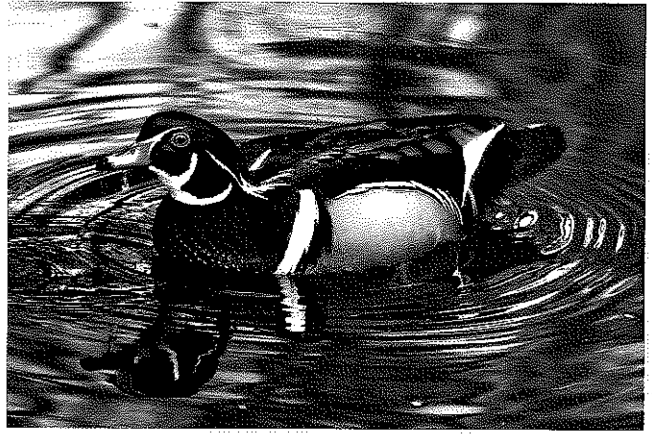
are provided at the end of the book. The combination of these excellent photos and the lovely artwork and page design by the Sinauer staff has made this edition as visually appealing as we could have hoped.

As scientific fields reach middle age, one often sees polarization into opposing camps on theoretical issues. Current debates in behavioral ecology include the role of information in animal communication, the relative importance of inclusive fitness versus network topologies in shaping the evolution of cooperation, whether sexual selection is cooperative or competitive, and which type of evolutionary model best predicts observed patterns of animal behavior. Because we are writing a text about "principles," we have often had to review the evidence for alternative viewpoints and indicate which way we think the issue is leaning. Our judgments will surely gratify some colleagues and elicit dissent from others. Only time will determine how often we got it right. However, it is important to point out that taking stands does not reflect excessive hubris on our part, but stems from our conclusion after 40 years of undergraduate teaching that a clear structure is a better starting point for students than the typical journal style of playing Dr. Jones off against Dr. Smith. There is room for both forms of pedagogy, but we find the latter works better in a lab or discussion group setting than in an undergraduate textbook.

Many colleagues have helped us with this new edition. Any errors or omissions are of course our responsibility and not theirs. Among the many who have given us input and feedback, we particularly thank Thorsten Balsby, Andy Bass, Carlos Botero, Mark Briffa, Alexis Chaine, Ken Clifton, William Cooper, Tom Cronin, Selvino de Kort, Stephanie Doucet, Neville Fletcher, Carl Gerhardt, Judith Hall, Oren Hasson, Simo Hemila, Ron Hoy, Sönke Johnsen, Bob Johnston, André Kessler, Josh Kohn, Frederich Ladich, Jürgen Liebig, Charles Linn, Irby Lovette, Kevin McGraw, Colleen McLinn, Molly Morris, Sirpa Nummela, Tomasz Osiejuk, Julian Partridge, Richard Prum, David Puts, Rob Raguso, Kern Reeve, Tommy Reuter, Edwin Scholes, Mohan Srinivasarao, Kerry Shaw, Rod Suthers, John Swaddle, Marc Théry, Stuart West, Jerry Wilkinson, and Tristram Wyatt. Copy editor Carrie Compton and artist Elizabeth Morales made major contributions. The talented Sinauer Associates' staff has been fantastically supportive and they deserve major credit for the look and feel of the final book. In particular, we want to thank staff artist Joanne Delphia, book designer Janice Holabird, Joan Gemme for her work on the photographs, art director Chris Small, website director Jason Dirks, licensing guru David McIntyre, and our project editors Sydney Carroll, Kathy Emerson, Laura Green, and particularly Azelie Aquadro, who was our guiding light through the difficult stages between writing the chapter drafts and finalizing the last page proofs. Since 1972, Andy Sinauer has continued to believe in a text on this topic and our ability to deliver something useful. We hope we have lived up to his expectations.

Jack W. Bradbury
Sandra L. Vehrencamp



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,

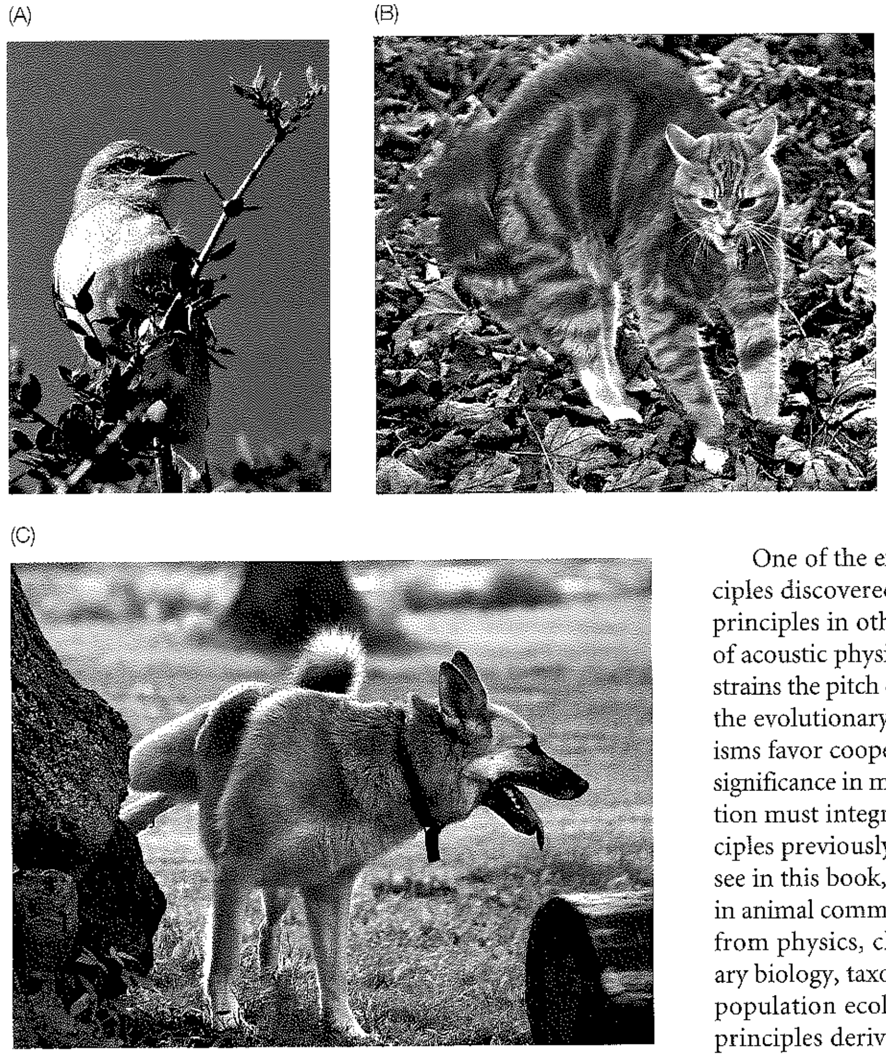


FIGURE 1.1 **Commonly encountered examples of animals communicating** (A) Male Northern Mockingbird (*Mimus polyglottos*) singing to defend its breeding territory from other males and attract a female mate. (B) Domestic cat (*Felis catus*) performing a defensive visual display when threatened. (C) Domestic 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 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.

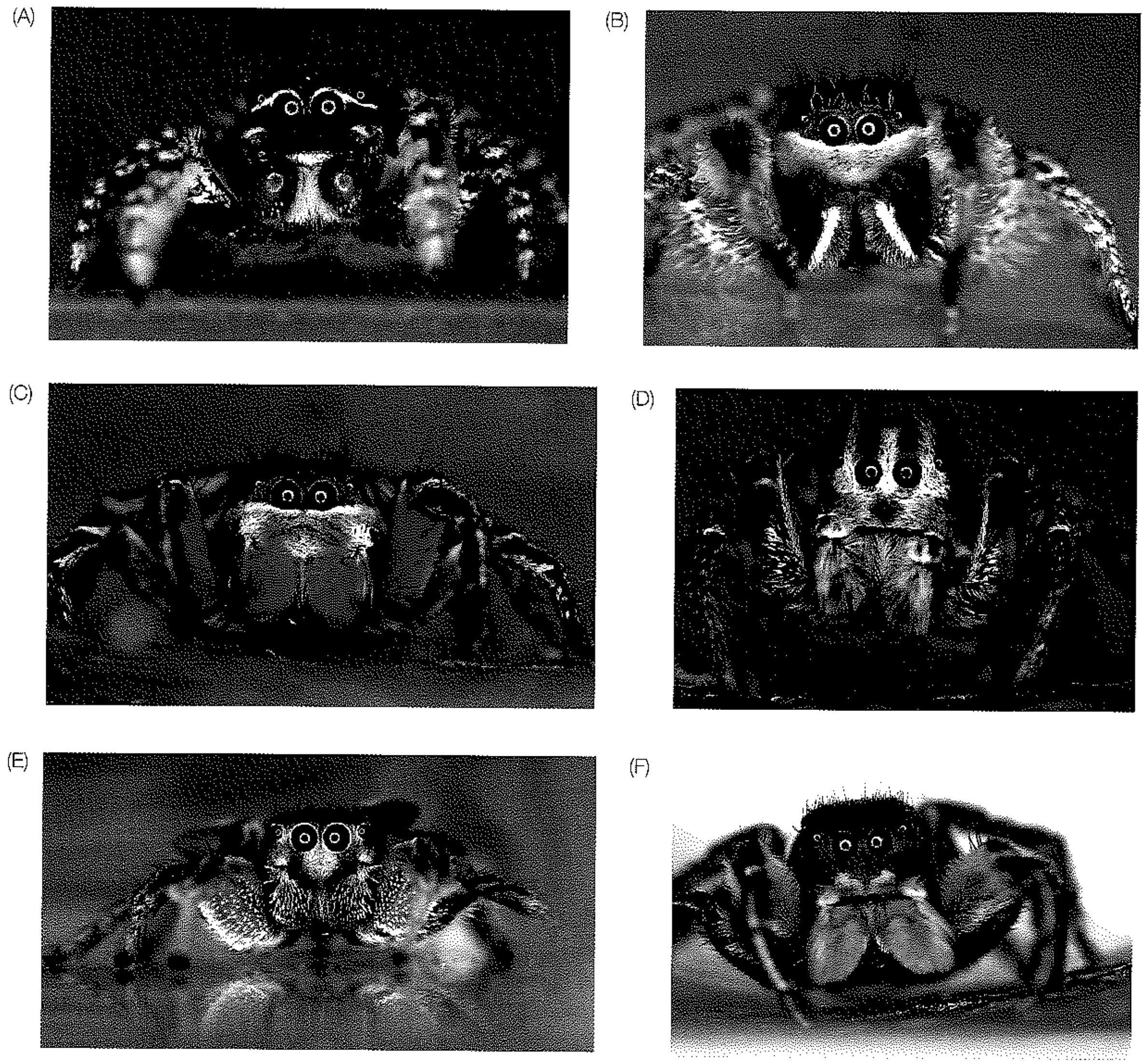


FIGURE 1.2 **Diversity in animal color signal patterns** A sample of the head and facial markings on males of different species of jumping spiders in the genus *Habronattus*. Although very closely related, these species show an amazing diversity of color patterns. A similar figure could be constructed 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.

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

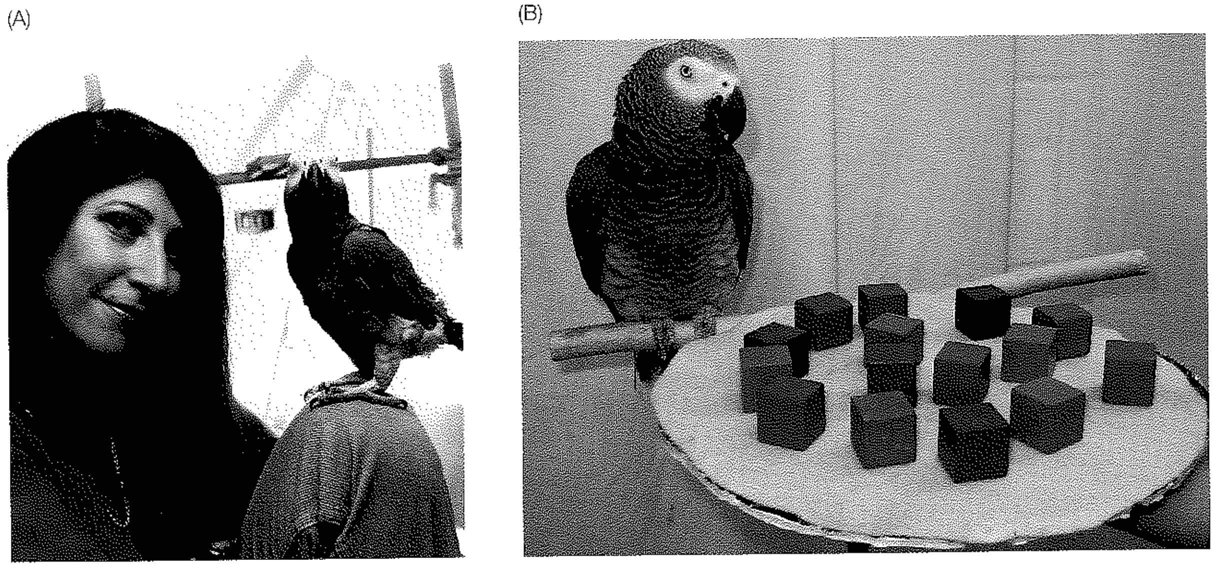


FIGURE 1.3 Studying the interface between animal communication and cognition (A) Dr. Irene Pepperberg and the late Alex, an African Grey Parrot (*Psittacus erithacus*). Alex was raised to respond to and reply with human speech in meaningful ways. In (B) Alex is shown being asked to identify the quantity 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 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

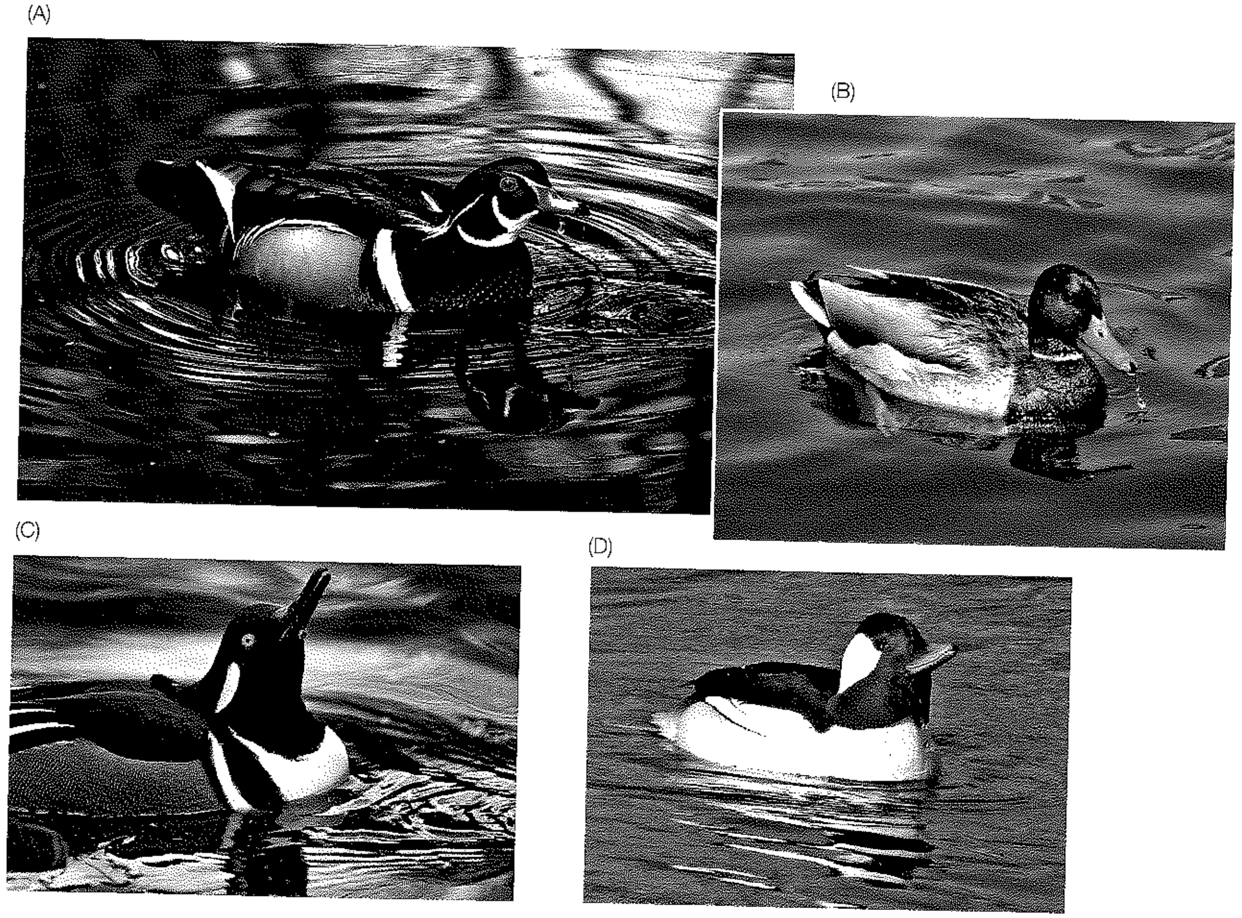


FIGURE 1.4 Evolution of display from behavior with other functions Most waterfowl drink by scooping up water in the bill and raising the beak high enough that the water runs into the throat. One puzzle is why waterfowl that have just spent extensive periods sitting on the water and filtering out food 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 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.

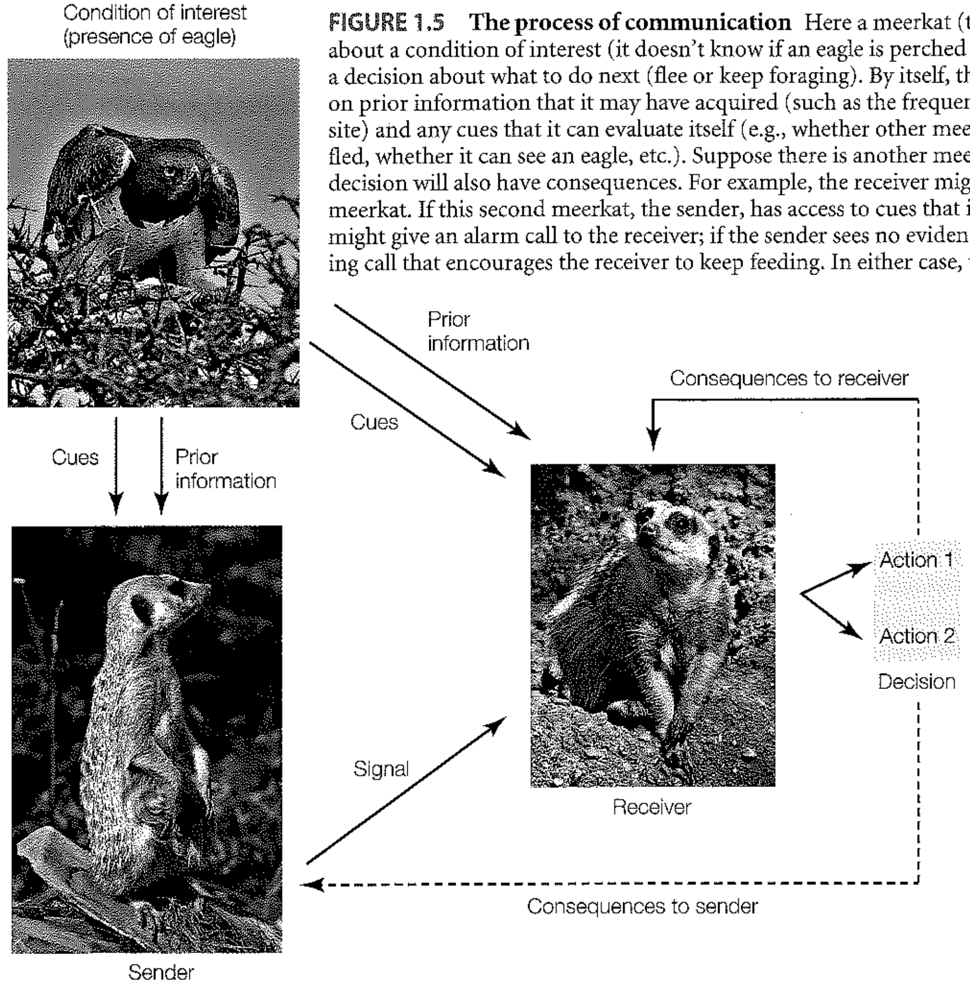


FIGURE 1.5 The process of communication Here a meerkat (the receiver) needs information about a condition of interest (it doesn't know if an eagle is perched nearby or not) before it can make a decision about what to do next (flee or keep foraging). By itself, the receiver has to base its decision on 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.

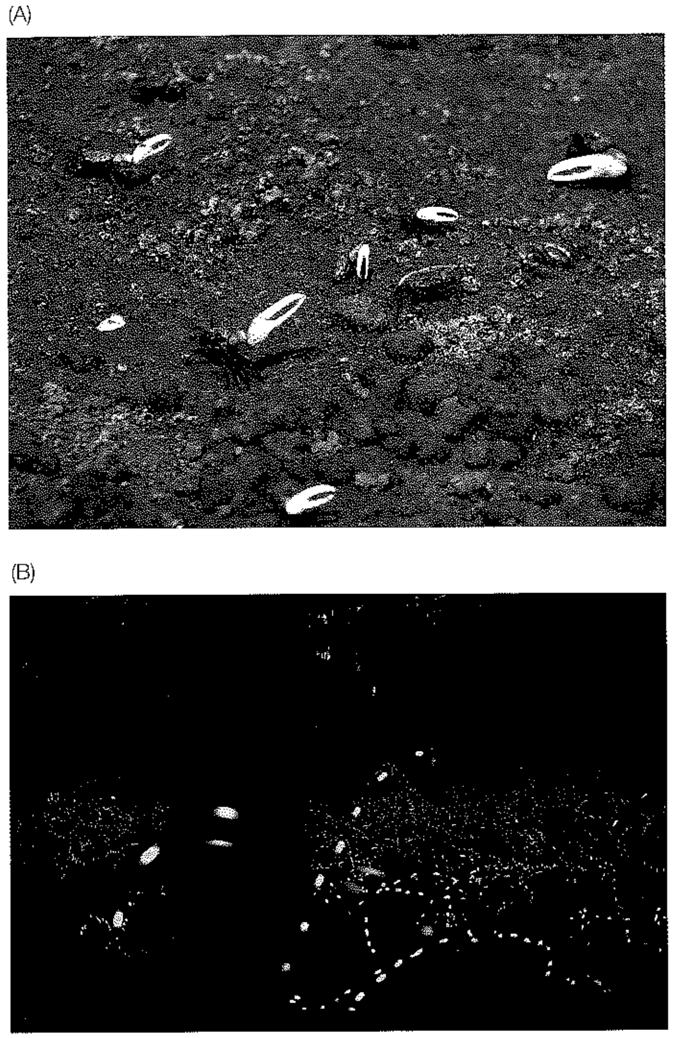


FIGURE 1.6 Visual signal networks (A) At low tide, each male fiddler crab (*Uca annulipes*) advertises himself and his burrow to females by waving his single grossly enlarged claw. When a female inspects the burrow of a particular male, other males cluster around the site and synchronize both their rate 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.

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

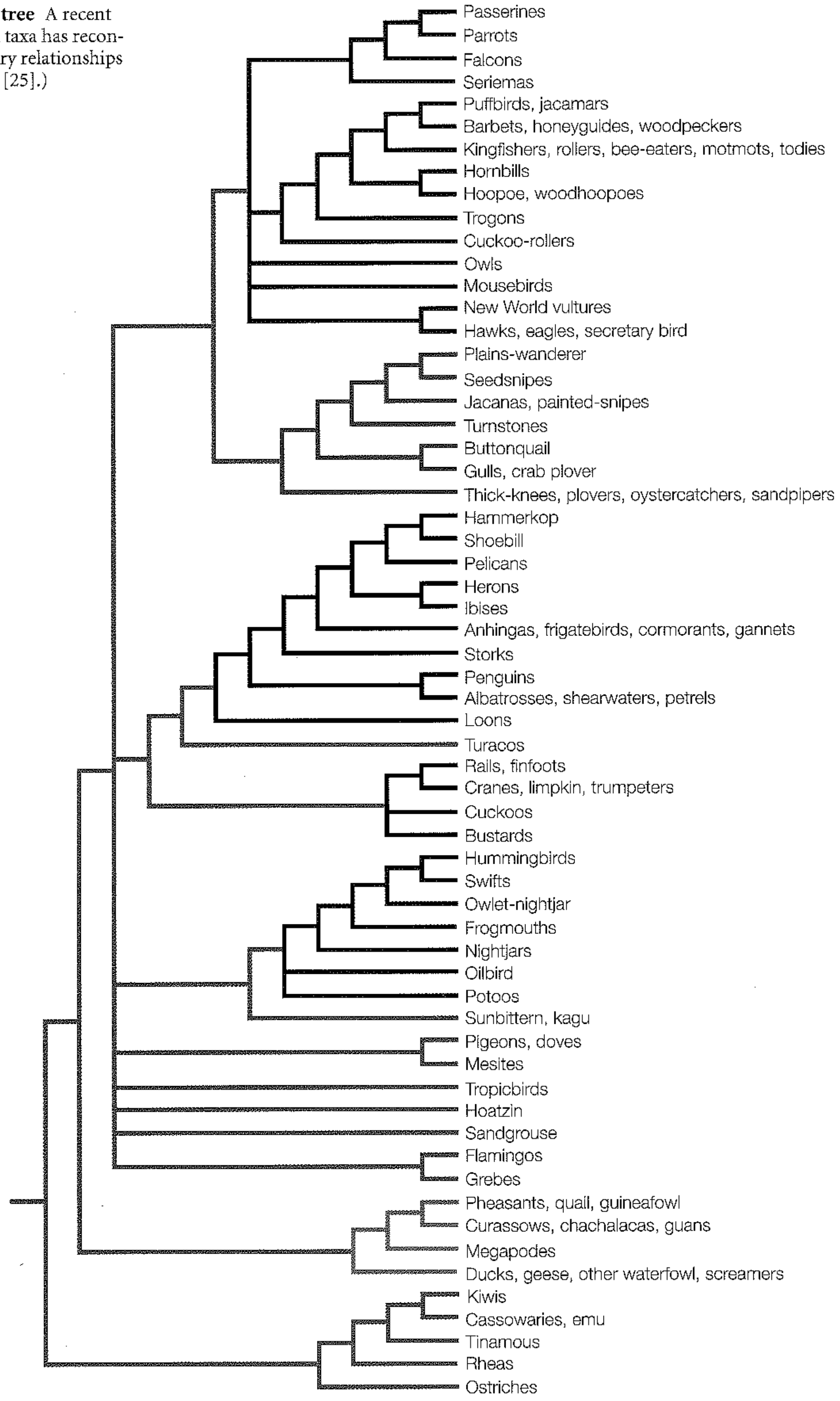


FIGURE 1.7 Bird phylogenetic tree A recent study using the DNA of living bird taxa has reconstructed the most likely evolutionary relationships between major bird groups. (After [25].)