# 14
# animal communication

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## INTRODUCTION

Many of the most spectacular and beautiful traits of animals function in communication. Especially striking to humans are certain visual signals, such as the vivid color patterns of coral reef fish and arrow poison frogs and the exaggerated feather ornaments of birds of paradise, egrets, and peafowl. Also obvious and beautiful to humans are the auditory signals of some animals, such as the songs of humpback whales, nightingales, and wood thrushes. Other animal signals tend to pass us by because of our sensory limitations; we miss out, for example, on most of the olfactory signals of insects such as butterflies and ants, and we are entirely oblivious to the electrical signals produced by some groups of fishes. Whether we are personally aware of them or not, animal signals pose interesting evolutionary questions. Natural selection should favor the evolution of signaling behaviors that benefit the signaler rather than the receiver, but then why do receivers pay attention to signals that have evolved to benefit others? Is it because signals contain information valuable to receivers? But why should such information be reliable (honest) enough to be worth attending to? Such evolutionary questions will be one focus of this chapter. A second focus will be the relationship between animal communication and human language. Human language is far more complex and cognitively sophisticated than the communication system of any non-human animal. Nonetheless we still can ask about specific ways in which human language is more advanced than animal communication, and about the nature of commonalities between the two. Before we get to any of these questions, however, we define communication and its relationship to information.

## Communication and Information

Communication can be defined as the production of acts or structures that affect the behavior of other individuals and that have evolved because of those effects (Wheeler et al. 2011). Such acts or structures are termed **signals**. The first part of this definition specifies that communication is considered to occur only if the signals produced by one individual influence the behavior of another. This influence can be overt and immediate or subtle and delayed. The second part of the definition specifies that communication involves signals that have evolved because of their effects on others. Acts or structures that affect other individuals but have not evolved because of those effects are termed **cues** rather than signals, and their production is not considered communication. An example of a cue is the compound 4-methylphenol, which is found in human sweat, and which has the effect of attracting *Anopheles* mosquitos (Hallem 2004). Attraction of *Anopheles* mosquitos (the vector for malaria) cannot be selectively advantageous for humans, so we cannot have evolved production of 4-methylphenol for that purpose. 4-methylphenol is therefore a cue and not a signal, and humans are not considered to be communicating to mosquitos when they produce this chemical.

Some definitions of communication add the requirement that information must be transferred for communication to occur. In this context **information** means a reduction in a receiver's uncertainty about the state of a signaler or its environment (Wheeler et al. 2011). Thus a begging call given by a nestling bird might reduce the uncertainty of the parents as to the nestling's state of need, and an alarm call given by one monkey might reduce the uncertainty of its fellows as to whether a predator is nearby. We have not included a stipulation of information transfer in our basic definition of communication because of the possibility that signalers in some cases have evolved to manipulate the behavior of receivers without providing any information. One way for such manipulation to occur is through **sensory bias** (Ryan et al. 1990): receivers have pre-existing response biases because of selection on their sensory systems in other contexts, and signals evolve to exploit these biases. An example that illustrates the idea involves the leg-trembling display used to court females by male water mites of the species *Neumania papillator*. The trembling display produces vibrations in the surrounding water at frequencies within the range produced by the copepod prey of the mites, and female mites react to both sets of vibrations by orienting towards and attempting to clutch the source (Proctor 1991). A male responds to being clutched by depositing spermatophores, which may then be taken up by the female to fertilize her eggs. The hypothesis that females respond to the male display as if it represents stimuli produced by prey is supported by evidence that hungry females are more likely to respond to male displays than are well fed females (Proctor 1991). Furthermore, phylogenetic evidence is consistent with the female foraging behavior having evolved first and the male display afterwards (Proctor 1992). The sensory bias interpretation is that female response to vibrations evolved to improve foraging, and that males evolved their trembling signal

to exploit this response. Under this interpretation, female response is explained without reference to any information provided by the male display.

Although non-informational explanations for signals can be plausible, as illustrated by the water mite example, such hypotheses make assumptions that are unlikely to hold in general. Figure 14.1 illustrates the assumptions made by informational and non-informational interpretations of communication. Both diagrams illustrate the evolution of the simplest kind of signaling system, one in which a single signaler communicates with a single receiver. The two interpretations make identical assumptions about the evolution of the signaler side of the system: in both, signaling is assumed to evolve to change the receiver's behavior in the signaler's interests. Where the two interpretations differ is in how the receiver side of the system is assumed to evolve. The non-informational interpretation assumes that there is no evolutionary response on the part of the receiver to the actions of the signaler; receivers continue to be manipulated in the interests of the other party, and do not respond to that manipulation evolutionarily. In contrast, the informational interpretation assumes that receiver response does evolve, and of course the evolution of receiver behavior, if it occurs, should be in a

## Two Evolutionary Interpretations of Animal Communication

### Non-Informational

signaling evolves to influence receiver in signaler's interests                                    response does not evolve

signaler ————————————→ receiver

### Informational

signaling evolves to influence receiver in signaler's interests                                    response evolves in receiver's interests

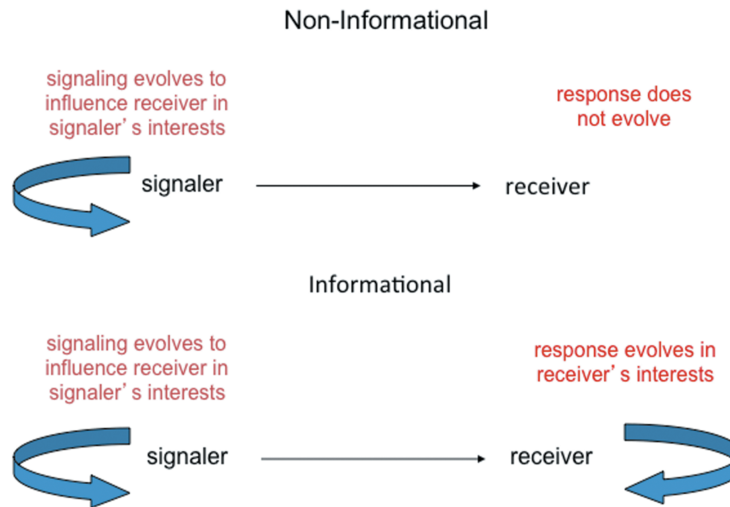signaler ————————————→ receiver

**Figure 14.1**  Non-informational and informational interpretations of animal communication. Under both interpretations, signaling behavior evolves to influence receiver behavior in the signaler's interest. Under the non-informational interpretation, receiver response does not evolve in response to the signaler's actions, so signalers are able to continue to manipulate receivers in the signalers' interests without providing information useful to the receivers. Under the informational interpretation, receiver response evolves to benefit the receivers, so response is only maintained if the signals provide information of benefit to the receivers.

direction that increases the receiver's fitness, not the signaler's. If receiver response does evolve, then to maintain receiver response there has to be some benefit to the receiver in attending to the signal, and the only plausible benefit is an informational one. Receivers thus are expected to maintain response only to signals that on average provide sufficiently valuable information to make their response adaptive.

Under the informational interpretation, signaling systems are expected to be at an evolutionary equilibrium, in which neither party can do better given what the other party is currently doing. Under the non-informational interpretation, signaling systems are viewed as being out of equilibrium, in that superior response behaviors are possible for receivers but for some reason have not evolved. The broad explanation for why superior response behaviors have not evolved is the existence of evolutionary constraints; in the water mite case, for example, females are constrained from evolving more advantageous responses to male signals by the necessity of maintaining proper responses to prey. Many cases exist, however, in which receiver responses are known to have evolved, or in which evolutionary constraints on receiver response seem unlikely. All such systems should be at equilibrium, and therefore should be informational.

## Signal Reliability

Signal reliability is an important issue for any communication system that is informational. **Reliability** in this context basically means honesty; signals are reliable if they are honest. A more formal definition is that signals are reliable if some characteristic of the signal is consistently correlated with an attribute of the signaler or the signaler's environment, and receivers benefit from knowing about that attribute (Searcy & Nowicki 2005).

Signal reliability presents a puzzle whenever the interests of signaler and receiver are not identical. The puzzle is most easily understood with respect to signaling during aggression, as this is the context in which interests are most clearly opposed. Assume that two individuals are contesting for a resource that is not shareable, such that if one wins the other loses. Assume also that the two contestants are evenly matched in fighting ability, but that one is willing to fight harder than the other to claim the resource; if the contest comes down to a physical fight, this more aggressive individual will win. An efficient solution would be for both individuals to signal their respective levels of aggressiveness honestly, with the individual producing the less aggressive signal giving way to the other. The resource would then be allocated in the same way as if there had been a fight, with both individuals benefiting from avoiding the costs associated with fighting. The problem with such a system is that it is vulnerable to cheating: animals that exaggerate their aggressiveness would benefit by winning additional contests and garnering more resources. Selection should favor exaggeration, and as the tendency to exaggerate spreads through the population, reliability of the signal

will be undermined. Once reliability is sufficiently low, receivers should evolve to cease responding to the signal, and once that has happened, signalers should evolve to cease giving the signal. The result of unchecked exaggeration should thus be the disappearance of the signaling system.

Problems with signal reliability are also possible in a variety of other signaling contexts. In mate choice, for example, males might benefit from exaggerating signals used to communicate their quality to females, in that exaggeration might induce additional females to choose them for mating. In systems in which offspring beg for food from their parents, individual offspring might benefit from exaggerating their neediness, either from securing a larger proportion of the food the parents have gathered or by inducing the parents to work harder. The fact that these signaling systems persist implies that some mechanism or mechanisms are at work to maintain signal reliability. Figure 2 shows a classification of the possible mechanisms for ensuring reliability and the kinds of signals they lead to (Hurd & Enquist 2005). In the rest of this section, we explain each of these mechanisms in turn.

## Signaling When Interests are Not Opposed

For equilibrium signaling, the first division in the classification in Figure 14.2 is between cases where the interests of signalers and receivers do or do not oppose. What we have said above about the temptations of unreliability applies only to cases in which interests do oppose. If interests are congruent, then unreliability has no benefits for the signaler, and selection can act to maximize information transfer between signaler and receiver, as used to be imagined for animal communication as a whole. Interests are most likely to be congruent in systems in which signaling occurs between close genetic relatives. The best known such systems are found in eusocial insects of the order Hymenoptera.

Eusocial ("truly social") species are ones in which castes of individuals exist that for the most part do not themselves reproduce, and instead work to aid the reproduction of others (Crespi & Yanega 1995). In Hymenopteran colonies, the worker caste consists only of females, who are usually the daughters of a single queen and are thus each other's sisters or half-sisters. Because the workers do not normally reproduce directly, they experience fitness gains only by helping the queen and each other to raise the queen's offspring. In the absence of worker reproduction (Ratnieks 1988), conflicts of interest between workers are minimal, and under these conditions communication systems especially rich in information have evolved. The most remarkable of such communication systems is the dance language of honeybees.

The dance language was first described by Karl von Frisch, who was awarded a Nobel Prize in 1973 largely for this work. The dancers are worker bees who have gone out from the hive and found food, and who use the dance to signal information about their discoveries to other workers. The dance is performed on the vertical surface of the honeycomb. The dancer moves in a figure eight pattern, the center part of which
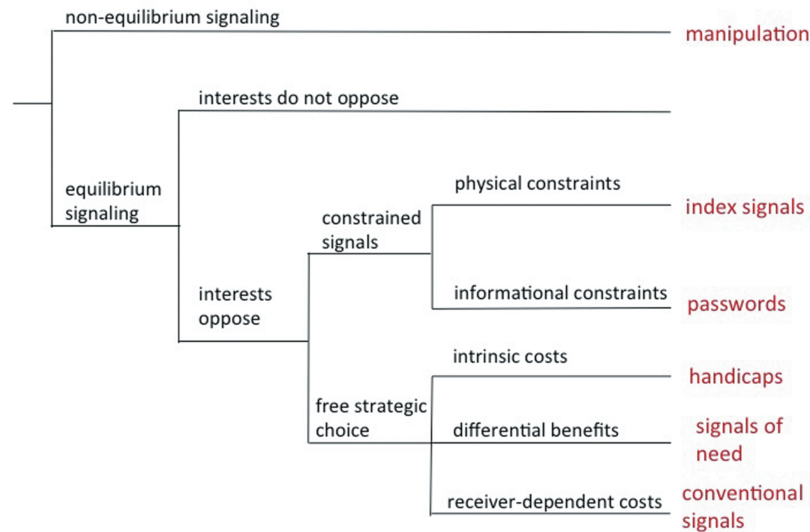
## A strategic taxonomy of animal signals

Figure 14.2   A taxonomy in which signals are classified according to the mechanism that maintain their reliability. See text for explanations of the mechanisms. Based in large part on Hurd and Enquist (2005).

is called the "waggle run" because the bee waggles her abdomen during this segment. The dance contains three kinds of information about the food that the bee has visited. First, the quality of the food source, specifically in terms of its sugar concentration, is positively correlated with both the rate of waggle run production and the total time spent dancing (Seeley et al. 2000). Second, the distance to the food source is positively correlated with the duration of each waggle run (Seeley 1997). Third, and most remarkably, the direction of the food is signaled by the direction of the waggle run relative to the vertical, with the convention that the vertical represents the direction of the sun (Von Frisch 1967). If, for example, the food is located 60 degrees to the right of the sun, the waggle run points 60 degrees to the right of vertical. The precision of the dance is such that 50% of the bees recruited by the dance arrive within 7 degrees of the food source (Gould 1976).

In the context of signaling between fellow workers from the same colony, both signalers and receivers benefit if receivers assess the food source accurately and locate it efficiently. Thus interests are not opposed, and the reliability of the signal is not surprising. What is surprising is the volume and sophistication of the information that we infer is communicated by an animal as small and as distantly related to humans as a honeybee. Critics have questioned this inference and have given an alternative explanation for receiver behavior that does not depend on communication via the

dance: that recruits find the food using odor cues alone (Wenner 2002). Von Frisch (1967) himself had shown earlier that bees both pick up scents at food sources and release pheromones there, and later experiments showed that bees rarely arrive at food sources that are unscented even if they are indicated by dancing (Wenner et al. 1969). The hypothesis that recruits follow odors rather than the dance is attractive in providing a parsimonious explanation for the behavior of recruits but leaves unexplained why bees would perform elaborate dances if no one acts upon them.

A variety of evidence has since upheld the dance hypothesis. In an especially ingenious test, harmonic radar was used to track the flight paths of individual bees as they responded to dancing (Riley et al. 2005). The dance was performed for a food source that was placed 200 m east of the hive and that none of the tracked bees had previously visited. Radar tracking showed that almost all the bees responding to dancing flew quite close to the correct easterly direction and flew out for distances close to the correct 200 meters (Figure 14.3). Although the tracked bees arrived in the vicinity of the unscented food source, none actually found it. Recruits that were displaced by the researchers to new release points again flew the direction and distance indicated by the dance, though (because of the displacement) their flights brought them
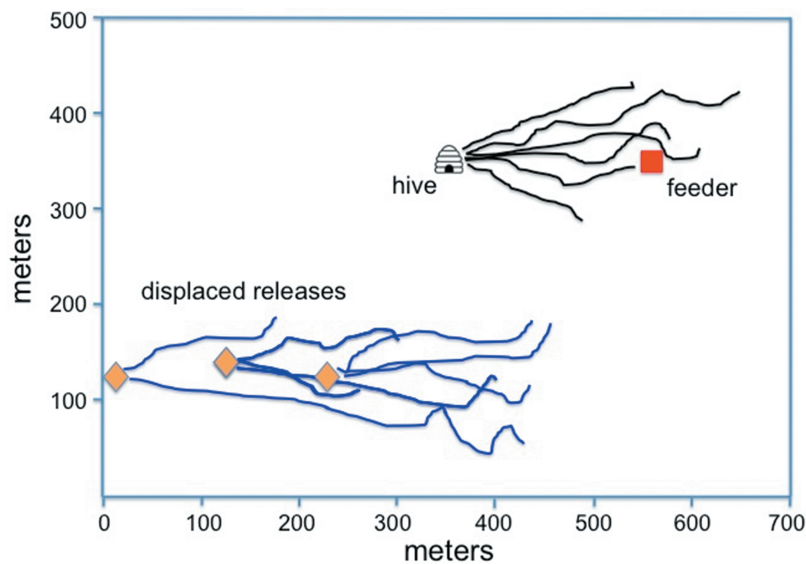


**Figure 14.3**   Representative flight paths taken by honey bees after observing a waggle dance at the hive indicating the location of a feeder (red square). Some bees departed directly from the hive (black lines) whereas others were released at displaced points (blue lines). The fact that the displaced bees flew in approximately the right direction for approximately the right distance is particularly strong evidence that the bees followed the information given in the dance rather than following cues emanating from the food. Based on the results of Riley et al. (2005).

nowhere near the food source (Figure 15.3). Thus, receivers do get fairly precise direction and distance information from observing dances, but the final approach to the food seems to require odor cues.

## Constrained Signals

Within the category of signals given between individuals with opposing interests, a distinction is made between signals that can be made by any individual and those whose production is somehow constrained (Figure 14.2). Two types of constraints are considered, physical and informational. A physical constraint means that some individuals are unable to produce certain types of signals or certain signal features because of the physical limitations of their signal production mechanisms, whereas an informational constraint means that some individuals cannot produce certain signals because they lack the necessary information.

Signals subject to a physical constraint are termed **index signals** and are often considered to be inherently honest because of an inescapable relationship between a signal feature and the physical characteristics of the signaler (Maynard Smith & Harper 2003). A now-classic example involves formant frequencies in red deer (*Cervus elaphus*). Male red deer produce loud roaring vocalizations during the fall breeding season. As in other mammals, the sound of any vocalization is initially produced by vibrations of vocal folds in the larynx, and then passes to the outside through the vocal tract, which in red deer is essentially a tube formed by the throat and oral cavity. Passage through this tube emphasizes certain frequencies, those whose wave lengths correspond to the acoustic resonances of the tube. These emphasized frequencies are termed **formants**, with the frequency of successive formants and the spacing between them being inversely related to the tube's length. Because the length of the vocal tract is likely to be greater in larger animals, one would expect these formant characteristics to be inversely correlated with body size (Fitch & Reby 2001). In red deer, as expected, body mass is strongly correlated with certain formant traits, especially with the minimum spacing between formants. These correlations are not perfect, but are nevertheless informative; variation in formant spacing, for example, predicts about 40% of the variation among males in body mass (Reby & McComb 2003). Both sexes of red deer respond to such information: females prefer to approach playback of roars with low formant spacing, while males vocalize more themselves in reply to such roars (Reby et al. 2005; Charlton et al. 2007).

The responses of other red deer suggest that it would be advantageous for a male to produce roars with lower formant spacing in order to exaggerate his apparent size. In theory, cheating on the roar in this way should not be possible, because only a truly large individual can have the long vocal tract needed to produce the formant attributes indicative of large size. Nevertheless, evidence exists of both past and present exaggeration of this signal (Fitch & Reby 2001). The larynx of most mammals is situated high in the throat, but has descended deeper in the throat in the evolution of humans.

The "descended larynx" was long thought to be a uniquely human characteristic, until it was shown that the larynx of red deer is also found in a similar descended position. One explanation for the descended larynx of red deer is that natural selection has favored lowering the larynx because doing so elongates the vocal tract, thus changing formant characteristics in a way that exaggerates apparent size. Natural selection for size exaggeration thus would have led to the gradual evolution of the larynx's descended position. In addition to this evolutionary exaggeration of apparent size, red deer manipulate apparent size behaviorally by using muscles to pull the larynx even lower when they roar. Despite the evidence for cheating on the signal on both evolutionary and behavioral time scales, it can still be argued that if all males have the descended laryngeal position and all pull down on the larynx when roaring, then any remaining variance in vocal tract length and thus in formant characteristics is still constrained to reflect body size.

An example of an informational constraint is provided by song type matching in songbirds. In many species of songbirds, each male sings multiple versions of the species song; the different versions are termed "song types." Song type matching is a behavior in which one individual replies to another with the same song type that the other has just sung. Matching has been suggested to be a signal of attention, demonstrating that the matcher is paying attention to the bird that it matches. The signal is constrained to be honest, because matching at above chance levels is only possible if the matcher is indeed paying attention to the other, so that it knows what the other has just sung. In this sense, having information about what song type was sung and the ability to match it functions as a kind of "password" in the signaling interaction. The constraint is an informational one because it is information on what the other male has sung that limits ability to match, rather than physical ability to produce the signal.

## Handicaps

Signals that are not subject to constraints are sometimes said to represent a **free strategic choice** (Hurd & Enquist 2005) (Figure 14.2): "free" because all individuals are able to produce such signals, and a "strategic choice" because each individual chooses whether or not to produce the signals based on the costs and benefits of doing so. It is then the relationships between costs and benefits together with individual attributes or environmental circumstances that can combine to make such signals reliable.

The best known hypothesis for how signal costs can produce signal reliability is the **handicap principle** of Amotz Zahavi. Zahavi (1975) proposed that display characters used in mate choice will be honest about signaler quality if they lower the signaler's survival. Those individuals that survive despite the costly display have passed a test that individuals of lower quality cannot pass. Possession of the trait thus conclusively demonstrates an individual's quality. Zahavi (1977) later amended the idea to allow the development of the display to be adjusted to individual quality within the lifetime of a

signaler, removing the assumption that death must act to cull through the signalers in order to produce reliability. A costly signal whose development depends on individual quality is referred to as a **condition dependent handicap**. Such traits are handicaps not in the sense of a physical disability but rather in the sense of the extra weight that an especially fast racehorse is made to carry.

Particularly important in convincing scientists of the validity of the handicap princi-ple were mathematical models by Grafen (1990), which demonstrated that the assump-tions of the handicap principle can lead to signals that are both evolutionarily stable and reliable. The models are complex, but their essentials are easily grasped from a graphical version proposed by Johnstone (1997) and illustrated in Figure 14.4. The model graphs the fitness costs and benefits of a signal against a measure of its inten-sity, which might be size or color for a visual display, or amplitude or production rate for an auditory display. The model shows the fitness benefit of the display increasing with signal intensity. If, for example, the display is a male courtship signal, this rela-tionship would arise because the higher a male's signal intensity, the more females he attracts, leading to more offspring and thus higher fitness. The benefit curve reaches an asymptote, based on the reasonable assumption in this mating signal example that there is some upper limit to the number of females a male can mate with. Two costs curves are shown, both having fitness costs that increase linearly with increasing signal intensity. The reason there are two cost curves is that the model assumes that fitness costs increase more steeply for low quality signalers than for high quality ones, another reasonable assumption. Suppose that the signal is a call used in mate attraction, such as a frog call, and that calling takes considerable energy, as is indeed true for calling in frogs. In this system, a low quality signaler would be one with poor energy reserves, and a high quality signaler ones with good energy reserves. The fitness costs of ex-pending energy by calling would then increase more rapidly with calling rate for a low quality signaler than for a high quality one. Only a single benefit curve is drawn because we assume that receivers cannot judge signaler quality independent of the signal, making the fitness benefit of a signal solely dependent on its intensity.

The optimal signaling level is that value of signal intensity at which the difference between signal benefit and signal costs is greatest. Because of the difference in cost curves, the optimum level is higher for signalers of good quality than for signalers of poor quality (Figure 14.4). Therefore, if all individuals signal at their optimum levels, signal intensity reveals signaler quality. Cheating is not favored, because signalers of poor quality that raise their signal intensity beyond their equilibrium level experience a greater increase in signal costs than in signal benefits. The signal is reliable, however, only along the dimension in which it is costly. A fitness cost that arises from an energy cost, for example, makes the signal reliable about energy balance, but not about other attributes such as age or agility.

An example of a signal that illustrates the assumptions of the handicap model is courtship drumming in the wolf spider *Hygrolycosa rubrofasciata*. In this species, males court females by drumming their abdomens against dry leaves, producing both sub-strate vibrations and an air-borne sound. Females respond preferentially to higher
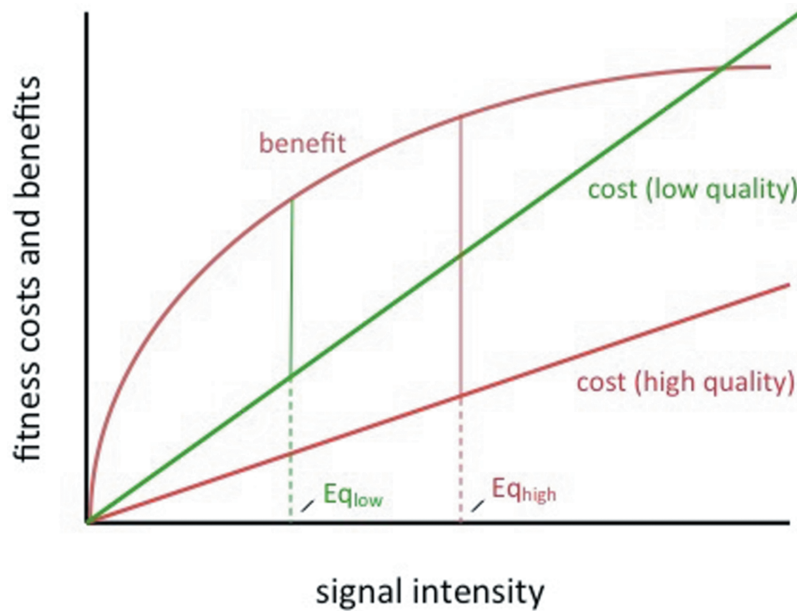
**Figure 14.4** A graphical version of the handicap mechanism. The fitness costs of giving the signal increase linearly with signal intensity, with a greater slope for low quality than for high quality signalers. Fitness benefits increase in the same curve for both categories of signalers. The optimum signaling level is found where the difference between benefit and cost is maximized; that level is greater for a high quality signaler than for a low quality one. Model based on Johnstone (1997) and Grafen (1990).

drumming rates both when choosing among live males (Kotiaho et al. 1996) and when responding to playback of drumming presented in the absence of males (Parri et al. 1997). Captive males provisioned at higher levels drum more than males provisioned at lower levels, demonstrating that drumming is condition-dependent (Kotiaho 2000). As assumed in the handicap model, the signal has a fitness cost: males induced to drum at a high rate (by proximity to females) lose weight more rapidly and suffer higher mortality than males drumming less (Mappes et al. 1996). In an experiment in which both food level and drumming rate were manipulated simultaneously, the two factors interacted in their effects on survival (Kotiaho 2000), supporting the assumption that the fitness costs of signaling are greater for males in poor condition than for males in good condition.

In the wolf spider case, it is the energy cost of producing the signal that leads to a fitness cost that maintains signal reliability, as we suggested in laying out the general logic of the handicap theory. Other types of costs are also possible. In some species of birds, such as the barn swallow, females prefer males with longer tails (Møller 1988a; Vortman et al. 2011), and tail length is a predictor of aspects of male quality (Møller

1994). Producing longer tail feathers may impose a trivial energy cost in many cases; the major cost of this signal instead appears to be that tail elongation reduces flight performance (Rowe et al. 2001). In certain species of fish, such as three-spined stick-lebacks (*Gasterosteus aculeatus*) (Millinksi & Bakker 1990), and birds, such as house finches (*Haemorhous mexicanus*) (Hill 1991), females prefer males that are redder in color. The red color is typically produced by carotenoid pigments, which vertebrates are unable to synthesize, and which consequently must be obtained in food. One cost to red coloration is that carotenoids allocated to producing color are taken away from their alternative functions in promoting health (Lozano 1994). Finally, some signals have costs that are not experienced when the signals are used in communication, but instead are experienced earlier in life, when the signals are developing. For example, learned aspects of bird song may have a developmental cost because song learning requires considerable investment in the brain regions that support song during a period of early life when resources are limited (Nowicki et al. 1998, 2002).

## Differential Benefits

In many species of birds, offspring remain in the nest and are fed by their parents for some days or weeks after hatching. When a parent visits the nest with food, the young produce a mix of signals: stretching their necks upwards, opening their mouths widely, and producing shrill calls. The common sense interpretation of these signals, that they function to beg food from the parents, turns out to be well justified. Young are fed more the more intensely they beg (Krauss & Yasukawa 2013) and experimental enhancement of begging calls via playback results in an increase in feeding by the parents (Burford et al. 1998). Begging intensity increases with increasing time since the last feeding (Kilner et al. 1999), so the signal contains reliable information about the hunger (or need) of the nestlings. Begging signals that communicate need from offspring to parents are also found in mammals such as seals (Smiseth & Lorentsen 2001) and meerkats (Manser et al. 2008).

Begging has some costs, as would be expected under a handicap interpretation. Begging requires energy expenditure (McCarty 1996; Leech & Leonard 1996), which, though slight, appears to be enough to lower growth (Kilner 2001). Lower growth should have negative effects on fitness. Begging also may attract predators (Haff & Magrath 2011), which again has negative fitness consequences. Furthermore, the energy cost of begging seems likely to act differentially according to signaler quality, as assumed in the handicap model. Nestlings that have been fed recently, and thus are not very hungry, should pay a lower fitness cost for expending a given amount of energy by begging than would a nestling that has not been fed recently, and is accordingly nearer starvation. Given that signal costs exist and that they increase with signal intensity at different rates for high and low quality signalers, reliability of begging seems well explained by our handicap model – except that the predicted relationship between
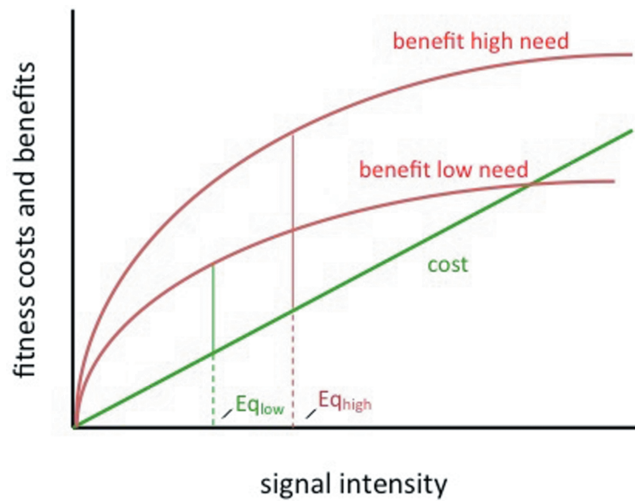
**Figure 14.5** A graphical version of a differential benefits model. The benefits of signaling are assumed to increase with increasing signal intensity more rapidly for signalers of high need than for those of low need, while costs follow the same line for both categories of signaler. The optimum signaling level is found where the difference between benefit and cost is maximized; that level is greater to signalers of high need. Model based on Johnstone (1997) and Grafen (1990).

hunger and begging intensity is directly opposite to that observed! Note with reference to Figure 14.4 that because the very-hungry chicks are the group for which fitness costs increase more steeply with increasing signal intensity, and the not-very-hungry chicks are the group for which fitness costs increase less steeply, the handicap model predicts lower begging from the very-hungry chicks than from the not-very-hungry ones, which is the reverse of what is observed.

Although the reliability of begging cannot be explained by our handicap model (Figure 14.4), it can be explained by an alternative version of Grafen's general model (Grafen 1990). In this second version (Johnstone 1997), illustrated in Figure 14.5, a single cost line is assumed to apply to all signalers. Two different benefit curves are assumed, one for signalers of high need and the other for signalers of low need. The benefit curve rises more steeply for signalers of high need than for those of low need because the delivery of a given amount of food has a greater impact on the fitness of a starving chick than on the fitness of a well-fed chick. The equilibrium signaling level is again the signal intensity at which the difference between signal benefit and signal cost is greatest. This model predicts a higher signaling level for signalers of high need than for signalers of low need, which is in accord with what is observed.

This alternative model may or may not be considered a handicap model, depending on one's perspective. Signal costs are needed to stabilize the signaling system, but it is really the differential benefits experienced by different categories of signalers that create the predicted relationship between signal intensity and signaler attributes. We therefore refer to this as a differential benefits model (Figure 14.2).

## Conventional Signals

The final category of explanations for signal reliability invokes **receiver dependent costs** (Figure 14.2). These are costs that are not intrinsic to the production or development of the signal but are instead generated by the response of receivers. When signals are subject to a physical constraint (like red deer roars) or a production cost (like wolf spider drumming), the meaning of the signal, in the sense of its information content, is determined by the signal's physical makeup. Signals that are not subject to physical constraints or production costs, but only to receiver-dependent costs, have meanings that are arbitrary with respect to their physical makeup, and that are instead determined only by convention. For this reason, signals that are of this type are often referred to as **conventional signals** (Guilford & Dawkins 1995).

One possible example of a conventional signal is soft song in song sparrows (*Melospiza melodia*) and other songbirds. Songs are long, elaborate vocalizations produced in the context of mate attraction and territory defense. Soft songs are simply low amplitude versions of these vocalizations. Although in some species soft songs are produced mainly during courtship (Dabelsteen et al. 1998), in song sparrows they are produced only during aggression. In fact, of the array of signals that song sparrows use during aggressive interactions, soft song is the one best predictor of aggressive escalation, more specifically of an actual attack (Searcy et al. 2006; Akçay et al. 2013). The physical attribute that separates soft song from normal, broadcast song is its low amplitude, a physical feature that is neither costly to produce nor constrained to be associated with aggression. At the same time, as a highly aggressive signal soft song does appear to provoke aggressive retaliation from rivals and thus to be subject to a receiver dependent cost (Anderson et al. 2012).

As emphasized earlier, aggression is a context in which conflicts of interest are most extreme, and in which unreliable signaling seems most likely to be advantageous. Can receiver-dependent costs actually produce reliable signaling in such cases? An answer to this question was first provided by Enquist's (1985) game theoretical model. The model assumes there are two possible signals: a signal of strength that we will call A and a signal of weakness that we will call B. An honest signaling strategy is to give A if strong and B if weak. Individuals giving B concede defeat if their opponent gives A and fight if their opponent gives B. Individuals giving A wait for their opponent to concede if it gives B and fight if it gives A. Given these assumptions, there is a temptation for weak individuals to cheat by giving the signal of strength: a weak individual

giving A will cause honest weak individuals to concede, thus winning contests it might otherwise lose. This benefit of cheating is balanced by a cost: weak individuals that give the signal of strength will be attacked by strong opponents, thus getting into fights that they will necessarily lose, and which honest weak individuals can avoid. Game theory analysis shows that if the cost of fighting a stronger opponent is high relative to the value of winning contests, then cheating will not have a net advantage, and reliability will prevail. Thus, reliable signaling is not inevitable in such a system, but can be a stable outcome with the right parameter values. Note that in such a conventional signaling system, honest individuals do not actually pay a signal cost, so honesty can be thought of as being maintained by the potential costs of cheating rather than by realized costs (Számadó 2011).

## Deception

Thus far we have laid out a number of hypotheses to explain why animal signals are often reliable, but we have not considered the opposite possibility: that animal signals are sometimes deceptive. When applied to humans, the term deception implies that one individual has an intention to cause another to form a false belief. Intentions and beliefs are mental states that are difficult, if not impossible, to assess in nonhuman animals. Accordingly, scientists have adopted a definition of deception in animal communication that does not stipulate such mental states. Here deception is defined as occurring when a signaler produces a signal Y that is usually associated with condition X; a receiver gives a response to Y that is appropriate under condition X and that benefits the signaler; and condition X does not actually hold (Searcy & Nowicki 2005). An example helps to clarify this definition. Suppose that signal Y is an alarm call that is usually given when a predator is present (condition X), that receivers usually respond to the alarm by freezing, and that freezing is appropriate in that it makes the freezing individual less likely to be observed and attacked by the predator. Alarming would be considered to be deceptive when the alarm is given in a context in which no predator is actually present and the signaler benefits from the receiver's freezing response.

Instances that meet this definition of deception have long been known from interspecific communication. Batesian mimicry, in which a harmless prey species evolves a resemblance to a dangerous one, provides many examples. Such examples typically involve visual resemblance, as when a non-poisonous king snake evolves a pattern of red, yellow, and black rings similar to that of a highly poisonous coral snake, and visual predators such as birds are thereby deterred from attacking the king snake (Greene & McDiarmid 1981; Brodie 1993). Because the visual signals provided by the king snake have evolved in order to influence the behavior of the predators, such a case meets our definition of communication. Mimicry can also occur with respect to other sensory modalities, as when palatable moths mimic the ultrasonic clicks that noxious moths use to warn off predatory bats (Barber & Conner 2007).

Evidence has also been found for intraspecific deception. A particularly clear example is provided by topi (*Damaliscus lunatus*), a species of savannah antelope (Bro-Jørgensen & Pringle 2010). In topi, both males and females give alarm snorts when they detect a predator such as a lion or cheetah, and then stand staring at the predator with ears pricked. Male topi give false alarms, that is alarms in the absence of any preda-tor, in one particular circumstance: when a sexually receptive female is on the male's territory and is starting to leave it. A female is sexually receptive for one day, and dur-ing that day she typically visits about 10 male territories, mating with about four of the owners. Territory owners are much more likely to give false alarms when a receptive female is on their territory than when no females are present, and they are especially likely to give false alarms when the receptive female attempts to leave. False alarms are acoustically indistinguishable from true alarms, and males giving them prick their ears and stare into the distance, just as they do when giving true alarms. Females respond to playback of both true and false alarms by first standing still briefly and then walking away from the source of the sound. Because males give false alarms when positioned between the female and the nearest boundary, the walking away response usually brings the female back toward the center of the male's territory, thus delaying her departure. Males on average achieve about three extra matings by using this false alarm tactic. Males thus give a false signal and benefit from doing so, as required by our definition of deception. Such a system can remain at evolutionary equilibrium despite the occurrence of deception if a sufficient proportion of the signals are reli-able to make response advantageous on average. Thus, female topi may be selected to continue to respond to alarm calls despite the occurrence of false alarms because the fitness consequences of failing to respond to an honest alarm are potentially disastrous.

False alarms are used for other purposes in other species, for example to draw com-petitors away from food in birds (Møller 1988b) and monkeys (Wheeler 2009) and to cause sexual rivals to cease moving in squirrels (Tamura 1995). Deception is also known in non-alarm systems, for example in threat displays in stomatopod crustaceans (Steger & Caldwell 1983) and in food calls in domestic chickens (Gyger & Marler 1988).

## Eavesdropping

**Eavesdropping** refers to the use of signals by unintended receivers and represents another way that signaling systems can be diverted from the functions for which they originally evolved. That receivers are actually unintended is clearest in cases in which the receivers are predators or parasites that use the signals of their victims to locate individuals to attack. A case in point is provided by the túngara frog (*Engystomops pustulosus*), whose mate attraction calls are exploited by both predators and parasites. Male túngara frogs can produce either simple calls, consisting of a frequency-modulated whine, or complex calls, consisting of a whine plus one or more broad-band chucks. The calls function in mate attraction; female túngara frogs approach calling males or

playback of calls and prefer to approach complex calls over simple ones (Rand & Ryan 1981). A frog-eating bat, *Trachops cirrhosus*, is also attracted to the male calls (Tuttle & Ryan 1981), and like the female frogs the predatory bat is more likely to approach complex calls than simple ones (Ryan et al. 1982). Several species of blood-sucking flies of the genus *Corethrella* are also attracted to the calls, and again respond more to complex calls to simple ones (Bernal et al. 2006). Complex calls appear to be easier for the bats to localize (Page & Ryan 2008), but this does not seem to be true for the flies (Bernal et al. 2006). Although it is not always clear why these natural enemies prefer complex calls, the existence of this preference helps explain why the male frogs sometimes produce simple calls even though complex calls are more effective mating signals.

Eavesdropping has also been suggested to occur within species. When a territorial male songbird countersings with an intruder on his territory, or with song playback simulating an intruder, information derived from the exchange of signals may be acted on by other, neighboring territory owners (Peake et al. 2005) or by nearby females (Otter et al. 1999). Such third party receivers probably should not be classified as "unintended" in the sense that predators and parasites are, in that influencing these other conspecifics may have been one of the selective advantages that originally led to the evolution of the signaling behavior and that still favors its maintenance. Nevertheless, the perspective that communication often occurs in extended "networks" (McGregor & Dabelsteen 1996), rather than exclusively in signaler/receiver dyads, is an important one and should be kept in mind when analyzing signaling systems.

## Animal Communication and Human Language

The animal signals discussed thus far have for the most part been capable of communicating only rather simple information: the body size of the signaler, for example, or its aggressive intentions or level of hunger. The simplicity of these signaling systems contrasts greatly with human language, as well as with the way that animals are imagined to communicate in works of literature such as *Watership Down* and *The Jungle Book*. In this section we consider whether non-human animals are capable of greater sophistication in communication than we have thus far seen, using human language as a point of comparison.

## Animal Signals as Symbols

In 1960, the philosopher Charles Hockett published a now-classic paper on the "design features" of human language, features that he thought all human languages possess and that are essential to their functioning. Hockett started his paper by asserting that "man is the only animal that can communicate by means of abstract symbols." Philosophers
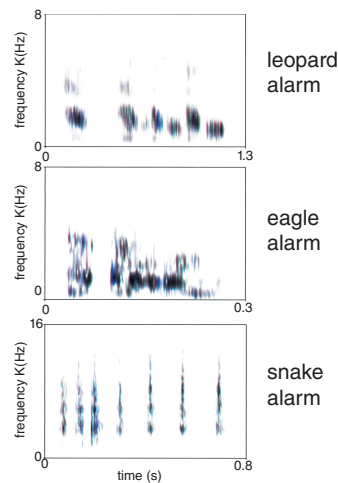
**Figure 14.6** Spectrograms of three alarm calls given by vervet monkeys in response to three specific types of predators: leopards, eagles, and snakes. Note that the acoustic structure of each alarm call is distinctive, allowing receivers to discriminate between them. Vervets respond differently to hearing each of the call types. Calls kindly provided by R. M. Seyfarth and D. L. Cheney.

debate how to define symbols, but Hockett's list of design features included attributes that he thought necessary, including 1) "semanticity", the property of being able to convey meaning, especially with reference to objects and events external to the signaler; 2) "arbitrariness," in the sense that that the meaning of the signal is arbitrary with respect to the signal's physical features, and 3) "displacement," meaning that the signal could be used to refer to things that are remote in space or time from the signaling event. Hockett suggested that some of the animal signals known to him had one or two of these properties, but that none combined all three.

Much has been discovered about animal communication since Hockett's landmark paper. One important set of animal signals discovered in the intervening years are predator-specific alarm signals, as exemplified by the alarm calls of vervet monkeys (*Chlorocebus pygerythrus*) (Seyfarth et al. 1980a, 1980b). Vervets possess three distinct alarm calls (Figure 14.6), each given when a different type of predator has been encountered: 1) leopard alarms – a series of short tonal calls given for large mammalian carnivores such as leopards, lions, and cheetahs; 2) eagle alarms – low frequency, staccato grunts given for large raptors such as martial eagles; and 3) snake alarms – high pitched "chutters" given for large snakes such as pythons and cobras (Seyfarth et al. 1980a, 1980b). Vervets hearing these alarms react differently to each: for leopard alarms they run up into trees, for eagle alarms they look up into the sky or run into dense bushes, and for snake alarms they look down at the ground (Struhsaker 1967; Seyfarth et al. 1980a). In each case, the response ought to make the monkey safer from

the specific type of predator associated with that alarm. Although vervet alarm calls clearly contain information on predator identity, it can be claimed that this information is not communicated to listeners, and that instead an alarm simply alerts the monkeys to the presence of some danger, whereupon they look around, see and identify the predator, and then take the proper action. This alternative interpretation was disproven in experiments in which vervets were played alarms from a loudspeaker in the absence of any predator; under these conditions, the monkeys still made the correct response for each of the three alarm call types (Seyfarth et al. 1980a, 1980b).

Although vervet alarm calls appear to refer to different classes of predators, we cannot say whether these signals have meaning to vervets in the same way that words do to humans. Does a snake alarm produce in an animal's mind a mental image of a snake, the way the word "snake" does for us? To address this question, Suzuki (2020) presented to coal tits (*Periparus ater*) a quasi-snake-like object, a wooden stick made to move in a snake-like manner, paired with playback of one of three call types from the vocal repertoire of the Japanese tit (*Parus minor*), a related species that occurs in the same habitat. Coal tits were significantly more likely to approach the stick when paired with the Japanese tit's snake alarm than when paired with its general alarm call or recruitment call. Coal tits failed to respond to the stick paired with snake alarms if the stick moved in a non-snake-like manner. The results suggest that the snake alarm evokes a mental "search image" for snakes in coal tits. Although suggestive, these results do not conclusively demonstrate that predator-specific alarms have meaning to non-human animals equivalent to the meaning of words and other symbols to humans. Consequently, these and similar signals in other animals are said to be **functionally referential** (Macedonia & Evans 1993), implying that they function as if they refer to things external to the animals, without committing to whether they are fully referential.

Functionally referential alarms arguably have the property of semanticity. These signals also have the property of arbitrariness, in that there is typically no apparent tie between the acoustic structure of the calls and the predator type they are associated with. These alarms, however, lack the third property specified for symbols, namely displacement: the calls are used only in the immediate presence of a predator, and not when the predator is distant in either space or time. Functionally referential signals with a similar mix of properties are found in other animals in food calls (Slocombe & Zuberbühler 2006) as well as in alarms (Manser 2001).

Hockett (1960) credited one animal signal with the property of displacement: the honeybee waggle dance described earlier. Recall that the dance conveys the quality of a food source by the rate of waggle run production and the time spent dancing, the distance to the food by the duration of a waggle run, and the direction to the food by the direction of the waggle run relative to vertical. Because the waggle dance can be used to describe a food source that is kilometers distant, it clearly exhibits displacement. Hockett also credited the waggle dance with semanticity, as it is used to refer to things external to the dancer. Hockett denied, however, that the waggle dance has the property of arbitrariness. Although one can agree with Hockett that some of the conventions in

the dance are not arbitrary, such as the use of a longer waggle run to indicate that the food is farther away, the convention for indicating direction could be considered arbitrary. At any rate, the honeybee dance language probably comes closest to meeting the criteria for symbolic communication of any of the animal communication systems that have thus far been studied, a remarkable feat for a tiny invertebrate.

## Vocal Learning

Another design feature that Hockett ascribed to all human languages is "traditional transmission," by which he meant that the "detailed conventions" of any particular language are acquired through learning. Because human languages are primarily vocal, language transmission is typically through "vocal learning," though humans also have the capacity to acquire fully functional sign languages through "gestural learning." Most animals, including many that rely heavily on vocal communication, are incapable of vocal learning; in particular, primates other than humans have relatively little capacity in this regard (Egnor & Hauser 2004). This generalization applies specifically to vocal production learning, in which animals learn how to form their vocalizations by imitating others. Other aspects of vocal learning, such as learning how to respond to vocalizations, are more widespread (Janik & Slater 2000).

Among animals other than humans, vocal production learning has been most thoroughly studied in songbirds. All songbirds appear to learn their songs, but as there are over 4000 songbird species, there is a great deal of scope for variation in patterns of learning (Beecher & Brenowitz 2005). One common pattern is illustrated by song sparrows. Male song sparrows prevented in early life from hearing the songs of adults grow up to produce songs that are obviously abnormal (Kroodsma 1977), but which nevertheless preserve some species-typical features (Marler & Sherman 1985). Isolated males tutored with recorded songs learn the details of those songs and show a strong preference for learning own-species songs rather than songs of a closely related species (Marler & Peters 1988). Young male song sparrows are particularly likely to learn from recorded models that they hear during a "critical learning period" that spans approximately 10 to 100 days post-hatching (Marler & Peters 1987). The existence of a critical learning period provides one striking parallel with human language development; a second parallel is that song sparrows and other songbirds pass through a subsong phase in which they sing relatively unformed versions of their song, similar to the babbling stage shown in human infants (Marler & Peters 1982). In the wild, young male song sparrows do not learn songs from their own fathers (Cassidy 1993), and instead learn from males they encounter after dispersing from their natal territories and that are likely to become their territorial neighbors (Nordby et al. 1999).

Vocal production learning occurs in two groups of birds other than songbirds, hummingbirds and parrots, and in a few groups of mammals other than humans, such as whales, dolphins, and bats (Searcy & Nowicki 2019). Why vocal learning has evolved

in these various groups and not others is not well established, but one idea is that the selective advantage of vocal learning lies in allowing the expansion of the repertoire of vocal signals (Nowicki & Searcy 2014). In humans, expansion of the vocal repertoire may have originally been advantageous mainly in allowing information sharing among kin (Fitch 2010) through increases in numbers of referential signals. In the other vocal learners, however, signals subject to learning are not referential, but instead are most often sexual signals used in mate choice and aggressive competition, as is true of songbird song. Increases in the vocal repertoire in such cases do not lead to greater information sharing in the same way as seen in humans. Because vocal production learning involves learning new referential signals in humans but not in other animals, non-human animals can be considered at most to approximate this design feature of human language.

## Syntax

**Syntax** refers to rules governing how smaller signal elements, such as words, are assembled into longer strings, such as sentences. Syntax in this simple sense is fairly common among animals. Many species of songbirds, for example, sing multiple song types, each of which conveys the same two messages: an aggressive, keep-away message directed at same sex conspecifics, and a courtship, mate-attraction message directed at opposite-sex conspecifics. Some species sing such song types with "eventual variety," meaning that a singer produces a series of renditions of one song type before switching to a bout of a second song type, while other species sing with "immediate variety," continually switching song types after a single rendition of each. Although a species may follow one of these syntactical rules faithfully, syntax in these songbirds is fundamentally different than in human language in that how signal elements are combined has little or no effect on meaning (Berwick et al. 2011).

Some nonhuman primates show a more complex level of syntax, in which signal elements have meanings that change when those elements are combined. In Campbell's monkey (*Cercophithecus campbelli*), for example, two boom calls mean that a male is separated from his group, two booms followed by a series of krak-oo calls mean that a tree is falling, and a pair of booms plus krak-oo calls interspersed with hok-oo calls mean that another group of monkeys is approaching (Ouattara et al. 2009). Note that in this example, meaning is affected by what calls are combined, and there seems to be regularity in the order in which call types are given, but it is not explicitly shown that order affects meaning. Syntax of this order of complexity is known for several nonhuman primates (Zuberbühler 2019).

The most complex level of syntax known for a nonhuman communication system occurs not in a primate but in a bird, the Japanese tit (Suzuki et al. 2019). Japanese tits produce A, B, and C notes as alert calls when they perceive a nearby predator and produce D notes to recruit others to social contexts that are not threatening. Playback of

ABC notes causes listening birds to scan their surroundings, while playback of D notes causes listening birds to approach. Playback of ABC-D combinations causes listeners to approach while scanning. Crucially, ABC-D sequences are much more effective in causing the approach while scanning response than are D-ABC sequences (Suzuki et al. 2016), demonstrating that element order affects response and suggesting that order affects meaning. Japanese tits also respond to tää recruitment calls produced by willow tits (*Poecile montanus*), a species that they often flock with (Suzuki et al. 2017). Japanese tits again respond with both approach and scanning to playback of completely novel ABC-tää combinations, while showing very little response to equally novel tää-ABC combinations (Suzuki et al. 2017). Thus, novel sequences are also interpreted with respect to their element order.

Although Japanese tit syntax is surprisingly complex, it is still far simpler than the widely varying syntactical rules of human languages. What the essential differences are between human and nonhuman syntax has been much debated. One proposal is that the one truly distinguishing feature of the human "faculty of language" is that only humans have a "capacity of recursion" (Hauser et al. 2002), where **recursion** refers to the sequential placement of components inside other components of the same type. An example is provided by the sentence "the car the doctor drove broke down," in which the phrase that describes what the car did (the car broke down) has embedded within it a specification of what car we are talking about (the one the doctor drove). Humans are sometimes said to have an infinite capacity of recursion, but in fact adding one more level of recursion is more than we typically attempt in speaking and is almost more than we can comprehend, as in "the car the doctor Sally knew drove broke down."

Although there is currently no clear evidence that any non-human animal uses recursion in its natural signaling system, studies have asked whether animals can learn to recognize recursive structures in human-imposed systems. In one such study, Gentner et al. (2006) trained European starlings (*Sturnus vulgaris*) to discriminate between two categories of sequences made up of two types of starling phrases, rattles (R) and warbles (W). One category included strings such as RRWW and RRRWWW, with a general form that can be written as $R^nW^n$. These strings have a recursive structure, with RW pairs embedded within other RW pairs. The second category consisted of sequences such as RWRW and RWRWRW; these can be written as $(RW)^n$ and do not have a recursive structure. Starlings proved capable of discriminating between the two categories of training sequences and of generalizing this discrimination to new examples of the sequence types. Probe stimuli were used to show that the starlings were not using simple rules-of-thumb, such as classifying based on whether the first two phrases were the same (RR = recursive) or different (RW = non-recursive). One classification strategy that was not eliminated was counting: starlings might have counted the number of R's given first and then the number of W's given subsequently, and accepted the sequence as recursive when those numbers were equal (Corballis 2007). Ironically, counting is a strategy that humans often follow to solve this discrimination problem. Another even simpler

possibility is that the starlings used overall acoustic similarity (i.e. which strings sounded similar) to classify sequences, without doing any kind of syntactic analysis at all (Van Heijningen et al. 2009). Acoustic similarity may also explain the results of other studies in which non-human animals appear to discriminate stimuli based on artificial syntactical rules (Beckers et al. 2017).

Although it is still debated whether birds and other non-human animals can be taught to judge whether strings of signals have a proper recursive structure, no one has suggested that non-human animals can recover meaning from such structures. It is after all both much easier (and less useful) to discern that the sentence "the car the doctor Sally knew drove broke down" has the correct number of verbs relative to subjects than to figure out that the car broke down, the doctor drove, and Sally knew. Once again, the communication capabilities of other animals fall short of those shown in human language.

## Pragmatics

In the study of human language, **pragmatics** concerns how context influences communication in general and meaning in particular. Context definitely has important effects on meaning in human speech, effects that are traditionally illustrated using statements that are ambiguous without knowledge of the context in which they are given. As one example, the statement "the missionaries are ready to eat" (Mey 2001) has a different meaning if given when a group of religious workers are sitting down to dinner than if given after the same individuals have been captured by cannibals. Context also affects communication acts in humans, with speakers altering their speech with respect to the composition of the audience they are addressing, the presumed state of knowledge of the individuals in that audience, and so forth.

Context has been demonstrated to affect the interpretation of signals in non-human animals just as in humans. In song sparrows, for example, territory owners are normally less aggressive towards playback of a neighbor's song than towards playback of a stranger's song, as long as the neighbor's song is played from the correct boundary, that is the one shared with the neighbor in question (Stoddard et al. 1991). If, however, playback is first used to simulate the intrusion of a neighbor onto a male's territory, that male is subsequently much more aggressive towards boundary playback of the song of this "bad neighbor" than towards song of an unoffending "good neighbor" (Akçay et al. 2009). Moreover, if playback is first used to simulate the intrusion of one neighbor (the "defector") onto the territory of another neighbor (the "victim"), subjects are subsequently more aggressive towards boundary playback of the defector's songs than of the victim's songs (Akçay et al. 2010). Song sparrows thus modulate their aggressive response to song not just with respect to the presumed signaler's past behavior towards themselves, but also with respect to the presumed signaler's past behavior towards others.

Context in non-human animals can affect signaler behavior as well as receiver response. In **audience effects**, for example, the presence and identity of potential receivers affects patterns of signaling. One of the first demonstrations of such effects was in chickens: roosters that encountered food were found to be very likely to give a food call when a female was present, less likely to call when no audience was present, and not at all likely to call when only a rival male was present (Marler et al. 1986). Audience effects have also been found in non-human primates: for example, the latency with which capuchin monkeys (*Cebus apella*) give food calls in response to the discovery of bananas was found to decrease as the number of nearby monkeys increased (Di Bitetti 2005). More subtle audience effects have been demonstrated in chimpanzees: in experiments in which playback was used to simulate the approach of another individual to a silently feeding chimpanzee, subjects were more likely to give food calls for the approach of a closely associated individual (a "friend") than for less closely associated individuals (Schel et al. 2013).

Altogether, non-human animals have been shown to exhibit considerable abilities with respect to pragmatics aspects of communication. Humans undoubtedly do far more, in particular in terms of adjusting signaling with respect to the state of knowledge of their receivers. Nevertheless, pragmatics may be the aspect of communication in which animal signaling systems most closely resemble human language.

## SUMMARY AND CONCLUSIONS

Communication is defined as the production of acts or structures that affect the behavior of others and that have evolved because of such effects. Signals often contain information of value to receivers, and this value explains the maintenance of receiver response over evolutionary time. The vulnerability of such systems is that signalers may be selected to manipulate receiver response by providing false information; most communication systems can be evolutionarily stable only if such deception is somehow held in check. One way that deception can be limited is for signaling to be constrained by inescapable relationships between signal features and physical characteristics of the signaler, producing what are termed index signals. Another possibility, which applies especially to signals of quality, is for signals to have a fitness cost that is higher for low quality than for high quality signalers, so that optimal signaling levels are higher for those of high quality. A third possibility, which applies especially to signals of need, is for the fitness benefits of signaling to be higher for individuals of high need than for those of low need. Finally, conventional signals are signals that are not physically constrained and that have negligible intrinsic costs and are instead stabilized by costs imposed by receiver responses.

Although some animal signaling systems are impressively complex, none approaches the complexity of human language. A subset of animal signals have some of the properties of symbols, such as the ability to refer to things external to the signaler, but none are accepted

as being fully symbolic. A few animal groups learn to produce their signals, but none are known to learn to produce new referential signals with new meanings, as do humans. Some animals follow rules about signal order, but it seems to be very rare for signal order to affect meaning, as occurs pervasively in human language. Animal signals approach human language most closely with respect to pragmatics, the effects of context on meaning and on signaling behavior, but even here non-human animals seem not to adjust their signals with respect to the state of knowledge of their audience.

## FURTHER READING

*Principles of Animal Communication* by Bradbury and Vehrencamp (2011) provides comprehensive coverage of all aspects of animal communication. Those interested specifically in issues relating to signal reliability and deception might consult the books by Maynard Smith and Harper (2003) and Searcy and Nowicki (2005), while those interested in the relationship of animal communication to human language will find much of value in *The Evolution of Language* by Fitch (2010). Monographs on specific systems of animal communication that are both authoritative and entertaining include Von Frisch (1967) on the dance language of honeybees, the two books by Cheney and Seyfarth (1990, 2007) on communication in non-human primates, and Catchpole and Slater (2008) on birdsong.

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