natural ordering when it comes to the theoretical and empirical approaches. Does theory come before or after empirical work? The answer is, "It depends." Good theory can precede or postdate data collecting. On some occasions, an observation or experiment will suggest to a researcher that the results obtained call for a mathematical model of behavior to

FIGURE 1.21. **Observation and experimentation.** Imagine your observations led you to predict that red-winged blackbirds will decrease foraging when under predation pressure. To experimentally examine causality, you could allow a trained falcon to fly over a red-winged blackbird area and observe how its presence affects the amount of foraging.

be developed. Models of reciprocity and cooperation, for example, originally emerged from observations that many animals appeared to sacrifice something in order to help others. Given that natural selection should typically eliminate such unselfish actions, the observations cried out for mathematical models to explain their existence. Mathematical models were then developed, and they provided some very useful insights on this question, as well as stimulating more empirical work.

In turn, theoretical models can inspire empirical studies. The foraging models discussed earlier in the chapter preceded the large number of empirical studies on foraging that ethologists and behavioral ecologists continue to undertake. While it is true that ethologists have long studied what and when animals eat, controlled experimental work designed to test specific predictions about foraging were initially spurred on by the theoretical work in this area. Regardless of whether theoretical work predates or postdates empirical work, however, a very powerful feedback loop typically emerges wherein advances in one realm (theoretical or empirical) lead to advances in the other realm.

An Overview of What Is to Follow

Following this chapter are five "primer" chapters that provide an overview of natural selection, phylogeny, and animal behavior (chapter 2);

hormones, neurobiology, and animal behavior (chapter 3); molecular genetics, development, and animal behavior (chapter 4); learning and animal behavior (chapter 5); and cultural transmission from an ethological perspective (chapter 6). The topics reviewed in the primer chapters are intertwined in the remaining eleven chapters, which cover sexual selection (chapter 7), mating systems (chapter 8), kinship (chapter 9), cooperation (chapter 10), foraging (chapter 11), antipredator behavior (chapter 12), communication (chapter 13), habitat selection and territoriality (chapter 14), aggression (chapter 15), play (chapter 16), and animal personalities (chapter 17). In addition, studies of our own species, *Homo sapiens*, are woven into the fabric of many chapters. In this way, the reader receives a truly integrative view of animal (nonhuman and human) behavior.

Interview with Dr. E. O. Wilson

The 25th anniversary edition of your classic book *Sociobiology*, **a landmark book in the field of animal behavior, was published in 2000. What prompted you to write** *Sociobiology*?

In the 1960s, as a young researcher working in the new field of population biology, which covers the genetics and ecology of populations of organisms,

I saw the logic of making that discipline the foundation of the study of social behavior in animals. At that time a great deal was known about societies of bees, ants, fish, chimpanzees, and so forth, but the subject largely comprised descriptions of each kind of society in turn, and with few connections. There had been little effort to tie all that information together. I had the idea of analyzing animal societies as special kinds of populations, with their characteristics determined by the heredity of behavior of the individual members, the birth rates of the members, together with their death rates, tendency to emigrate or cluster, and so forth—in other words, all the properties we study and put together in analyzing ordinary, nonsocial populations.

Sociobiology as a discipline grew from this idea and was born, not in my 1975 book with that name (*Sociobiology: The New Synthesis*), but in my 1971 *The Insect Societies*. In this earlier work I synthesized available knowledge of the social insects (ants, termites, the social bees, and the social wasps) on the base of population biology. I defined the term *sociobiology* that way, and predicted that if made a full unified discipline it would organize knowledge of all animal societies, from termites to chimpanzees. In *Sociobiology: The New Synthesis* I added the vertebrates to the social insects (and other invertebrates) to substantiate this view, then in the opening and closing chapters, the human species. In the latter chapters, I suggested that sociobiology could (and eventually would) serve as a true scientific foundation for the social sciences. This was a very controversial notion then, but it is mainstream today.

What do you see as *Sociobiology's* legacy to date?

The legacy of *Sociobiology*, which took hold and generated interest and discussion as *The Insect Societies* never could, is indeed the discipline of sociobiology, with journals and many new lines of research devoted to it. This advance was greatly enhanced by the rapid growth of studies on animal communication, behavioral ecology, and, in population genetics, kin selection. Of ultimately equal and probably even greater importance, it showed how to create a link of cause-and-effect explanation between the natural sciences, including especially the study of animal social behavior on the one side and the social sciences on the other.

What sort of debt do ethologists owe Charles Robert Darwin?

Ethologists owe an enormous debt to Darwin, by encouraging the deep and now well-established concept that instincts are biological traits that evolved by natural selection. A word on terminology is worth introducing here. *Ethology* is the systematic (i.e., scientific) study of the behavior of animals (including, by extension, humans) under natural conditions. *Sociobiology* is the study of the biological basis of all forms of social behavior and social organization in all kinds of organisms, including humans, and organized on a base of ethology and population biology. *Evolutionary psychology* is a spin-off of both ethology and sociobiology, including both social and nonsocial behavior with special links to traditional studies of psychology.

After Darwin, whose work has had the most profound impact on the scientific study of animal behavior?

In 1989 the Fellows of the International Animal Behavior Society voted *Sociobiology: The New Synthesis* the most influential book on animal behavior of all time. The most important individual discoveries of all time would have to include sign stimuli, ritualization, the multiple modalities of nonhuman communication, the neurological and endocrinological basis of many forms of behavior, and the amazingly diverse and precise manifestations of kin selection.

Why should a talented undergraduate studying biology care about animal behavior?

Animal behavior is of course a fundamental and extraordinarily interesting subject in its own right. But it is also basic to other disciplines of biology, all the way from neuroscience and behavioral genetics to ecology and conservation biology.

Why should social scientists pay attention to what is happening in the field of animal behavior? What can they gain by doing so?

The social sciences desperately need biology as their foundational discipline, in the same way and to the same degree as chemistry needed physics and biology needed chemistry. Without biology, and in particular genetics, the neurosciences, and sociobiology, the social

sciences can never penetrate the deep wells of human behavior; they can never acquire the same solidity and explanatory power as biology and the other natural sciences.

You and Bert Hölldobler won a Pulitzer prize for *The Ants*. Why have you devoted so much time and effort to studying this taxa?

There are two kinds of biologists: those who select a scientific problem and then search for the ideal organism to solve it (such as bacteria for the problems of molecular genetics), and those who select a group of organisms for personal aesthetic reasons and then search for those scientific problems which their organisms are ideally suited to solve. Bert Hölldobler and I independently acquired a lifelong interest in ants as children, and added science to that fascination later.

You have written much on the subject of conservation biology. How does work in animal behavior affect conservation biology studies, and vice versa?

The understanding of animal behavior is crucial to conservation biology and its applications. Consider how important to ecosystems and species survival are the behaviors of mating, territorial defense, dispersal, pollination, resource searching, and predation. To be successfully grasped, these phenomena have to be studied in an organized, scientific manner, not just added haphazardly to conservation strategies.

What do you believe will be the most important advance in animal behavior in the next twenty-five years?

My prediction: the complete linkage of a number of complex behavior patterns from genes to proteonones to sensors and neuron circuits to whole patterns of behavior. Biologists will learn how to scan the whole range of levels of organization to account for each animal behavior in turn.

Will animal behavior be a discipline fifty years from now, or will it be subsumed by other disciplines?

Today the study of animal behavior is the broad gateway to a wide array of different modes of study. But in fifty years—who knows? It may well be subsumed by other disciplines, some as yet undefined.

Dr. E. O. Wilson is an emeritus professor at Harvard University and a member of the National Academy of Sciences. He is the recipient of two Pulitzer prizes, and his book *Sociobiology* (Harvard University Press, 1975) is regarded as one of the most important books on evolution and behavior ever written.

SUMMARY

1. The scientific study of animal behavior, which dates back hundreds (if not thousands) of years, is called *ethology*.

2. The process of natural selection, the ability of animals to learn, and the process of cultural transmission are all important concepts for developing an integrative view of animal behavior.

3. Niko Tinbergen suggested that ethologists ask four types of questions: What are the immediate causes of behavior? How does behavior change as an animal develops and matures? How does behavior affect survival and reproduction? How does behavior vary as a function of evolutionary history?

4. Ethologists examine behavior from a proximate perspective by examining immediate causes of behavior, and from an ultimate perspective by examining evolutionary factors responsible for a behavior.

5. Work in ethology, like in all scientific fields, can be conceptual, theoretical, or empirical. Empirical work can be further subdivided into observational and experimental studies.

DISCUSSION QUESTIONS

1. Take a few hours one weekend day and focus on writing down all the behavioral observations you've made, as well as any, even indirect, behavioral hypotheses you have constructed over the last 24 hours. Think about your interaction with both humans and nonhumans. How has your very brief introduction into ethology reshaped the way you observe behavior?

2. Why do we need a science of ethology? What insights does this discipline provide both the scientist and the layperson?

3. Imagine that you are out in a forest, and you observe that squirrels there appear to cache their food only in the vicinity of certain species of plants. Construct a hypothesis for how this behavior may have been the product of (a) natural selection, (b) individual learning, and (c) social learning.

4. Why do you suppose that mathematical theories

play such a large part in ethology? Couldn't hypotheses be derived in their absence? Why does mathematics force an investigator to be very explicit about his or her ethological hypotheses?

5. Discuss the pros and cons of each of the bulleted definitions of behavior in this chapter.

SUGGESTED READING

Alexander, R. D. (1974). The evolution of social behavior. *Annual Review of Ecology and Systematics*, *5*, 325–383. This paper, published just before E. O. Wilson's *Sociobiology*, provides the reader with a good overview of how one approaches behavior using "natural selection thinking."

Dewsbury, D. (Ed.) (1985). *Studying animal behavior: Autobiographies of the founders*. Chicago: University of Chicago Press. A fascinating introduction to the lives of early ethologists.

Galef, B. G. (2009). Strategies for social learning: Testing predictions from formal theory. *Advances in the Study of Behavior*, *39*, 117–151. In this review, Galef formalizes predictions from social learning models, and puts those models to the test.

Levitis, D. A., Lidicker, W. Z., & Freund, G. (2009). Behavioural biologists do not agree on what constitutes behaviour. *Animal Behaviour*, *78*, 103–110. A review of different definitions of the word *behavior*.

Strassmann, J. E. (2014). Tribute to Tinbergen: The place of animal behavior in biology. *Ethology*, *120*, 123–126. An modern overview of proximate and ultimate causation as applied to behavior.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift fur Tierpsychologie*, *20*, 410–440. A classic paper that outlines Niko Tinbergen's approach to animal behavior.