Principles of ANIMAL COMMUNICATION

Second Edition

Jack W. Bradbury | Sandra L. Vehrencamp

Cornell Lab of Ornithology and
Department of Neurobiology and Behavior
Cornell University

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Chapter 1

Signals and Communication

Overview

The evidence that animals communicate is all around us. But what accounts for the conspicuous diversity of signals that animals seem to be using? Is there any order or pattern to this diversity? Research on animal communication seeks to identify general principles from biology, the physical sciences, and economics that together can explain why one animal species relies on one type of signal and another animal species relies on a different type of signal. In this chapter, we provide an overview of the important principles and how they will be presented in more detail later in this book.

Why Study Animal Communication?

Do animals communicate?

Any observant person knows that animals communicate (**Figure 1.1**). When your dog hears a cat jump up onto your porch at night, it begins barking and soon, all the neighborhood dogs are also barking despite the fact that they cannot possibly have heard the cat's soft thump. It does not take musical training to notice that when one songbird in your backyard starts singing, its neighbors not only sing back, but may even match the theme sung by the first bird. If you are good at imitating bird songs by whistling, you can easily provoke a currently silent cardinal, mockingbird, or titmouse to start singing back at you, often with a similar theme. Given these widely experienced examples, most people presume that the roars of lions, the chirping of crickets, the deafening choruses of cicadas, and the songs of whales are also used by these animals for communication.

Sound production is just one clue that animals communicate. Anyone who has had to wait interminably while their dog meticulously sniffed the roots of a tree before finally adding its own urine cannot help but surmise that the dog is checking out odor signals left previously by other dogs and then leaving its own "message." Surely the bright red coloration of the male northern cardinal, which makes it extremely conspicuous to predators against a green background, has to serve some compensatory utility to the birds bearing it. The color might provide insurance that males and females can recognize members of their own species for mating; serve as an early morning advertisement to potential intruders that a territorial owner has survived another night; or create a plumaged "canvas" that helps females to assess the health of potential mates. Sound, odor,

(A)

(B)

(C)

FIGURE 1.1 Commonly encountered examples of animals communicating (A) Male Northern Mockingbird (*Mimus polyglottos*) singing to defend its breeding territory from other males and attract a female mate. (B) Domestic cat (*Felis catus*) performing a defensive visual display when threatened. (C) Domestic dog (*Canis lupus familiaris*) urinating on a tree to leave scent mark for other dogs in the neighborhood.

and visual signals are only some of the various stimuli that we find animals using to communicate.

So, if most reasonable people have already concluded that animals communicate, what else is there left to say about the subject?

Diversity and principles

Diversity is a ubiquitous property of nature. The major task of science is making sense of this diversity by extracting and then verifying general principles that singly or in combination explain most of the variation in a particular aspect of nature. As demonstrated by the earlier examples and those in **Figure 1.2**, animals can show enormous diversity in whether, when, and how they communicate. Rabbits barely make a sound except when grabbed by a predator, whereas male hammer-headed bats devote two thirds of their anatomy and a quarter of their waking hours to producing honking calls that attract females. What basic principles can explain these differences? Or put another way, what principles might we discover by comparing the sound signals of rabbits and hammer-headed bats?

One of the expectations of modern science is that principles discovered in one discipline will be compatible with principles in other disciplines. Biologists invoke principles of acoustic physics to explain why body size ultimately constrains the pitch of animal communication sounds. Similarly, the evolutionary principle of kin selection, in which organisms favor cooperation with genetic kin, has proved to have significance in medicine [58]. Studies of animal communication must integrate and in some cases can help refine principles previously identified in other disciplines. As we shall see in this book, an understanding of the diversity observed in animal communication requires the melding of principles from physics, chemistry, genetics, physiology, evolutionary biology, taxonomy, behavioral ecology, community and population ecology, informatics, and economics. In turn, principles derived from studies of animal communication are providing new insights and tools for fields such as conservation biology and wildlife management, pest control, linguistics, developmental biology, immunology, epidemiology, neurobiology, and psychology (**Figure 1.3**).

Beyond the pursuit of scientific inquiry and tests of concordance across disciplines, even a minimal knowledge of animal communication principles can enrich anyone's daily life. It is hard to find a location on earth where one is not exposed to the signals of communicating animals. Knowing what they are doing, why they are doing it, and why they do it the way they do makes a walk in the woods or a snorkeling trip on a shallow reef a far richer experience. A birder so preoccupied with checking off newly sighted species that she fails to stop and attend to what the birds are doing is truly missing half the story. Even when one cannot see a forest bird, one can often hear it exchanging vocalizations with other birds. Why is the bird using such low-frequency sounds? Why does it use such a slow tempo? Is it defending a territory or attracting a mate? If one knows what questions to ask, it is amazing how much more one can get out of that walk or snorkeling dive. You do not need fancy equipment to eavesdrop on most of the communicating animals that you are likely to encounter. Human senses may not be as well tuned to every animal

FIGURE 1.2 **Diversity in animal color signal patterns** A sample of the head and facial markings on males of different species of jumping spiders in the genus *Habronattus*. Although very closely related, these species show an amazing diversity of color patterns. A similar figure could be constructed for closely related species of crabs, butterflies, fish, lizards, or birds. (A) *H. pugillis*; (B) *H. tarsalis*; (C) *H. americanus*; (D) *H. sansoni*; (E) unnamed species 1; (F) unnamed species 2.

signal as those of the intended receivers, but we are amazingly well equipped to monitor a very broad range of stimuli, more than enough to make a knowledgeable person's walk in the park the highlight of the day.

Web Topic 1.1 ***Animal communication and science education***

Because most students naturally like animals, and animal communication integrates so many disciplines, the topic can be used as an entry point for science education in middle and high school curricula. Here we provide some background and relevant links.

Cues, Signals, and Signal Evolution

Cues

All animals have **sense organs**. These provide current **information** about the physical, ecological, and social conditions surrounding the animal. This information is then used by the animal's brain and associated systems to adjust physiological states and refine decisions about subsequent actions. Most sense organs do not measure external conditions directly, but instead monitor **cues**. Cues are assessable properties that are at least partly correlated with a condition of interest. While one animal might rely on thermoreceptor neurons that directly measure ambient temperatures, others may attend to cues such as visible heat waves rising from the substrate or the dryness of an exposed tongue. Many conditions of interest, such as the health of a potential mate or the intentions of a nearby predator, are nearly impossible to measure directly. Instead, animals have evolved sense organs that are tuned

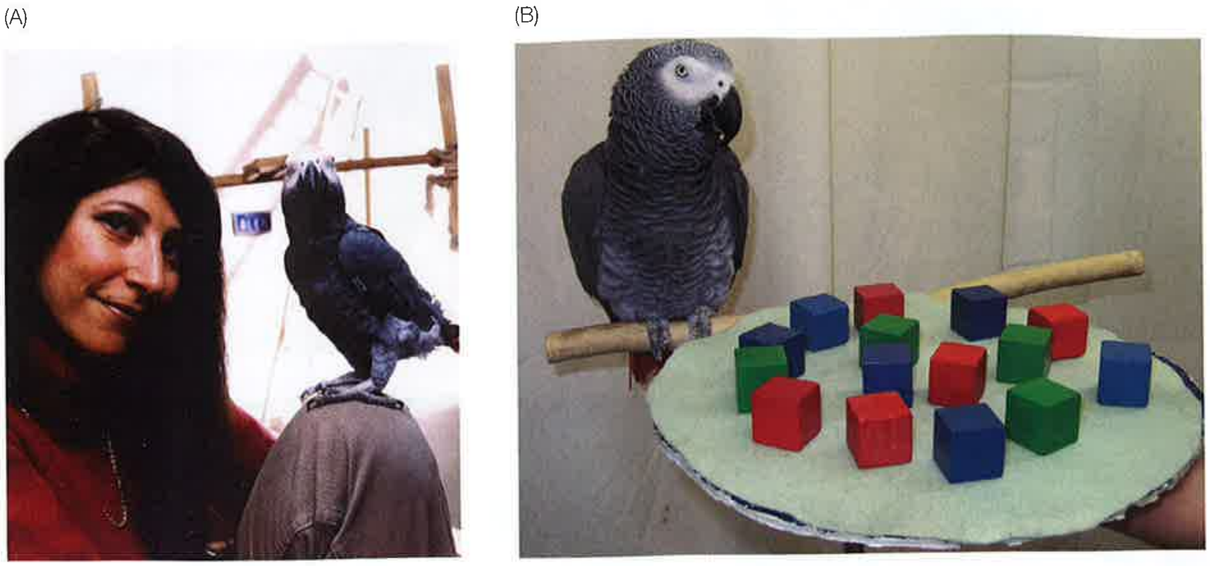

FIGURE 1.3 Studying the interface between animal communication and cognition (A) Dr. Irene Pepperberg and the late Alex, an African Grey Parrot (*Psittacus erithacus*). Alex was raised to respond to and reply with human speech in meaningful ways. In (B) Alex is shown being asked to identify the quantity of a specific set of objects defined by their shape and color. At his death, he could identify over 100 different items, including locations, foods, and objects made of various materials, colors, and shapes; assign items to labeled categories; understand concepts such as object permanence, same versus different, and bigger versus smaller; count to eight; recombine the elements in his labels to form other novel labels; and say "None" if asked to find something that was not there. This work demonstrated that parrots can use complex communication to perform cognitive tasks with a very high rate of accuracy [68]. How parrots might use these abilities in the wild remains to be studied.

to one or more cues correlated with those conditions. Few cues are perfectly correlated with conditions of interest, so an animal is often faced with a trade-off between relying on a cue that is easy to measure but imperfectly correlated with a condition of interest versus trying to measure the condition directly. In the majority of cases, animals opt for the most quickly evaluated cues despite their imperfect correlations with the properties of interest.

Humans monitor cues, just like other animals. When it is hot, and our sweat does not evaporate, we conclude that the humidity is probably high. We do not have direct humidity sensors and so rely on a related cue. We assume that a person with a wrinkled face and gray hair is probably old. However, there are diseases that can produce wrinkles and gray hair in younger people; the correlations between the cues (wrinkles and gray hair) and the property of interest (age) are imperfect. However, they are usually good enough for us to continue to monitor these traits as useful cues. We even make important behavioral decisions about how to interact with others based upon such imperfect correlations.

Animals behave similarly. Many species have sensory organs and associated brains that can track changes in ambient cues with great speed and accuracy. Simultaneous input from sensors monitoring different but related cues facilitates cross-checking to correct for imperfect correlations between any one cue and conditions. Mammalian predators combine olfactory, visual, and auditory cues to detect and locate prey. Interacting animals usually alter their behaviors more rapidly than the nonbiological environment changes. It thus pays for animals to monitor the cues that predict future actions of nearby conspecifics, predators, and prey more often and more accurately than they monitor atmospheric conditions. Most animals stop other activities, alter their posture, or otherwise prepare themselves before making a significant change in their actions. Observer animals can watch for these subtle antecedents and use them as cues to the subsequent behaviors of others. In fact, monitoring the behavioral cues generated by other nearby animals (including predators and prey) is the dominant task for the sensory organs and brains of most animal species.

Signals

Signals are stimuli produced by a **sender** and monitored by a **receiver**, to the average net benefit of both parties. Like cues, signals are correlated with conditions outside the receiver and thus provide potential information to it. Unlike cues, which are generated either inadvertently or for purposes other than communication, the function of most signals is to provide information to another animal. If this provision of information benefits both sender and receiver, mutations in either party that refine and improve the process will be favored over evolutionary time. We thus might expect that the correlations between signals and their referent conditions will usually be higher than the correlations between cues and conditions. As we shall see, this is often true, given sufficient evolutionary time and a commonality of interests between sender and receiver.

In practice, sender and receiver may not have identical interests, senders can err in their evaluation of the condition about which they are signaling, and noise and other factors may distort signals during propagation. This does not necessarily mean that communication is a waste of time. On the contrary, even a slight net benefit to one or both parties may favor the continued production and reception of imperfect signals. If the costs of further improvement by either party are higher than the benefits, evolution will not favor refinement, and the animals will continue to communicate imperfectly. This fact has generated some confusion in the study of animal communication about when senders are or are not deceiving receivers. True **deception** occurs when a sender produces a signal whose reception will benefit it at the expense of the receiver regardless of the condition with which the signal is supposed to be correlated. An observation that a sender produces a "wrong" signal, given the actual state of the referent conditions, could be an example of deceit, but it could also reflect economics that favor continued reliance on imperfect signals [7, 10, 34, 56, 75, 89]. Determining whether a misleading signal is a case of true deceit or imperfect signaling invariably requires more refined data, careful economic and sensory analysis, and often, a critical experiment based on the relevant principles. Research has shown that misleading signals are most often the outcome of economic constraints on signal perfection and only rarely due to deceitful intent on the part of the sender.

Many actions by animals have both signaling and nonsignaling functions and thus are not easily assigned to discrete categories. While the song of a nightingale or the dance of a honeybee fit most scientists' definition of a signal, other behaviors do not fit the definition as neatly. Philosophers of science spend considerable time debating definitions for natural phenomena with the hope that everything can be clearly assigned to one discrete category or another. Evolution tends to favor economics over philosophy: if a single animal action can efficiently serve multiple functions, it is often favored by natural selection. A threat display at close range may function both to place the sender in a better tactical position for attacking its opponent and provide information to the opponent about the sender's estimation that it would win an escalated fight [84, 85]. Grooming of one primate by another provides hygienic benefits and information to both the recipient and any nearby observers about the groomer's perceived affiliations with the recipient [86]. Males of many birds provide food samples to courted females; this provides nourishment that may later contribute to egg production, but also provides information to the female about the courting male's future abilities as a provisioning parent [61]. These actions, which combine signaling and nonsignaling behaviors, are not easily assigned to tidy, discrete definitions. Not surprisingly, there is continued debate over suitable definitions of biological signals, information, and communication [4, 10, 23, 30–33, 35, 36, 38, 51–53, 55, 59, 60, 71, 76–79, 82, 83].

In this textbook, we shall invoke a broad and quantitative (as opposed to discrete) definition of signals. We accept that actions such as threat displays, shared grooming, and courtship feeding can have both tactical and signaling functions, and that the impacts of these combined functions on both an actor and a recipient of the action can vary continuously. This approach has the advantage of expanding the range of phenomena that can be considered in trying to extract general principles. At the same time, it makes the detection and quantification of signal content in an action more challenging. A careful examination of the contexts in which an action is performed and its economic consequences, followed by informed experiments and manipulations, can be very helpful in evaluating signal content. For example, roosters often emit a specific call when they find food. This is not some uncontrollable expression of excitement [45, 71], but instead is given most often when hens are nearby [14, 15, 44]. Males will even pick up and present samples of food to nearby females [14, 44, 80, 81]. The economic benefit of this selective calling for the rooster is greater access to hens for mating [87]. Given this motivation, roosters will sometimes call falsely and proffer inedible objects to hens [24, 46]. Similar economic data have been used to confirm and quantify signal content in a variety of actions and a variety of taxa [2, 3, 9, 11, 12, 19, 40, 41, 47, 48, 57, 62, 63, 66, 67, 69, 70, 72]. We shall provide other examples in later chapters, where contexts, economics, and experiments combine to demonstrate and quantify the signal content in animal actions.

Web Topic 1.2 ***Information and communication***
Some scientists feel that the role of information provision should be downplayed in definitions of animal communication. A few even recommend elimination of the term when applied to animal interactions. Here, we outline the case for information as a useful and even key concept in understanding the evolution and diversity of animal signals.

Signal evolution

Since most animals have already invested inordinately great amounts of time, energy, and anatomical specialization in monitoring cues generated by other animals, the evolution of signaling is relatively easy. Consider a female bird that routinely examines the plumage of potential mates for ectoparasite infestations. She might do so to avoid becoming infected during mating contact, or because she is looking for evidence of parasite-resistance genes in males that could be passed on to her offspring. Relevant cues that he is unhealthy might include excessive feather dust, missing vanes and elements in key feathers, lethargy, slow reaction times, or discolored skin. If a mutant male with low parasite infestations adopts a posture or activity that makes the female's assessment of his plumage easier or more accurate, he is more likely to be selected for mating. His many offspring will carry the genes that promote this display behavior as well as the genes of his mate, who responded to it. As a result, the trait could become increasingly common in successive generations. While males

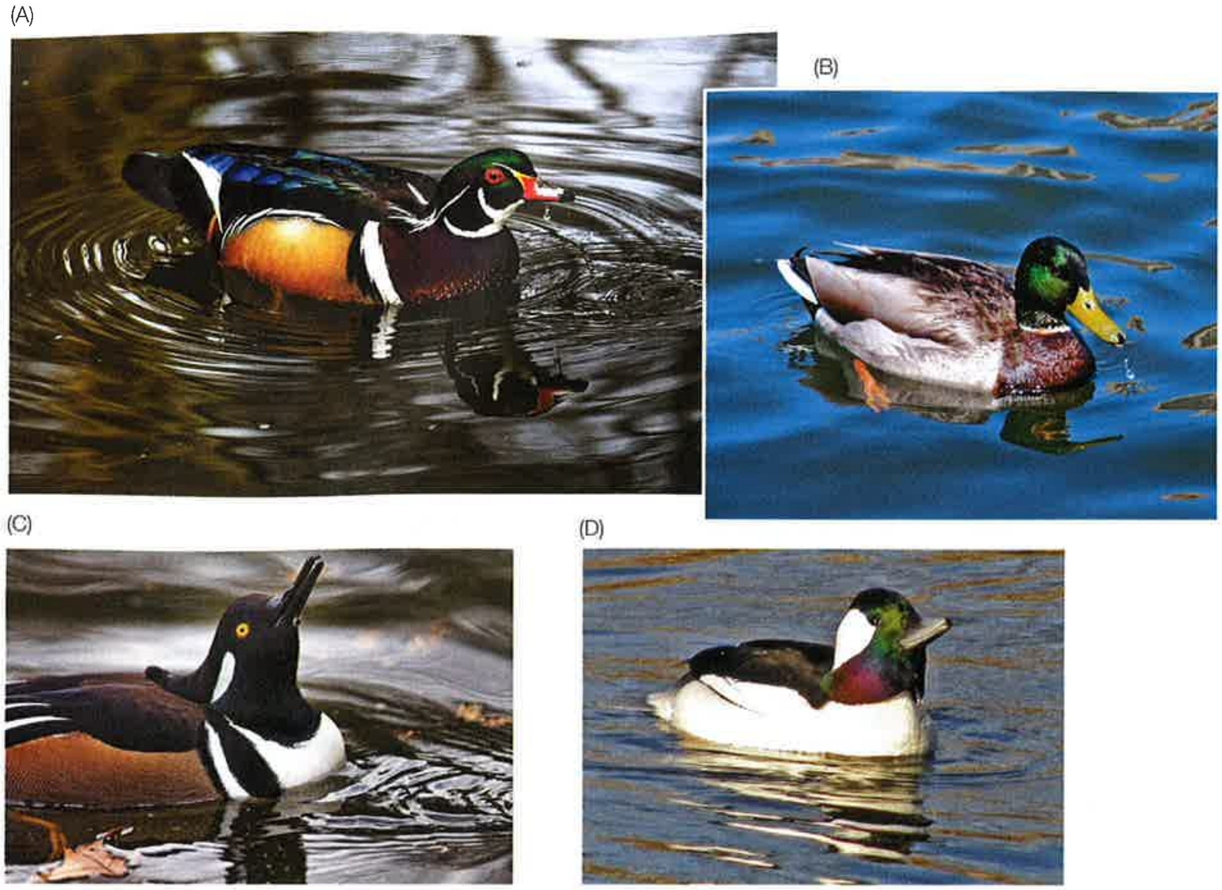

FIGURE 1.4 Evolution of display from behavior with other functions Most waterfowl drink by scooping up water in the bill and raising the beak high enough that the water runs into the throat. One puzzle is why waterfowl that have just spent extensive periods sitting on the water and filtering out food items appear to drink and to do so repeatedly. Why would they drink when it seems they have had plenty of opportunity for accumulating water during feeding? It turns out that many species have ritualized the drinking movements into a display that is used to mediate conflicts, courtship, and social integration [37]. Careful observation shows that the motions are similar but the contexts and functions are quite different. Here we see examples of ritualized drinking displays by a male (A) wood duck (*Aix sponsa*), (B) mallard (*Anas platyrhynchos*), (C) hooded merganser (*Lophodytes cucullatus*), and (D) bufflehead (*Bucephala albeola*).

with higher parasite loads penalize themselves when they perform the display, once enough males perform it, females should reject not only males that clearly have high infestations, but also males that refuse to perform the display. If the only way to obtain a mating is to display, the behavior becomes obligatory in all males if they wish to reproduce.

In this example, we assumed that the mutation generated a new posture or action. However, it is not necessary that the new behavior be entirely novel. As we noted earlier, most animals adopt postures or perform subtle actions that precede major changes in behavior. A careful watcher can use these cues to anticipate what the animal is likely to do next. If it pays both parties to have the watcher anticipate the actor's next behavior, mutations that favor exaggeration of the actor's cue posture or action might be favored over evolutionary time. This is surely how many displays performed during aggressive encounters have evolved. In the case of the hypothetical interaction just discussed, the antecedent of the male's display might simply be normal preening activities. Birds spend considerable effort to keep their feathers cleaned, arranged, and oiled. Any of the normal hygiene activities of the male could be exaggerated slightly to make it easier for a nearby female to assess his ectoparasite load. Subsequent mutations might exaggerate this action further and shape the preening behavior such that the exaggerated form is used only when receptive females are nearby; when they are absent, the male might continue to use the original unexaggerated form of preening. Preening is just one of many examples of animal behaviors that have both nonsignaling and signaling versions (**Figure 1.4**). Such examples have proved very useful in understanding the process of signal evolution.

We shall discuss how signals evolve in Chapter 10. But at this stage, the general point is that the extensive monitoring of cues by animals sets the stage for the subsequent evolution of signals. Usually, the relevant cues are linked to the same condition that is subsequently the focus of the signals.

However, there are cases in which a mutant sender produces a stimulus that mimics some cue that is already of major interest to receivers but fails to provide any new information. Examples might be sender production of a color or sound that receivers typically associate with food or predators. A mutant sender could exploit this general sensitivity of the receiver to attract the latter's attention and then try to induce it to behave in ways that benefit the sender. This type of sensory exploitation usually leads to stable communication only if receipt of the signal provides some incidental benefit to the receiver, or if subsequent sender mutations cause the signal to become correlated with information that the receiver can use. For example, a male display that by chance exploits existing female sensory biases might benefit the male by catching the attention of more females, while ameliorating the task faced by females of finding and comparing potential mates. Whether an incipient signal exaggerates a cue already being monitored or instead exploits a sensory bias to get another animal's attention, prior cue monitoring is the key preadaptation for the evolution of communication.

Principles and Animal Communication

Luckily, explanations for the observed diversity in animal communication systems do not require that we invoke principles from all of the relevant disciplines at once. Instead, it is possible to divide up relevant principles into general topics, and then tackle the topics serially. Because signals evolve from cue monitoring, the **physiological mechanisms** with which senders develop signals and receivers process them are those that the animals are already using before signals evolve. These physiological precursors of communication have been shaped over prior evolutionary time by constraining principles of physics and chemistry. The **physical constraints** differ depending upon the animals' ambient medium (air, water, solid substrates); habitat (e.g., forest versus open plains); circadian rhythm (diurnal versus nocturnal); mobility; position in the food web; and body size. Different physiological preadaptations for monitoring cues in these different situations are a major source of diversity in animal communication systems and constitute the focus of Chapters 2–7 in this book.

A second source of diversity in animal communication systems arises from the taxonomic affiliations of each species. Without the effects of historical and phylogenetic constraints, we might expect all species, regardless of taxon, to utilize similar signals when the physical, chemical, and functional contexts are identical. In practice, this is not what is found. Most birds have wings and can fly (although a few groups have lost this ability), and most mammals have four legs but no wings (although one group has turned the front legs into wings, and a few others have turned theirs into flukes and flippers for swimming). As a result of these different heritages, flight displays are not an option for gorillas (at least over the time scales considered in this book), whereas they are a common signal among many bird taxa. It is thus important when considering the contributions of physical, chemical, and physiological principles to animal signal diversity to also specify the taxonomic limitations on options. We have noted these taxonomic constraints throughout Chapters 2–7.

The third source of diversity in animal signal systems concerns the **economics of communication** (**Figure 1.5**). A signal emitted by a sender should be sufficiently correlated with conditions of interest to the receiver that it pays the receiver to attend to the perceived signal and incorporate the new information into its future decisions and physiological states. Similarly, a sender should only send a signal if its reception makes a receiver more likely to behave in ways that benefit the sender. In short, both sender and receiver should benefit, at least on average, by communicating.

The economics of communication can be both subtle and complicated. Both senders and receivers will pay costs for participating in communication: these costs include energetic, temporal, and anatomical investments; increased exposure to predators, disease, and parasites; and the risks of being deceived or manipulated by other parties. If the correlations between the condition being monitored and the signals perceived by the receiver are sufficiently poor that the average costs exceed the average benefits for either party, there will usually be no communication. The tightness of these correlations can vary with the accuracy of the sender's assessment of the conditions of interest, the modalities of the signals used (sound, light, odor, touch, electrical fields), the physics and chemistry of the environment in which the signals propagate between sender and receiver, and the accuracy with which a receiver can perceive and discriminate between alternative signals. All of these factors are constrained by the differing physiological heritages of each taxon.

Because it would be unrealistic for receivers to insist on perfect cue and signal correlations before making decisions, they usually choose what to do after receiving some intermediate amount of information. Refinement of the communication process above this level would only increase the costs on either or both parties with little if any benefit. The optimal level of signal accuracy can vary depending upon the context in which a given species is communicating. A population of birds living on islands, where predators generally tend to be less common, can likely afford to invest in a higher level of signal accuracy than can a population of the same species on the mainland, where the risks of a predator detecting the signal and attacking the sender or receiver are more severe. Basic principles of optimality economics and information theory have proved very useful in explaining the economic bases of animal signal diversity. These principles are the focus of Chapters 8 and 9.

The fourth source of signal diversity follows from the degree to which sender and receiver have commensurate interests in successful communication. At one extreme, fighting animals have minimal common interests, and one might think that it would not pay to engage in communication at all. In fact, a significant portion of most social species' signal repertoires is dedicated to conflict mediation. As we shall see, the distrust between sender and receiver in aggressive contexts places special constraints on the kinds of signals that are used in these contexts. Partners in cooperative groups such as mated pairs of birds raising offspring, pack hunters, or large flocks or schools sharing predator vigilance might be assumed to have identical interests. However, there is always a temptation to take more than one's fair share of the spoils or let a partner do more of the work. Thus even in apparently cooperative contexts, some conflict of interest is usually present. In fact, the only communication in which there are no potential conflicts of interest occurs when an animal "talks" to itself. An example of this is echolocation by bats and dolphins, in which the animal emits a sound, listens for the echo, and then uses differences between the two to infer the presence of nearby obstacles, predators, or prey.

When sender and receiver experience **conflicts of interest**, it would seem that the optimal level of signal accuracy might degenerate over evolutionary time until it did not pay to communicate. Despite this, animals continue to communicate across the entire spectrum of conflicts of interest. The answer to this puzzle is that receivers facing a conflict of interest often limit responses to those signals that have some **honesty guarantee**. How these guarantees are achieved has been clarified by invoking principles from **evolutionary game theory**. This is a discipline that merges classical game theory from human economics with basic principles from behavioral ecology and evolutionary biology. We introduce the basic ideas of evolutionary game theory and its links to signal evolution in Chapters 8–10, and then review the diversity of mechanisms discovered for ensuring signal honesty over the full range of potential conflicts of interest in Chapters 11–14.

The traditional approach to studies of animal communication focuses on a single sender and a single receiver. To the degree that natural communities of interacting animals can be described by summing up the interactions of each dyadic pair, such approaches to animal communication are sufficient. However, many animals broadcast signals expressly because it pays to contact many receivers at once. This can set off a wave of successive responses that both radiates away from the signalers and feeds back on them in complicated ways. The pooled interactions within the **network** of communicating animals can produce emergent properties that are not predictable from dyadic interactions alone (**Figure 1.6**). The nature of these emergent properties will vary with the physiological heritage, physical and ecological

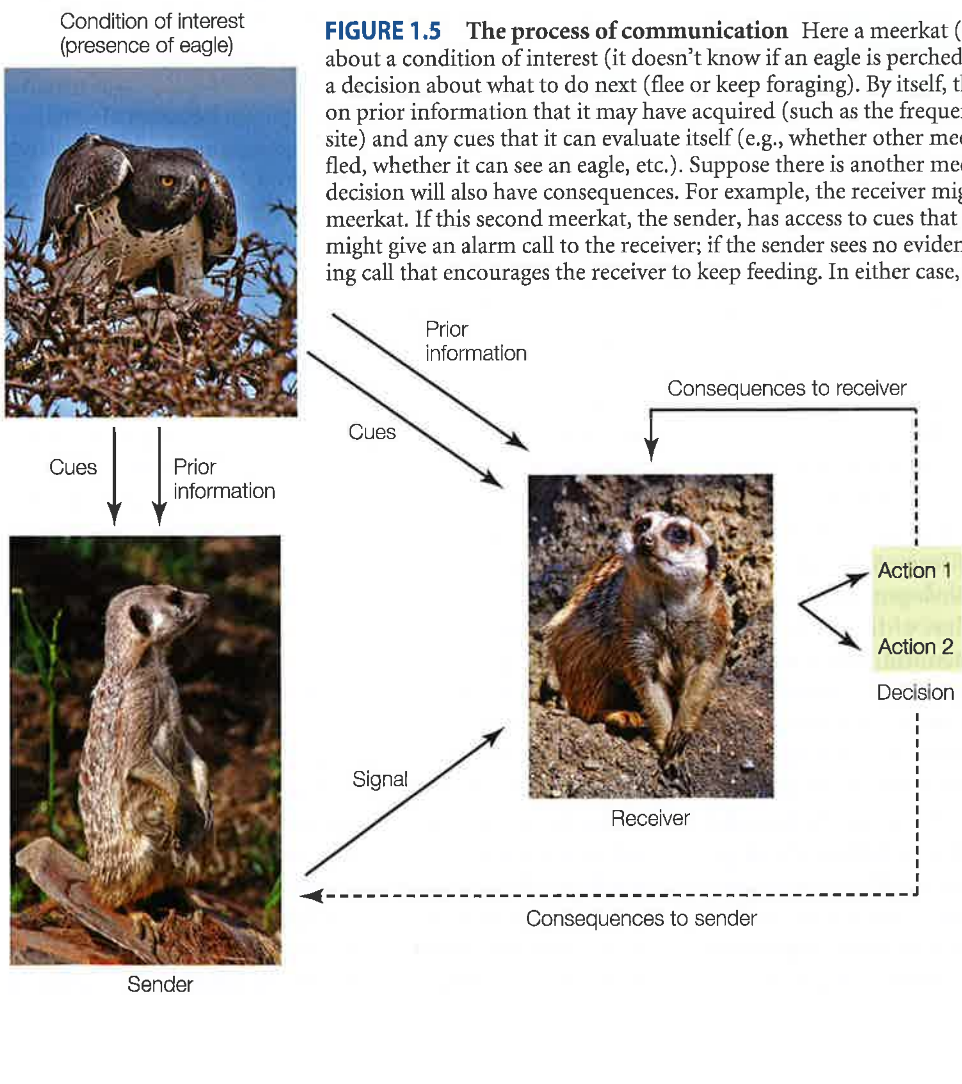

FIGURE 1.5 The process of communication Here a meerkat (the receiver) needs information about a condition of interest (it doesn't know if an eagle is perched nearby or not) before it can make a decision about what to do next (flee or keep foraging). By itself, the receiver has to base its decision on prior information that it may have acquired (such as the frequency with which eagles occur in this site) and any cues that it can evaluate itself (e.g., whether other meerkats and small mammals have all fled, whether it can see an eagle, etc.). Suppose there is another meerkat nearby for whom the receiver's decision will also have consequences. For example, the receiver might be a close relative of the other meerkat. If this second meerkat, the sender, has access to cues that indicate the presence of an eagle, it might give an alarm call to the receiver; if the sender sees no evidence of an eagle, it could give a foraging call that encourages the receiver to keep feeding. In either case, the receiver can combine its prior information, its own cue assessment, and the nature of the signal given by the sender to make a better decision than it would by itself. If the benefits of the receiver making a good decision outweigh both parties' respective costs of giving the signal and attending to it, evolution will favor their participation in this communication.

FIGURE 1.6 Visual signal networks (A) At low tide, each male fiddler crab (*Uca annulipes*) advertises himself and his burrow to females by waving his single grossly enlarged claw. When a female inspects the burrow of a particular male, other males cluster around the site and synchronize both their rate of waving and the phase of their wave display with those of the visited male. This synchrony provides no advantages in avoiding predation or attracting additional females, but is solely an emergent property of the local competition between males [5]. (B) Males of some species of fireflies (here *Photinus carolinus*) synchronize their flashes when attempting to attract female mates [8]. Like the fiddler crabs, the firefly males adjust their display behaviors according to those of their neighbors. In both species, the interactions between a single male and female cannot be considered independently of the presence and activities of neighboring males. The best approach is to study these systems as communication networks.

environment, and the appropriate economics for each taxon. Extraction of the principles governing the diversity of communication networks in animals is still in its infancy, but it is clearly a critical approach that is needed to complete the story. We review current principles of network communication in Chapter 15.

Finally, can the principles elucidated by studying the diversity of animal communication signals pass the test of taxonomic generality? For example, it is now widely recognized that communication occurs in bacteria and archaea, the diverse protist groups, and plants. Do these taxa follow similar rules? Humans are, of course, animals: to what degree are principles extracted by studying animal communication applicable to humans? In Chapter 16, we briefly review recent studies that have sought to extend the principles of animal communication to other taxa.

Principles of Evolutionary Biology

Evolution is increasingly seen as the core concept integrating all of the biological sciences. It is a *theory* in the scientific sense that although there is overwhelming evidence supporting it, scientists remain willing to refine or even refute aspects of the current version should new and persuasive evidence become available. The atomic basis of chemical reactivity and the well-known tenets advanced by Newton for object motion are theories that have been sufficiently tested and confirmed that they are now effectively referred to as *laws* or *principles*. Evolutionary theory has reached the same level of maturity: centuries of research, quantitative and experimental challenges, and tests of consistency across taxa and between disciplines have convinced nearly all scientists that the basic precepts of evolution are as likely to survive further tests as are the laws and principles of physics and chemistry [6, 18, 50, 73]. In this book, we thus refer to these precepts as *principles of evolutionary biology*.

The principles of evolutionary biology are relevant to every aspect of the study of animal communication. The physiological substrates that senders and receivers recruit for communication are considered by evolutionary biology to be **adaptations**: that is, they are likely to be those combinations of traits that in prior generations most effectively promoted their owners' survival and reproduction in their current contexts. Variants that were less effective resulted in early death or reduced reproduction of their owners. The process of differential contribution to future generations is called **sexual selection** when the relevant traits focus on competition for mates within a sex, and **natural selection** otherwise. Since most traits are to some degree **heritable** through **genetic transmission** to progeny, differential offspring production results in some trait combinations becoming more common over successive generations while other traits disappear. This is the process of evolution. Because new variants are continually appearing through **mutations** in the genes affecting traits, selection and evolution are continuing processes.

One evolutionary principle relevant to animal communication is that most traits suitable for signal production or reception are already adapted to specific functions and contexts. This why ears in aquatic animals like fish are likely to have very different structural designs from those in terrestrial animals such as birds. Evolutionary biology does not predict that every trait will be as adaptive as possible. Many traits have multiple effects and selection to improve a trait's effectiveness for the most crucial consequences may result in reduced suitability of the trait for other consequences. In addition, selection can only improve the effectiveness of a trait if mutation provides sufficient variants. Over evolutionary time, there may be adequate mutational variation to optimize the trait given the animal's basic anatomical constraints. But that is not necessarily the case for all traits. While we can expect most traits to be relatively adapted given a species' recent history, we should be alert to possible exceptions.

A second relevant evolutionary principle is that all organisms have arisen by descent. Ducks and geese appear to have evolved from a common ancestor, and humans and chimpanzees had a common ancestor. In increasing numbers of cases, extinct ancestors are now known from the fossil record. Because most traits have at least some heritable basis, it is possible to reconstruct a **phylogenetic tree** of organisms by examining fossil forms and looking for similarities and differences in the anatomy, physiology, and genetic structure of current taxa (**Figure 1.7**). Most phylogenetic trees show increased branching over evolutionary time, with no branches fusing and many branches arrested when a taxon goes extinct. However, there are notable exceptions. Many bacteria and archaea exhibit extensive gene transfer between species, and there are examples of taxa descended from quite different branches apparently combining into a new kind of organism. This is the most likely mechanism by which archaea evolved into eukaryotic organisms and by which some eukaryotic algae fused to create new algal taxa [39, 54]. There is little evidence that any animal taxa were created by organismal fusion, although one such claim remains controversial [29, 90]. On the other hand, specific genes can move between animal taxa, even between phyla, when transmitted by parasites with multiple host species [22].

This second principle of evolutionary biology means that closely related species are likely to have similar physiological substrates and physical constraints on the evolution of their signals. They are also likely to have similar ecologies, including diets and predators, and often relatively similar body sizes. All of these shared contexts favor similar economic constraints on their signal systems. The advantage is that once one understands the signaling economics of one member of a group, this often provides immediate hints as to the relevant economics of related taxa. Note that when initially related taxa move into different environments (e.g., some terrestrial mammals becoming aquatic), physiologies, ecologies, and signals are likely to diverge. Ecology and phylogeny then become two independent factors affecting signal diversity.

The third principle of evolutionary biology relevant to animal communication is a corollary of the first: behavior, like anatomy and physiology, is often an evolved and heritable trait. This means that communication behavior should largely be adaptive, and related species should perform similar communication tasks in similar ways. The courtship displays of dabbling ducks are strikingly similar, although some species use more of an ancestral repertoire than others [37]. The howls of dogs, wolves, and coyotes are quite similar, due to the similar preadaptations and functions of the howls [20, 21, 28, 65, 74].

The ubiquity of these principles should encourage us to ask of any animal signal system why the animal performs it the way it does. How much of the system is due to inheritance of signals evolved in immediate ancestors and shared with slight modification by related species? Why is a particular signal system adaptive, given the ecological contexts and phylogenetic constraints faced by the species? Answers will require us to compare the economics of the observed system with likely alternatives that may have been eliminated by selection in previous generations or may even be present in related species. At each of the stages of analysis outlined in this book—physiological and physical constraints, phylogenetic heritage, economics, and honesty guarantees—we can ask how particular aspects of animal communication are likely to have evolved and why the current form is adaptive compared to alternatives. As noted earlier, evolution provides a very powerful schema for examining any set of traits in organisms, and animal communication is no exception.

Classifying Communication Systems

Scientists classify natural phenomena in ways that reflect currently accepted principles. The taxonomy that defines species of living organisms and lumps them into genera, families, orders, and higher categories is based on the evolutionary principle of historical descent: species that share a common ancestor are combined into the same higher-level category. The utility of this classification is that the biology of a species about which little is known can often be inferred from knowledge of other species that, based on their anatomy, genes, and the fossil record, appear to be related by descent to the lesser-known form. Chemists classify atomic elements into the families of the periodic table based on the principle that the chemical reactivity of atoms is largely determined by the structure of their outer electronic shells. Classification is thus a way to summarize and predict similarities and differences among a diverse set of examples given underlying scientific principles.

It will be useful in this book to reduce the enormous diversity of animal communication systems down to a more manageable set of categories. If done properly, specific animal examples assigned to the same category would share many properties: knowing details about one example in that category may allow us to predict with reasonable confidence the properties of other yet-unstudied examples in that category. Our review of relevant principles above suggests four different schemes with which we might try to classify signal systems based on: (1) shared physiological and physical pre-adaptations for communication; (2) the informational economics of signals; (3) signal honesty guarantees; and (4) context. None of these schemes meets our goal perfectly by

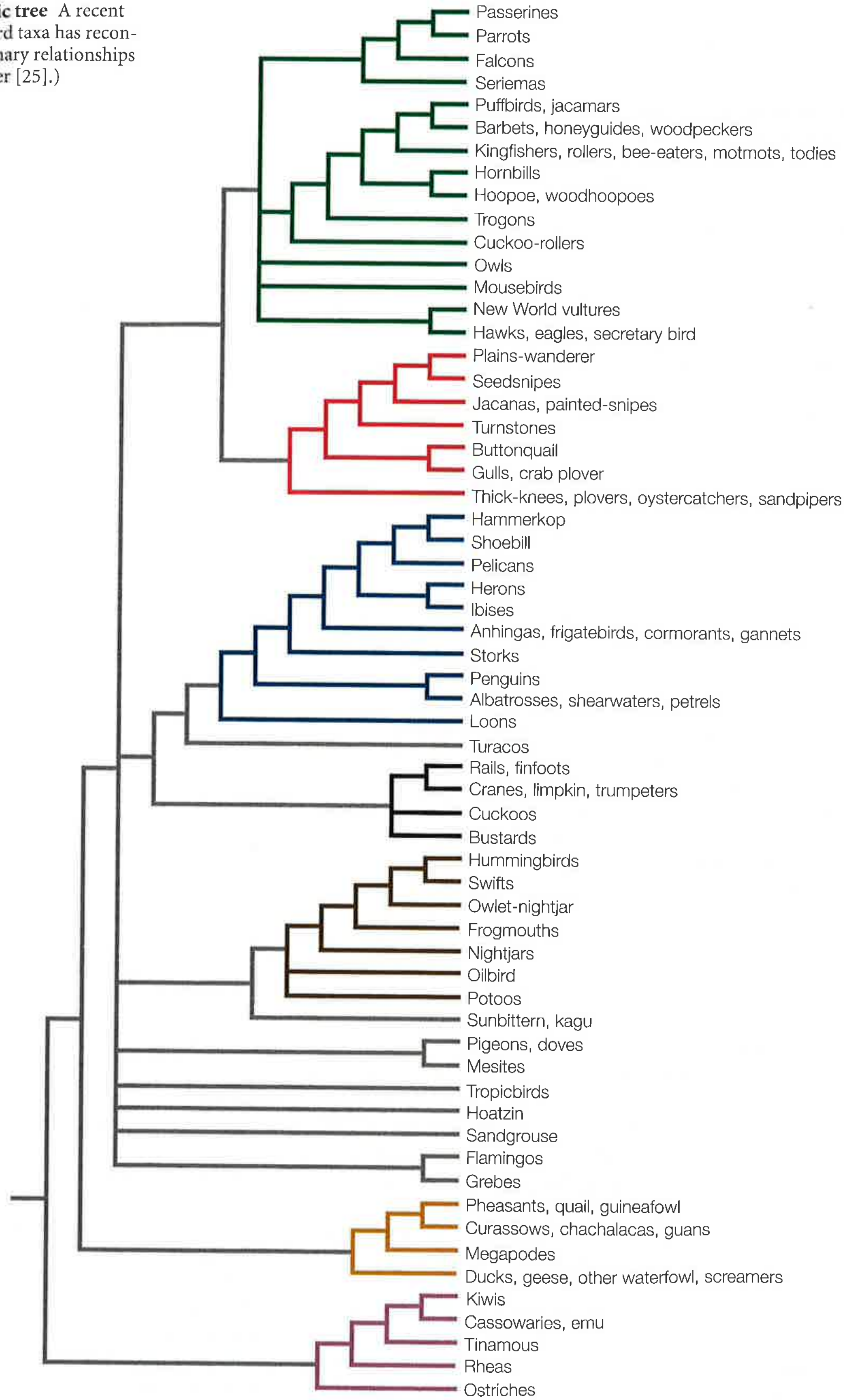

FIGURE 1.7 Bird phylogenetic tree A recent study using the DNA of living bird taxa has reconstructed the most likely evolutionary relationships between major bird groups. (After [25].)

itself; but taken together, they do a pretty good job of sorting out the diversity seen in animal communication systems.

Classifying by preadaptation, modality, and medium

Animals monitor cues conveyed by sound, light, ambient chemicals, electric fields, hydrodynamics, and touch. Each of these modalities has also been recruited to convey signals by at least some animals. Although a remarkable number of species are capable of detecting magnetic cues [16, 17, 42, 43], so far no animals have been shown to use this modality for communication. The preadaptations required for the production and reception of signals vary markedly depending upon the modality. This is particularly true for receivers: for example, adaptations for monitoring sound cues are very unlikely to be recruited for detecting visual signals.

The medium (air, water, or solid substrates) in which animals monitor cues and exchange signals can have a dramatic effect on the adaptations required. Some modalities, such as electrical fields, simply do not propagate sufficiently between terrestrial animals to be useful for signaling. Vision is of little use for animals that spend their lives tunneling in the earth. Even where the same modality is feasible in multiple media, the constraints imposed by each medium on that modality can be markedly different. The many possible combinations of medium and modality thus provide a major source of diversity in animal communication systems. On the other hand, all animals trying to communicate with the same modality in the same medium face the same physical constraints. To the degree that each taxon's existing preadaptations allow, we should expect these shared constraints to produce at least some convergence in their signaling systems.

It thus seems that one useful way to classify animal signals would invoke the criteria of modality, medium, and taxonomic affiliation (in that order). As examples, we might expect fish and whales to show some convergence in the ways in which they produce and receive sounds, whereas both might be expected to show significant differences from terrestrial vertebrates such as toads or rats. Within the whales, the design of underwater hearing organs differs somewhat given the different evolutionary trajectories of the toothed whales (Odontocetes) and baleen whales (Mysticetes). As we shall see, a signal classification scheme based on modality and medium, with some taxonomic fine-tuning, can be very useful in interpreting the observed signal diversity of animals. This is the logic used to organize Chapters 2–7 in this book.

While many signals rely on only one modality, others are **multimodal**. Many vertebrates produce courtship displays that combine visual and acoustic components. Signals of insects, spiders, and aquatic invertebrates often combine visual and olfactory components; some even contain acoustic components as well. Multimodal signaling permits a wider variety of distinctive signals to be generated, but it also requires sufficient preadaptations in the relevant ancestors for manipulating and detecting more than one modality. Coordination of multiple modality components may also require additional nervous system integration not required for single modality signals

Classifying by informational focus

CODING RULES The utility of communication to receivers hinges upon the ability of senders to correlate alternative signals with specific conditions of interest to receivers in a consistent way. As we have seen, this correlation need not be perfect, but it does have to be sufficiently reliable that attending to a signal improves a receiver's chances of making an appropriate decision or adjustment in its physiological state. To interpret signals, receivers must have prior access to the likely correlations that a sender will use to select signals. The correlations between a set of signals and conditions invoked by either party are called the **coding rules** for the exchange.

For communication to be effective, there must be some degree of concordance between the coding rules used by senders and those expected by receivers. There are several factors that can limit this concordance. One factor is the means by which each party acquires its coding rules. Species in which coding rules for both parties are largely heritable generally show a good match between sender and receiver coding. In contrast, species in which one or both parties largely acquire their coding rules by learning are prone to making mistakes. The most general procedure for acquisition combines some broad and heritable template for coding rules in both parties with subsequent refinement by learning and experience. For example, the canvas on which individual identity signals develop is largely heritable in most species, but the actual pattern in those signals depends on many different and unpredictable factors such as diet, injury, weather, local habitat conditions, and so on. Although the canvas is the same, individuals end up with at least slightly different signal variants. Receivers must then learn to associate specific signal variants with particular individuals to be able to discriminate identities.

A second factor limiting sender and receiver coding rule concordance is the degree to which signal propagation distorts the form of the signals. For close-range signals, this is usually not an issue. But for animals communicating over a distance, signal distortion can become a major problem. Clever receivers may thus use slightly different coding rules for long- and short-distance communication; receivers would continue to use the same rules. Alternatively, senders might only use signals that resisted propagation distortions, and then both parties could again share the same coding schemes. In Chapter 8, we outline a number of independent axes along which coding rules can vary depending upon functions, contexts, and taxa.

INFORMATION AND CLASSIFICATION Sender and receiver coding rules must have a minimal level of concordance before signals can provide **information** to a receiver. The term information often has a different practical significance to animals than it does to literate humans. When we read a book or attend a lecture, we often learn of new facts that we might never have imagined before. The coding rules for animal signal systems rarely provide sufficient flexibility for this type of information acquisition. Instead, the possible *facts* have been discovered long ago during the species' evolution or more recently by the receiver's prior experience. The typical problem facing a receiver is which of several known alternatives is currently the case. Suppose the receiver is assessing whether or not there is a predator nearby. It recruits its own prior experience, any inherited biases favored over evolutionary time, and its monitoring of ambient cues to estimate the probability that a predator is present. If it then detects a conspecific's alarm call, which is usually correlated with predator presence, it will use this signal to **update** its estimates of predator risk before deciding what to do. As we shall discuss in more detail in Chapter 8, this change in probability estimates after receipt of a signal is what we mean by provision of information during animal communication. Properly scaled, it is also the best measure of how much information has been provided.

A consequent way to classify animal signals is by specifying the topic about which a sender is providing information to a receiver. A given topic might have several conditions of interest to receivers. To the degree that different species share interests in the same topics and conditions, we might expect relevant coding rules to show convergences. This provides a different perspective from which we might extract some general principles. Table 1.1 provides a hierarchical summary of topics and conditions that are most commonly encoded into animal signals. The broadest level divides signals according to three topic categories: (1) possible conditions of the sender; (2) possible conditions about the receiver that are uncertain or unknown to the receiver; and (3) conditions concerning a third party or entity.

For each topic, we list conditions that are of widespread interest across many animal taxa. We can further subdivide conditions into those that are relatively stable over time versus those that are more likely to vary over short time periods. We might expect signals reflecting fairly static conditions to require a different type of coding rule from those reflecting more rapidly varying conditions.

SIGNALS ABOUT THE SENDER Since senders know themselves better than they know others, it is not surprising that the majority of the conditions about which they can provide information relates to themselves. Relevant signals have been described as "self-reporting" [30, 31, 49, 53]. Among the most common conditions of senders that are stable over long time periods are specifications of the sender's **identity**. These include its **species**, local **population**, current **social group** (if stable), **kin affiliation**, **pair bond** if mated, and own **individual identity**. Each of these aspects might be declared through one or more signals augmented by additional cues. Other relatively stable conditions that might be associated with self-reporting signals include the sender's **sex** (male, female, hermaphrodite, or asexual), **age**, **body size**, **toxicity** and **palatability** (to warn off predators), and **dominance status**. Some species wear visible "badges" that reflect their current **dominance rank** in their group.

A variable sender condition that a receiver often needs to know is the **location** of the sender. Senders can make the estimation of their location easy or difficult by careful

TABLE 1.1 *Informational classification of animal signals by topic and topic condition*

Signal topic	Condition stability	Specific examples

Sender conditions	Stable conditions	Identity:
		  Species
		  Population
		  Social group
		  Kin affiliation
		  Pair group
		  Individual

		Sex (male, female, hermaphrodite, asexual) Age Body size Dominance status Toxicity and palatability

	Variable conditions	Location of sender
		Sender's intended next action
		Physiological condition:
		  Hunger
		  Thirst
		  Reproductive receptivity
		  Health
		  Physical stamina
		  Coordination
		  Agility
		Learned skills (foraging, parental care, nesting)

Receiver conditions	Variable conditions	Detection of second party's presence Receiver selection: pointers Receiver selection: declaration of choice
Third party/entity conditions	Variable conditions	Presence of third party/entity Location of third party/entity Quality or type of third party/entity Quantity of third party/entity Identity of third party/entity Urgency of response to third party/entity

adjustment of their signals' properties [64]. Another commonly signaled condition is the intended or threatened **next action** of the sender: this can be as obvious as exaggerated postures that anticipate that action or as subtle as an alerting note before a bird sings a complex song. Predators often seek to assess the **physiological condition** of alternative prey before selecting the most vulnerable to chase. Healthy senders may benefit by demonstrating their condition, and less healthy individuals will then have no choice but to do likewise or risk being hunted because they failed to signal. Receivers seeking mates may want to assess the **genetic quality** of potential candidates. While this is technically a stable condition, the most useful index of underlying genetic quality may be one or more current physiological conditions. In these and similar situations, senders often produce signals to indicate their current physiological states such as **hunger, thirst, reproductive receptivity, health, physical stamina, coordination**, and **agility**. A sender's level of **learned skills** with respect to foraging, parental care, or nest building can also be advertised using signals that mimic or demonstrate these abilities.

SIGNALS ABOUT THE RECEIVER Many prey species produce signals that notify a stalking predator that it has been **detected**. The receiver (the predator) thus receives information about itself from the sender. Similarly, social animals may acknowledge the arrival of another with greeting signals that make it clear to the arriving animal that it has been noticed. The selective direction of broadcast signals to particular individuals is often difficult in crowded social situations: any nearby animal may mistakenly think a threat was directed at it. Some animals solve this risk by using **pointer** signals that specify the receiver to which subsequent signals will be directed. In a similar vein, a sender comparing several possible partners for some subsequent activity may use a signal to indicate to the favored individual that it has been selected (**choice**).

THIRD PARTY SIGNALS Third party signals provide information about some individual or entity other than the sender or the receiver. The topic could be another conspecific, a member of another species, a predator, a nesting site, food, water, or a refuge. The simplest type of third party signal simply announces the **detection** of something of interest in the immediate environment. For example, many alarm signals announce the detection of predators, and food calls announce the discovery of a new food source. Information about the **location** of a third party or entity is often of great use to receivers. At one extreme, signals might only indicate whether the third party is nearby or far; at the other, they may actually indicate the direction and distance to be traveled to reach the third party or entity. Signals may also provide information about the **quantity** and **quality** of a food source, or the **type** of predator. In the case of a predator alarm, variant versions of the signal may indicate what the predator is doing and thus how **urgent** the situation may be.

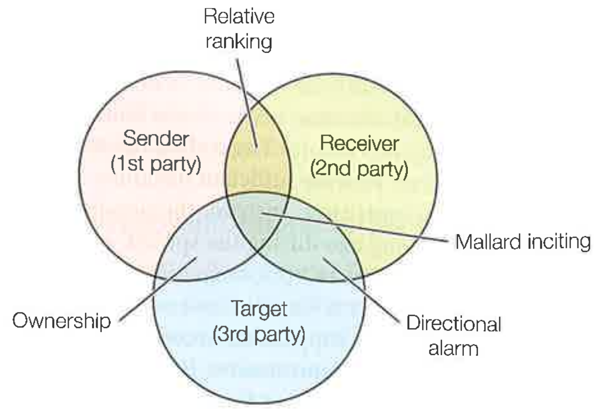

FIGURE 1.8 Examples in which information about more than one topic is provided by signals In relative ranking situations, a sender signals its estimate of the relative values of itself and a receiver along some biologically important axis. This axis might involve dominance status, chances of winning a fight, or suitability for group leadership. The signal provides information both about the sender and about the receiver. When a sender uses a signal to declare ownership of a territory, food item, or a sleeping site, it is providing information about both itself and the target commodity that it claims to own. Consider a sentinel in a foraging group that spots a predator approaching a particular group member. If it can provide an alarm directed either acoustically or by its stare at the vulnerable group member, it will be providing information both about the target (the predator) and the receiver (vulnerable group member) at the same time. Finally, the inciting display of female mallard ducks indicates to her consort receiver that she accepts a sufficient level of bonding with him and expects him to attack the other (third party) male nearby. This signal provides information to her consort about herself, about her perceived relationship with the consort, and her evaluation of the other male as an intruder who should be chased away.

In the case of social interactions, an animal may use signals to **identify** for a receiver which other individual will be the target of the sender's subsequent displays or actions.

MIXED TOPIC SIGNALS Some signals involve more than one topic and thus can be considered hybrids of the simpler examples listed in Table 1.1. Possible overlaps are summarized in **Figure 1.8**. For example, a sender may provide signals during a contest with a receiver that reflect the sender's estimate that it, rather than the receiver, will win the contest. It thus creates a **relative ranking** of the two parties. This type of signal provides a receiver with information about the sender's evaluation of itself and the sender's evaluation of the receiver.

Another type of hybrid signal occurs when a sender declares **ownership** of a territory, sleeping site, food item, or even another individual. The intended receivers are any possible intruders or competitors in the area, and the topics are both the sender's status as owner and the identity of the commodity that the sender claims to own. Alternatively, consider a sentinel watching for predators while its group's members forage. If it spots a predator approaching a particular group member, it might send a **directional alarm** signal toward a particular receiver to inform it that it is at risk from a predator. This type of signal provides information about both the receiver and a third party.

Finally, some animals produce signals that provide information on all three topic categories at the same time. One example is the inciting display of female mallard ducks. This display is performed as the female swims with her current male consort and approaches or is approached by a second male. The female's display is a repeated pointing of her bill at the intruder male, and her consort's response is often to attack the second male. This display indicates to the female's consort (the receiver) that she (the sender) feels sufficiently bonded to him that she expects him to ward off competitor males (the third parties).

MIXED CONDITION SIGNALS A signal may provide information not only about multiple parties, but also about multiple conditions. Information about identity is often combined with information about other conditions. For example, the odor trail that a worker ant lays on the ground to guide its nestmates back to a food discovery is also likely to provide information about the species, population, nesting colony, and even individual identity of the worker. Body size may be indicated by a male frog's call at the same time that he uses the signal to declare ownership of a territory in the pond and his readiness to mate with receptive females. In some cases, multiple conditions are encoded using different modalities in a multimodal signal; in others, different aspects of the pattern in a single modality can be used to provide different kinds of information.

Classification by honesty guarantees

We noted earlier that senders and receivers may have conflicts of interest and thus disagree as to the optimal decision by the receiver. This provides an incentive for senders to emit signals that cause the receiver to make a decision that is optimal for the sender but not for the receiver. These are considered deceitful signals. Since receivers usually have the upper hand in making decisions, they can minimize this risk, at least over evolutionary time, by attending only to those signals that carry some guarantee of honesty. There are several types of guarantees possible and we shall discuss them in considerable detail in later chapters. For the purposes of signal classification, we can focus on five common cases [27, 30, 31, 35, 49, 53, 84, 85, 88]. **Index signals** are sufficiently constrained by physiology, body size, or access to information that they are unbluffable. Only those senders with appropriate properties can produce them. **Handicap signals** are available to all senders, but the costs of their production are higher (or the benefits lower) for deceitful senders. The encoding rules for **conventional signals** are arbitrary, and thus lack the direct link between signal and honest content seen in index and handicap situations. However, honesty can still be enforced if receivers test senders at intervals and punish those found being deceitful. **Proximity signals** are largely used during aggressive encounters and place a sender in a vulnerable position where the risks of injury keep deceit at a minimum. Finally, if senders and receivers have minimal conflicts of interest, honesty is favored by both parties and no guarantees are necessary. Note that honesty in one component of a multimodal signal might be guaranteed because it is an index, whereas another component might be kept honest because of handicap costs. As with the other classifications listed above, a given multimodal signal may fall into more than one category of honesty guarantee.

Classification by context

We can also classify signals by the social context in which they occur. Receiver decisions made in different social contexts result in different kinds of payoffs to each party. In some contexts, payoffs are associated with health, successful foraging, physical integrity and survival; in others, the key payoffs are related to successful reproduction. The signal repertoires of most species can be partitioned among four general categories according to social context. Usually, a given signal is used in only one of these contexts, making for a natural criterion for signal classification. These four categories form the basis for our treatments of signals in Chapters 11–14.

Most species have at least some signals that are used in **aggressive** contexts. Such signals function as threats, opponent assessments, appeasements, and indications of dominance status. The diversity of signals in this category is highly variable among species. A second contextual category involves **mating signals**. We often find separate signals in a species repertoire for mate attraction, courtship, solicitation, copulation/gamete release, and postmating announcements. **Social integration signals** are largely devoted to activity coordination. The group being coordinated can range from a mated pair performing parental care to a large group of individuals that arrives, forages, and flees as a unit. Finally, **environmental signals** provide information about the presence, and in some cases the location, of predators, food, water, refuges, or other resources.

The payoffs of exchanging signals in a given context may differ significantly depending upon who is involved in the exchange. Close **kin** have shared genetic interests: production of offspring by one individual helps promote genes shared by its relatives. The benefits and costs that determine the payoffs of a given exchange will vary depending upon whether sender and receiver are or are not relatives. Similarly, some animals may have long-term relationships involving **reciprocity**: aid by one partner to the other at one time is compensated by a reversal of the roles on some later occasion. Again, the economics of a given signal exchange may differ depending upon whether sender and receiver have already established a reciprocal relationship. Threaded throughout the four contexts outlined above are adjustments in the magnitude of payoffs depending on relationships between the communicating parties. Classifications of signals based on context usually require qualifications based on who is involved in the interaction.

Categorization of signals based on context is at best a fuzzy set exercise. Many male songbirds produce songs that are designed to repel male intruders and attract potential female mates at the same time. Social integration signals can become complicated by aggressive considerations when exchanged by animals with differing dominance status in the group. Environmental signals can play key roles in maintaining social integration of cohesive foraging groups. It is important to recognize that none of the signal classification schemas outlined in this chapter produce exclusive categories, and there are, in fact, no reasons why the underlying principles should require such exclusivity. While mixes may require a higher level of anatomical and physiological integration, these costs may be made up by the economy of using one multimodal signal for multiple functions and contexts. We review the various types of mixed-function signals in Chapter 8.

Cross-classifications

In practice, most researchers in animal communication invoke two or more of the above classifications concurrently. Thus some workers have combined informational focus as one classificatory axis and honesty guarantees as a second axis [30, 35]. Another obvious combination might invoke social context and honesty guarantees. We might expect both the degree of conflict of interest and the relevant payoffs to vary in different social contexts. The literature on animal communication often mixes classification schemes rather blithely. In the same issue of major scientific journals, one can find articles with titles referring to *mating solicitation* (a context-specific term with no topic or modality information), *signature whistles* (a mixture of modality and informational content, in this case, sender identity), and *predator alarm pheromone* (a mixture specifying the olfactory modality, a third party subject, and environmental context). Many scientists working on animal communication are not hampered by this inconsistent approach, because they are sufficiently familiar with the alternative modalities, focal topics, honesty guarantees, and contexts to be able to identify a given signal system with any of these names. However, it can be confusing to students and others new to the field, and we need to be honest at this point and confess that there is currently no consistency in how animal signals are named and classified. Be warned!

At the same time, the fact that no single classification system has gained dominance testifies to the complex nature of communication. By definition, communication involves at least two active participants: a sender and a receiver. Each is out to promote its own interests, which may or may not be congruent with those of the other. The overall payoffs of an exchange to each party may vary in complicated ways. Add in the interests of referenced third parties and eavesdroppers, and the classification of animal signals can become very complex, indeed. Animal communication is subject to coevolutionary processes: as one party in the system gains an advantage, selection pressures on others increase, leading to subsequent changes in their contributions. This makes for a very large number of potential evolutionary forces and potential trajectories, and one might worry that there cannot be order or general rules in such a situation. In fact there are, and as the field matures further, more and more predictable structure is becoming apparent. There will always be diversity in signal systems as long as there is a diversity of animals to use them. But luckily, general principles and useful classification schemes are emerging, and these are the main focus of this book.

The Signaling Sequence

While the opportunity to create different signal patterns might initially seem limitless, in practice, the modality, medium, topic, and need for honesty guarantees impose severe constraints on which patterns will work as signals and which will not. In each modality, there are only certain patterns that a given sender will be capable of generating. After emission of the signal, there will be only certain patterns that can propagate between sender and receiver without serious distortion. And once the signal arrives at the receiver, there will be only certain patterns in that modality that a given receiver is capable of recognizing. When the constraints imposed at each stage of the communication process are added up, the number of useful signal patterns can be quite limited. This winnows down the actual coevolutionary trajectories and outcomes significantly. It is thus very important to understand both the possibilities and the constraints for each signal modality.

In the following six chapters, we examine these possibilities and constraints for acoustic, visual, chemical, tactile, hydrodynamic, and electrical communication, respectively. Although we treat only one modality at a time, it should be remembered than many real animal signals are multimodal. We take up the issues of multimodality later in the book. For now, it will be sufficiently challenging to get a good grasp of which patterns are possible and which not in each modality separately.

Regardless of modality, the **signaling sequence** involves seven steps (**Figure 1.9**). The first three steps occur in the sender. These are the initial **generation** of a patterned stimulus, the subsequent **modification** and refinement of the stimulus pattern, and finally the **coupling** of the modified stimulus to some **medium** that links the sender to the receiver. Usually, senders must evolve special adaptations and tricks to accomplish each step of their part of the signaling sequence.

Once emitted by a sender, a signal must then **propagate** through the medium to the receiver. During this fourth and intermediate step, the pattern so carefully crafted into the signal by the sender can easily be distorted and, if propagated over a long enough distance, can disappear in the ambient noise. For sound, the medium linking sender and receiver can be air, water, or a solid such as a plant stem or the ground. For light, no medium is needed, since light can propagate in a vacuum; however, no animals live in a vacuum, so light signals propagating between senders and receivers must pass through

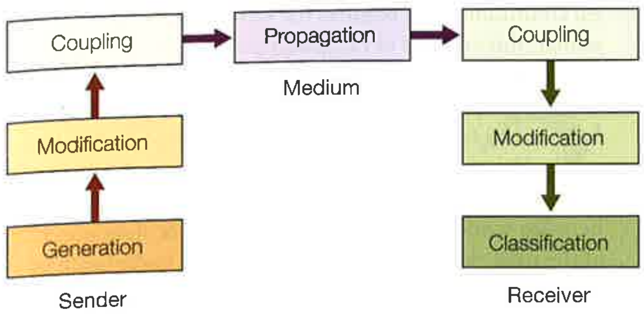

FIGURE 1.9 **The seven steps of the signaling process** Each modality will create its own challenges to communicating accurate information at any of these stages.

air, water, or even in certain cases, solids. Chemical signals propagate through air, water, or a few porous solids. Tactile, hydrodynamic, and electrical signals are all limited to short-range communication. Touch, of course, propagates directly from the surface of the sender to a surface on the receiver. Distortion is limited to interactions between the sender and receiver surfaces. Hydrodynamic signals tend to remain near to the location in which they were generated. However, they may persist long after the sender has moved away and thus may not be detected until the sender is at a considerable distance from the receiver. Air is a sufficiently poor conductor of electricity that electrical signals of animals are limited to aquatic environments. Distortion of electrical signals in water depends upon the nature of dissolved solutes and the proximity of objects with differing electrical properties.

The final three steps in the signaling sequence occur at the receiver and are the mirror images of those undertaken by the sender. First, the receiver must couple the incoming signal from the propagating medium into its sensory organs. Because the optimal propagation pattern may not be in the optimal form for information extraction, receivers often modify or transform the pattern of the signal once it enters their bodies. Finally, the receiver's sense organs and brain **identify** and **classify** the pattern that remains in the received and modified signal. At this point, the brain regions that oversee decision making step in and take over the remainder of the process.

SUMMARY

1. While most people acknowledge that animals communicate, they often lack the background needed to recognize common patterns and principles amidst the enormous diversity of animal signals.
2. The field of animal communication research, like other sciences, seeks to identify the basic principles that are required to explain and organize animal signal diversity. As is customary in modern science, these principles must be concordant with principles derived in other fields such as physics, chemistry, physiology, and economics, and they are proving general enough to provide insights for other disciplines such as psychology, medicine, conservation and wildlife management, and linguistics.
3. All animals monitor the ambient physical, ecological, and social conditions around them. Because many of the relevant conditions are not directly measurable, animals use their **sense organs** to monitor **cues** that are correlated with the conditions of interest. Because cues are only correlated with conditions, they typically provide imperfect information.
4. **Signals** are stimuli produced by one animal (the **sender**) and propagated to another animal (the **receiver**). Like cues, they are correlated with conditions of interest to the receiver, but unlike cues, which are generated inadvertently or as a by-product of some function other than communication, signals are generated expressly to provide additional **information** to receivers.
5. Because all animals have evolved the sense organs and sampling behaviors required to monitor ambient cues, the **evolution of signals** is often a relatively simple process. A mutant sender displays a slightly exaggerated anatomical feature or performs a slightly enhanced version of some action that another animal is already monitoring as a cue. If both parties benefit by this exaggerated or enhanced display, subsequent coevolution of the sender trait and receiver perception leads to further exaggeration and refinement and a new signal is created.
6. The relevant principles needed to explain animal signal diversity can be grouped into general categories: (A) those due to **physical constraints** imposed by the habitat in which each species lives and reflected in the **physiological mechanisms** that serve as **preadaptations** for signal generation and reception; (B) those due to different evolutionary histories for each taxon, that limit the kinds of preadaptations available for signal evolution; (C) those imposed by the **economics of communication**, which require that both senders and receivers benefit on average when exchanging signals; (D) those imposed by **conflicts of interest** between sender and receiver and the need for **honesty guarantees** in the design of signals; and (E) those imposed by the hordes of eavesdroppers that form the ambient **communications network** and may exploit the exchanges between any pair of animals.
7. As with all other fields of biology, evolutionary theory provides the backbone for studying all aspects of animal communication. Basic evolutionary principles such as the **genetic heritability** of traits, **sexual** and **natural selection** for some variants over others, **phylogenetic affinity**, and the perpetual introduction of new variation through

mutation are all critical to understanding the origins and maintenance of animal signal diversity.

8. Animal communication systems can be classified in several ways. One axis focuses on the **modality** (light, sound, chemicals, touch, hydrodynamics, or electricity) used to create signal stimuli, the **medium** (air, water, or solids) through which the signal propagates, and the preadaptations for that modality and medium that are present in each taxon.
9. A second axis for signal classification focuses on the alternative kinds of information that signals might provide. Since the sender knows more about its own status than any other animal, many signals provide information about sender conditions. Such information may include sender identity, sex, age, dominance status, and location. In some cases, the sender can provide information about the receiver that the latter cannot know on its own. Finally, the sender may provide receivers with information about other parties, such as predators or approaching conspecifics, or about objects, such as food.
10. A third method of classifying signals focuses on the mechanisms by which signals are kept honest when sender and receiver have a conflict of interest. **Index signals** are constrained in ways that make it impossible for a sender to be deceitful. **Handicap signals** impose higher costs or lower benefits on deceitful senders. Receivers can punish deceitful senders using **conventional signals**, and in aggressive contests, confident senders can confirm their self-assessment by making themselves vulnerable with **proximity signals**. Where there is minimal conflict of interest between sender and receiver, no honesty guarantees are needed.
11. A fourth axis classifies signals into one of four contextual categories that differ in the relevant payoffs that each party receives following communication exchanges. Usually, a species' signal repertoire can be divided into its **aggressive signals**, **mating signals**, **social integration signals**, and **environmental signals**. Different species may have more or fewer signals in each category, but most species have at least a few signals of each type.
12. Animals may use signals that mix categories both within and across the above classifications. **Multimodal signals** utilize two or more modalities at once, and each modality may invoke a different honesty guarantee. Birds often combine acoustic and visual displays, whereas insects combine visual and chemical components. Animals may also provide information about multiple conditions in the same signal: a frog's call can indicate the caller's body size and its species in the same signal. Finally, the same signal may be used in multiple contexts: the songs of many birds are designed both to repel male competitors and to attract potential female mates.
13. All communication requires the same seven steps. For the sender, this consists of (1) generating an initial stimulus, (2) modifying it to ensure proper pattern, and (3) coupling it to the propagation medium. These three sender steps are followed by (4) propagation in the medium, which usually results in some distortion of the released signal, depending on its design, the modality, the medium, and the distance between sender and receiver. The final three steps occur at the receiver and are the reverse of those undertaken by the sender: (5) coupling the propagated signal from the medium into the receiver's sense organs, (6) modifying it as necessary to improve detectability and resolution, and finally (7) identifying and classifying the perceived signal. Variations among species at each step contribute to the overall patterns of signal diversity seen in animals.

Further Reading

Good introductions to the evolution of animal behavior in general can be found in Alcock [1] and Dugatkin [13]. Signal classification and associated evolutionary processes are discussed by Hauser [33] who provides an in-depth review of the physiological preadaptations for signal evolution; Hailman [26], who classifies signals according to the complexity and redundancy of coding rules; and Searcy and Nowicki [77], and Maynard Smith and Harper [53], who review current thinking about conflicts of interest, honesty guarantees, and signal evolution.

COMPANION WEBSITE
sites.sinauer.com/animalcommunication2e

Go to the companion website for Chapter Outlines, Chapter Summaries, and References for all works cited in the textbook. In addition, the following resource is available for this chapter:

Web Topic 1.1 ***Animal communication and science education***
Because most students naturally like animals, and animal communication integrates so many disciplines, the topic can be used as an entry point for science education in middle and high school curricula. Here we provide some background and relevant links.

Web Topic 1.2 ***Information and communication***
Some scientists feel that the role of information provision should be downplayed in definitions of animal communication. A few even recommend elimination of the term when applied to animal interactions. Here, we outline the case for information as a useful and even key concept in understanding the evolution and diversity of animal signals.