# Communication

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## Synonyms

Language; Messages; Signals

## Definition

In humans, communication is one of those terms that everyone knows but may be a little more difficult for some of us to define. In animal communication, biologists have been arguing over the definition for decades (see Table 1 for some, but by no means exhaustive list, of animal communication definitions). There are three things that most biologists agree upon: (1) there has to be a sender and a receiver, (2) there has to be a signal, and (3) this signal has been shaped by natural selection for the purpose of communication (this last piece becomes important when we start to define cues versus signals below).

Where biologists disagree is the relationship between sender and receiver and what is being transmitted in the signal. The relationship between sender and receiver becomes important when we think about fitness and how natural selection acts on individuals. Dawkins and Krebs (1978) proposed that communication involves a sender manipulating the receiver but failed to take into account that the receiver is also under natural selection and is not a by-stander in the communication relationship. Later, they (Krebs and Dawkins 1984) clarified that, in general, a sender is manipulating the receiver and the receiver is trying to mind-read the sender. Viewed this way, both sender and receiver are under natural selection and both are essentially trying to trick the other into doing something that benefits them. This adaptationist definition was stated best by Maynard Smith and Harper (2003, p. 3) where they defined communication as: “a sender producing a signal, which alters the behavior of other organisms, which evolved because of that effect, and which is effective because the receiver’s response has also evolved.” This takes the sender and receiver into account, clearly defines a signal, and allows for natural selection to act on the sender and receiver. The next thing most biologists disagree on is what, if anything, is being transferred between sender and receiver in a signal.

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**Communication, Table 1** Some key definitions of animal communication

| Definition | References |
|---|---|
| Communication occurs when the sender does something that appears to be the result of selection to influence the sensory organs of the receiver so that the receiver's behavior changes to the advantage of the sender | Dawkins and Krebs (1978) |
| Building off of their definition in 1978: Communication is based upon manipulation and mindreading. They coevolve and signals are the result of this coevolution | Krebs and Dawkins (1984) |
| Communication involves a sender producing a signal, which is "any act or structure which alters the behavior of other organisms, which evolved because of that effect, and which is effective because the receiver's response has also evolved" (p. 3) | Maynard-Smith and Harper (2003) |
| Signals are characteristics fashioned or maintained by selection because they convey information to a receiver | Searcy and Nowicki (2005) |
| Signals are stimuli produced by a sender and monitored by a receiver to the net benefit of both parties and have evolved for the purpose of relaying information | Bradbury and Vehrencamp (2011) |
| Communication is "the use of specialized, species-typical morphology or behavior to influence the current or future behavior of another individual" (p. 771) | Owren et al. (2010) |
| A signal is "any act or structure that (i) affects the behavior of other organisms; (ii) evolved (or is maintained) because of those effects; (iii) is effective because it transfers functional information to receivers" (p. 663) | Carazo and Font (2010) |
| "Communication occurs if trait values of one organism (the informer) stimulate the sensory systems of another organism (the perceiver) in such a way as to cause a change in the behavior of the perceiver (compared to a situation where the trait values of the informer were different). We use 'communication' in the narrow sense of applying only to traits that were selected for their communicative function (that is, to signals). Thus, communication in this sense is sometimes called signaling and sometimes true communication (c.f. inadvertent information)" | Ruxton and Schaefer (2011) |

## The Role of Information in Communication

The idea that information is transferred between the sender and receiver is incorporated either explicitly or implicitly into many definitions of animal communication (Table 1). Information, like communication, is a word everyone knows but is difficult to define. For this reason, some biologists have raised issue with the use of the word information in the formal definition of animal communication (Owren et al. 2010; Scott-Phillips 2008). Formally, information is assumed to have been transferred when a signaler influences the behavior of a receiver. As Searcy and Nowicki (2005, p. 207) note, "The sole value of a signal to a receiver is as a source of information, information that it uses in choosing the behavioral, physiological, or developmental responses that will maximize its fitness."

The amount of information transferred can be quantified, in bits, as a reduction in uncertainty to the receiver following a communication exchange (Shannon and Weaver 1949). For instance, if a female bird is trying to select a potential mate, she has to determine whether a bird singing near her is the correct species, the correct sex, and potentially of the highest quality. Thus, signals produced by the signaler contain potential information about species, sex, and quality and this helps the female reduce her uncertainty when making a mate-choice decision. This definition is useful insofar as it permits an objective description of the value of information. Yet, few studies ever quantify the information content of animal signals; rather, the information content is assumed to exist and thus have value. By contrast, Scott-Phillips (2008) argues that Maynard Smith and Harper's (2003) definition of communication does not use the word information and thus, information is unnecessary in a definition of communication. But is assuming that such information exists useful?

Owren et al. (2010) had some additional arguments against the use of information, in particular "encoded information," in the formal definition of animal communication. First, they argued that because biologists cannot agree on a definition of information in an animal communication context, using the word information creates nothing but ambiguity and a lack of testable hypotheses grounded in evolutionary biology. They continue to argue that Shannon and Weaver's definition of information (the correlation between the occurrence of one event with the occurrence of another event (Shannon and Weaver 1949)) cannot be applied to an animal communication definition that contains the idea of encoded information because it implies a "meaning or a significance of that event" (Owren et al. 2010, p. 761). Second, they argued that the use of encoded information implies a cooperative co-evolution between sender and receiver because if a sender encodes information in its signal there must be a benefit to the sender for sharing that information. Third, they argued that using the idea of encoded information puts the proverbial carriage before the horse in our understanding of the evolution of language. Instead, they suggest a definition where the sender influences the receiver and the concept of information is explicitly excluded (Table 1).

In response to these concerns about the inclusion of information in the formal definition of animal communication came a flurry of responses arguing for the inclusion of information in the definition (Carazo and Font 2010; Ruxton and Schaefer 2011; Seyfarth et al. 2010). Among other things, the respondents noted that, by focusing solely on the sender's influence on the receiver, the important role of the receiver is downplayed, which is a problem given that the receiver is an entity that is also subjected to selection. Thus, researchers seem to have circled around to the original issue: what is the role of the receiver in a communication exchange? To date, there has not been a consensus but the conceptual idea of information has value, even if it is rarely quantified, and even if many definitions of communication do not require it to be explicitly defined.

And for the purpose of this entry, we adopt a recent definition by Carazo and Font (2010, p. 663): a signal is "any act or structure that (i) affects the behavior of other organisms; (ii) evolved (or is maintained) because of those effects; (iii) is effective because it transfers functional information to receivers." The Carazo and Font definition includes the manipulative or influential aspect of the sender on the receiver (i), it defines a signal (ii), and it acknowledges the receiver's role in the communication scheme and that, even if not intentional by the sender, information from the receiver's perspective may be obtained (iii).

## Signals Versus Cues

There is a formal but important distinction between signals and cues. Cues, like signals, modify the behavior of a receiver, but cues have not evolved specifically for the purpose of communication (Bradbury and Vehrencamp 2011; Scott-Phillips 2008). Rather, cues are attributes of or associated with other organisms that provide information to the receiver and, hence, influence the receiver's behavior. For example, when an owl uses the movement of the grass caused by a mouse foraging, the owl is using a cue not a signal because the movement of the grass has not evolved specifically for communication with the owl; rather, it is a by-product of the mouse's foraging behavior. Yet cues, like signals, may provide sources of information.

## Signal Modalities and Types

With this definition of animal communication (and the distinction between a signal and cue), the amazing diversity illustrated by animal communication systems can be explored. Animals communicate using visual, acoustic, olfactory/chemical, tactile/seismic, and electrical signals (Bradbury and Vehrencamp 2011). Furthermore, signals vary on a continuum of conspicuousness from subtle, close-range, direct signals to obvious, long-distance, broad audience signals (Laidre and Johnstone 2013). Each of these has a different active space – the effective range through which a signal can work, each is differentially localizable, and each has constraints on the rapidity with which they vary, which has implications on the maximum amount of information transmitted. Thus, the specific modality employed may depend on the habitat in which it must be used as well as constraints on signal propagation.

Visual signals, perhaps one of the more conspicuous modalities to humans, can include colors, patterns, and/or movements. An example of color, pattern, and movement all being used together comes from the mating dance of the bird-of-paradise Wahnes's parotia (*Parotia wahnesi*) from Papua New Guinea. Males flash their multicolored, patterned iridescent chest at females, while hopping around and moving the ornaments attached to their head (see https://macaulaylibrary.org/video/469253 for a video). The active space of a visual signal will be reduced in areas with physical obstructions, but because they can be dynamically varied, they can potentially transmit a lot of information.

Acoustic signals, another conspicuous modality to humans, include different frequency, temporal, and amplitude patterns and are thus an excellent example of signals that vary in their conspicuousness. Unlike visual signals, some of which, like color, can sometimes be "always on," acoustic signals are by default off until they are produced. Two examples of acoustic signals on the opposite ends of the conspicuous spectrum come from birds. Many bird species have a "whisper song" or a "soft song" that is quiet and meant for close range communication between a male and female breeding pair. By contrast, mobbing calls are predator-elicited acoustic signals designed to be heard by both the predator and conspecifics. Mobbing calls are generally broadband and harsh in their acoustic structure making them very conspicuous and able to travel long distances to many receivers. Acoustic signals can travel around visual obstructions and may have large active spaces (the low frequency elephant and whale vocalizations can travel many kilometers). Because they may be rapidly modified, they can contain a substantial amount of dynamically varying information. Human language, after all, is not communicated using olfactory signals for a reason.

Chemical signaling may be the oldest method of communication (Bradbury and Vehrencamp 2011). Humans detect chemical signals both by taste and smell. Chemical signals tend to be long-duration signals because they have a slower diffusion rate (although this can be environmentally dependent and different components of chemical signals vary in their volatility (Parsons et al. 2017). An example of chemical signaling is the track that ant species lay down to allow nest mates to follow their tracks to locate food. These chemicals are species and ant colony specific. A recent realization is that the odorants used in chemical signaling may be produced by symbiotic bacteria living on or in animals.

Tactile or seismic signaling can be more difficult to define. For example, if in a male-male contest one male pushes the other, is this considered a signal? In other systems, it is easier to define. For example, in spider courtship, the males will pluck the strings of their web to communicate to the female and the foot drums of kangaroo rats contain information about individual identity that are transmitted to others within seismic range.

Some fishes (knifefish, elephant fish) are able to create electrical signals with specialized electric organs. These signals are used in territory and aggressive interactions, courtship, dominance, social coordination, and identification (reviewed in Bradbury and Vehrencamp 2011). More species seemingly are sensitive to other species' passive electric discharges. For example, short-beaked echidnas (*Tachyglossus aculeatus*) have electroreceptors on the tip of their snout that they forage with to detect prey, but it is unknown if echidnas use this sensory ability for communicative purposes (Bradbury and Vehrencamp 2011).

## What Influences Signal Transmission?

Given these possible modalities, what determines the conditions under which a specific modality is used and how it transmits? Animals are constrained on the signals they can send based on the environments they live in and based on their own abilities to produce and receive potential signals. Endler (1992) coined the term "sensory drive" to recognize the inevitable relationship between environmental conditions, the sensory systems, and signals that work together to drive the evolution of signaling systems.

The medium in which the signal is produced can dictate choice of signal modality. For example, electric signals are used only in aquatic environments because water increases the active space of potential signals. Within a modality, the medium can have drastic effects on signal transmission and diffusion. For example, acoustic signals travel farther in water than in air.

Signals may be blocked or otherwise masked by environmental noise. For example, broad-spectrum water noise masks acoustic signals. Torrent frogs (*Odorrana tormota*) living near rapidly flowing, noisy streams in China have escaped this constraint by producing what we perceive as ultrasonic (very high frequency) signals that are able to communicate above the lower-frequency water noise. Birds vocalizing in a cicadia-filled forest or in an urban environment with road noise may shift the frequency of their songs or calls to avoid environmental masking.

Within a medium, signals both attenuate (lose amplitude and become more difficult to detect) and degrade (lose fidelity) when transmitted over space. For acoustic signals, Morton (1975) formalized this into the acoustic adaptation hypothesis where he predicted terrestrial acoustic signals will be structured to maximize transmission within the habitat they are produced. For long-distance acoustic signals, there is a small effect of the acoustic environment on signal structure. The best support for the hypothesis comes from large-scale comparative analyses of birds or studies that look at a single species across a range of environments. The effects of the environment effect signal design in other modalities as well. For example, in a paper discussing visual signals and environment, Karen Marchetti found that *Phylloscopus* warblers vary in their color patterns depending on the light intensity of their habitat with brighter species living in darker habitats (Marchetti 1993).

Finally, the sensory systems of both the sender and receiver will influence the signal modality and signal structure. Senders physiologically need to be able to produce a signal that receivers can perceive and process and thereby evolutionary influence the signal structure through their response (Endler 1992).

## Multimodal Communication

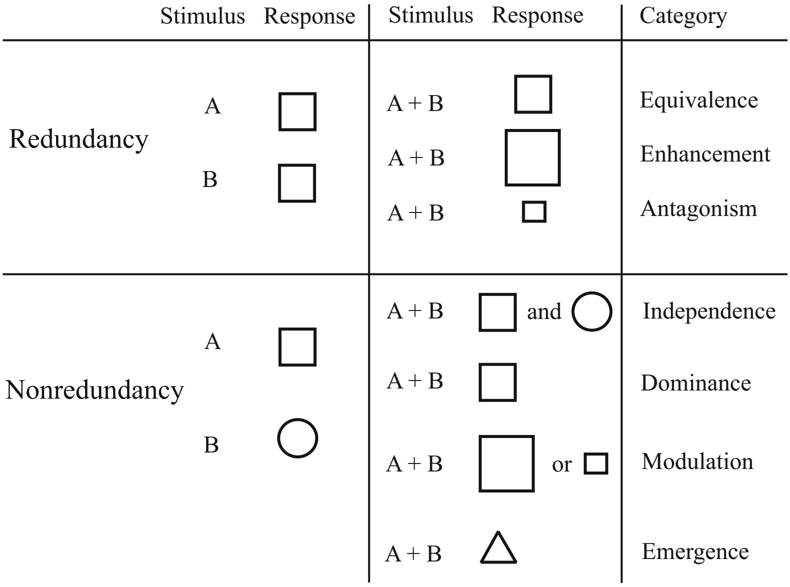
The examples of signals so far focus on a single modality. However, in reality, multimodal communication, where a sender uses signals from two or more different sensory modalities, may be relatively common. This section will discuss the evolution, use, and prevalence of multimodal signals in animal communication.

Why use a multimodal signal over a unimodal signal? After all, producing more than a single signal is assumed to be more costly than producing one. The two main hypotheses to explain the evolution of multimodal signaling are to increase content/reliability (i.e., content-driven selection; Hebets and Papaj 2004 or the multiple messages hypothesis; Johnstone 1996) and/or to increase robustness (i.e., efficacy-driven selection; Hebets and Papaj 2004 or the back-up signals hypothesis; Johnstone 1996). These ideas were formalized into a framework by Sarah Partan and Peter Marler in 2005 to describe redundant versus nonredundant multimodal signals (Fig. 1).

Redundant signals contain the same information in the signal components where nonredundant multimodal signals contain different information in their components. Apply this to the mechanisms suggested above and redundant signals may be used to increase robustness because if one modality is blocked, the information will still reach the receiver (back-up signals hypothesis). Whereas nonredundant signals may be used to increase information content because the signals contain different information (multiple messages hypothesis).

Furthermore, within redundant and nonredundant multimodal signals, Partan and Marler (2005) considered the inter-signal relationship or how the components within a signal may interact from the perspective of the receiver. For example, in the model organism of the fruit fly (*Drosophila*

**Communication, Fig. 1** Classification of multimodal signals after Partan and Marler (2005)



*melanogaster*), Fanny Rybak and colleagues found that males that use both an acoustic and a chemical component in their female courtship display have more successful matings than males that use only acoustic or chemical components (Rybak et al. 2002). This illustrates redundant enhancement (Partan and Marler 2005; Fig. 1), where both components provide information to assess male suitability (redundant), but when combined males have significantly more matings than from either component presented alone (enhancement).

Multimodal signaling, just like unimodal signaling, is subject to sensory drive and also is subject to selection for reliability. For example, Anne Leonard and colleagues focused on plant-pollinator signaling systems where most plants use both visual (color) and chemical (olfactory) signals to communicate nectar rewards to their pollinators (Leonard and Masek 2014). Selection for increased information and reliability about the nutritional reward (content-driven selection and robustness against a noisy background with multiple olfactory and visual signals bombarding pollinators (efficacy-driven selection) may increase the benefits from multimodal signals over unimodal signals.

Much of the research on multimodal communication has focused on intraspecific signaling systems, mainly antagonist and mate-choice signals. Yet, signaling systems can also exist across species. Many aspects of multimodal signaling systems are expected to be similar within and across species, and signal reliability underlies all signaling. Interspecific communication systems have an additional component that must be considered: the need for overlapping sensory systems, sensory thresholds, and cognitive abilities. As discussed above, the sensory systems and the threshold limits within those sensory systems are important for intraspecific signaling as well. However, in general, individuals of the same species share the same sensory system, thresholds, and cognitive abilities. Therefore, when examining interspecific signaling systems, researchers need to be especially aware of the sensory systems of each species involved to understand the signaling system as a whole. As research expands into multimodal signaling systems, researchers are beginning to discover that not only are most signaling systems multimodal, but that they often consist of three and potentially even four different modalities.

## Signal Reliability and the Evolution of Signals

To be useful to a receiver, signals must be reliable. Because selection acts on both the sender and the receiver, reliability must be considered from both the sender's and receiver's perspectives. By ignoring unreliable signals, receivers select for signals that contain reliable information. However, no signaling system is honest or reliable 100% of the time. Signals can be unreliable in two ways: they can unintentionally not be linked to a stimulus (false signals) or intentionally presented in the absence of the stimulus (deception) (Searcy and Nowicki 2005). For example, white-winged shrikes (*Lanio versicolor*) emit alarm calls to the rest of the mixed-species flock when they detect predators. This causes the rest of the flock to cease foraging and dive for cover. This species also emits deceptive alarm calls to manipulate the rest of the flock to dive for cover permitting them to forage without competition (Bradbury and Vehrencamp 2011). Whereas these alarm calls are sometimes deceptive and not completely reliable, the signaling system persists. Therefore, the mantra of signal evolution is that signals are honest or reliable *on average* (Searcy and Nowicki 2005).

Signals are often kept honest or reliable through production costs. The magnitude of the cost needed to keep a signal reliable is often dependent on the relationship between the sender and receiver. If the sender and receiver have aligned interests, the signal needs to be less costly because the aligned interest alone can maintain honesty because the fitness benefits are linked between sender and receiver. For example, although often temporary, mobbing signals directed at conspecifics are considered to have few costs because the interest between the sender and the receiver at the time are aligned: work together to drive a predator out of the area. However, as interests start to diverge, senders will be more tempted to provide unreliable information; therefore, the costs should be greater to ensure signal reliability. For example, when males compete, each male's interests are opposed; both want to win the encounter. Signals used in these situations are expected to be costly to ensure reliability, such as seen with the costly antlers of elk and fiddler crab's giant claws. More generally, because sender's and receiver's interests rarely completely overlap, most signals impose a cost to maintain reliability and honesty (Bradbury and Vehrencamp 2011).

An early explanation for variable costs is from Amotz Zahavi's handicap principle, where signals impose a handicap on the sender to ensure honesty, and not all senders can bear the cost (reviewed in Searcy and Nowicki 2005). They can indicate the quality or condition of the sender. All senders can produce the signal, but only certain individuals can bear the costs of the signal. The costs can be enforced in signal production, development, or maintenance. Production costs can be in the form of energy used in production, time spent signaling and away from other activities or increased conspicuousness to predators. Handicap signals can also have developmental costs. Development costs are born prior to signaling and often direct limited resources to signal development. Carotenoid expression in birds and fish is developmentally costly. Carotenoids must be acquired by foraging and are used in immunological defense systems. Therefore, any animals that can show evidence that they have acquired carotenoids (through carotenoid-dependent coloration) have demonstrated that they forage well and are of both high nutritional and immunological quality. Handicap signals can also impose maintenance costs (Bradbury and Vehrencamp 2011). Maintenance costs refer to the costs of maintaining a signal and can be energetic or act through increasing predation risk.

Index signals are signals that are constrained by the anatomy, physiology, or experience of the sender. Unlike handicap signals, not all individuals can produce the signal and honesty is enforced not by direct costs but by constraints. They most often indicate condition and quality. For example, song repertoire size in birds with open-ended learning can be considered an index signal because it cannot be faked: repertoire size is contingent on age.

Signals may also have third party costs. Third party costs can come in two forms: reciprocity or as an honesty check. Reciprocity exists in systems where individual recognition is present and previous actions are remembered. For example, allogrooming (the act of one individual grooming and removing ectoparasites from another) in primates and ungulates is often kept honest through reciprocity: if you do not scratch my back, I will not scratch your back next time. The other form of a third-party cost is when the signal is kept honest by the responses of other individuals. For example, the songs that male brown-headed cowbirds use to attract females are maintained by other male cowbirds. Males are attacked more when they sing the female-preferred interphrase unit, which means only strong males can endure being attacked, and the signal is kept honest through these checks (reviewed in Searcy and Nowicki 2005).

## Signal Design and the Evolution of Signals

Now that we understand how a signaling system evolves and is maintained, how do the signals themselves evolve? Darwin thought deeply about the evolution of communication in his book *The Expression of Emotions of Man and Animals* and many of his ideas persist (Darwin and Prodger 1998). For example, his principle of antithesis is that aggressive and submissive displays will be structured so that they will be opposite each other. The examples illustrated here may be extensions of behaviors used when approaching or retreating.

The early Ethologists viewed signals as evolving through a process called “ritualization.” Ritualization is the process by which a nonsignal (such as a cue), used in a particular context, becomes predictive of what follows and then becomes exaggerated or stereotyped so that what follows becomes clear. Ritualization involves formalizing parts of a movement pattern. Ethologists would refer to these parts as “intention movements” not because the animals intend to do something, but rather because those movements predict (to us at least) what will follow.

Some of the displays that Darwin thought about when coming up with his principle of antithesis can be explained as having evolved through the process of ritualization. Ruffling feathers before flying away might be an intentional movement that the sparrow ritualized into a submissive display. Putting the ruff up to increase apparent size and protect its neck might be an intentional movement that dogs used that later became ritualized into an aggressive display. Other sorts of examples include: breathing (a nonsignal) becomes ritualized into courtship song; a defensive posture (imagine a dog crouching down) becomes ritualized into a submissive signal (imagine that same dog crouching down after it has gotten caught eating your shoe); autonomic nervous system processes such as piloerection or feather ruffling often provide the source of the ritualized display. At that level, many ritualized signals may be honest indicators of how the animal perceives the world at that time. Ritualization should be straightforward to evolve because the signaler is already producing something that the receivers respond to in its own best interest.

This ritualized view of communication underlies the idea that communication functions to provide unambiguous information. However, because ritualization removes information by removing variability, once ritualized, additional signals are needed to emerge to provide more information. Thus, you could envision elaborate courtship rituals evolving by the process of ritualization of signal after signal. Cumulative selection like this is how we generally view the evolution of all sorts of complex traits.

But how do signals and signal receptors actually evolve: probably by a series of incremental fitness gains? Most are likely to be “exaptations” evolved from traits that already have some function but become specialized for another. Each step of a complex signal probably involved an incremental benefit and the potentially lengthy process of cumulative selection was driven by the fitness benefits of having a particular trait at each step of the way. Through these incremental fitness benefits, we can envision scenarios by which rather complex signals evolve.

There may be preexisting biases that make certain modalities or types of signals more likely than others. For instance, females of different taxa (some birds, some fish) find males with long tails particularly attractive, and studies of sword-tailed fish find that even in the absence of swords in a clade, sword-bearing fish are still found more attractive.

Structure is likely to reflect function. Thus, avian mobbing calls should be easily localizable if animals are to recruit others to help mob. Similarly, they should be broadband to ensure predator-directed mobbing calls are actually perceived by the predator. The mobbing call is much wider bandwidth than the avian aerial alarm “seet” calls. But even alarm calls will vary in their localizability. Bird alarm calls to terrestrial predators tend to be wider bandwidth and more localizable than those given to aerial predators. One possible explanation of this has to do with risk. Aerial predators move faster and generally are associated with a more compelling risk than terrestrial predators. Remember, not all animals call, nor do most animals call when they are really exposed to imminent predation (unless it is given to scare the predator into dropping them).

Thus, we see some convergence in the structure of aerial alarm calls in birds. Many songbirds produce similar calls when they detect raptors. This convergence in structure reflects convergent problems – warning others while not getting preyed upon themselves. The convergence works because of how the calls are structured. They fade in and fade out and are relatively high frequency as Peter Marler first pointed out in the late 1950s. The combination of fading in and fading out both in volume and also in their structure makes them relatively hard to localize. Rapid and sharp onsets are easier to localize than narrow-band, smoothly fading in sounds. Additionally, because they are high frequency, they transmit less than a lower frequency call of the same structure. Thus, birds can better target their recipients – and not advertise the fact that they have seen a raptor to all – including to the raptor. Additionally, call frequencies used are outside the best hearing range of some of their predators. Taken together, these similar selective pressures might lead to convergent call structure.

## Functionally Referential Signals

In addition to containing information that helps animals make decisions, calls may be said to have referential meaning. The referential meaning of signals has been most studied in alarm communication and in food calls.

Alarm calls are signals emitted when an animal detects a predator. For species that emit situationally variable alarm calls, two hypotheses have been invoked to explain the meaning of variable calls. Alarm calls may vary according to the “response urgency,” or imminence of predation, the caller faces. Thus, short calls may be produced when predation is imminent while longer calls may be produced when there is more time to assess and manage the risk of predation. By doing so, calls may communicate the degree of risk the caller experiences and may be a function of the caller’s arousal. Alternatively, different alarm calls may denote different types of predators (e.g., aerial vs. terrestrial predators), or even the exact species of predator. These alarm calls are known as “functionally referential” in that the calls refer to specific external stimuli. Labeling a specific external object or event is known as “referential communication.” Such referential communication is a required component of human language and therefore is of some interest. Philosophers debate what referential communication really entails. Does it mean that animals form “images” of objects? Does it require labeling (eagle!) or could it communicate the desired action (run up a tree now!)? Does it require complex cognitive abilities? Honeybee waggle dances, after all, communicate very specific information about the quality of food, the distance to the food, and the direction to the food. Is there any biological basis for saying that referential communication in monkeys is more complex than in bees? Some researchers care about this because they would like to use human language abilities as a metric by which to contrast humans with other species. If bees and monkeys share the same abilities, then perhaps humans are not that cognitively complex. Rather than engaging in this debate, Peter Marler, Chris Evans, and Marc Hauser shifted the discussion by defining the term "functionally referential" (reviewed in Evans 1997). Functionally referential makes no reference to higher-level cognitive processes but rather focuses on production and response specificity. Thus, to quantify referential communication, it is essential to have a high degree of production specificity – specific calls are elicited by specific predators, and it is essential that receivers respond uniquely to these calls; thus, the calls are contextually independent from the receivers perspective.

Vervet monkeys studied in East Africa (Uganda and Kenya) are a well-studied system of referential signaling. Classic work by Peter Marler, Dorothy Cheney, and Robert Seyfarth showed that monkeys produce acoustically different calls in response to different types of predators: they "chutter" to snakes, "bark" to leopards, and "cough" to eagles. Monkeys hearing chutters immediately stand bipedally and look for snakes, those hearing barks climb trees and retreat to the distal part of limbs where they will be safe from leopards, and those hearing coughs retreat to the center of trees where they are safe from eagles (Seyfarth et al. 1980). But do these signals really communicate predator type? The calls could signal information about predator behavior or act to instruct receivers about the appropriate response. These would not be referential in the same sense. For reasons like this, some have questioned the utility of using the term referential. Furthermore, recent work by Nicholas Ducheminsky, Peter Henzi and Louise Barrett with a different subspecies of vervets in South Africa has even questioned the inferences from earlier vervet studies (Ducheminsky et al. 2014). South African monkeys living in larger groups and under different predation risks did not have the contextual independence seen in East African vervets. If we accept that cognition is a trait subject to selection, we should expect both intra- and inter-specific differences in cognitive abilities based on their value. It is likely that the different conditions that the South African vervets lived under selected for different cognitive abilities.

Food calls are vocalizations emitted around food. Are they referential? Can they label specific types of food in ways that animals may label types of predators? The short answer is that food calls are rather complex and multipurpose. Food calls are given in both feeding and nonfeeding situations. Most species do not produce unique calls for different foods. The most common mechanism associated with food variation is changing the calling rate, suggesting that call structure reflects the caller's internal state rather than the food type. Additionally, there is no unifying function of calls either. Some food calls are used in situations where individuals recruit others to reduce predation risk. Some food calls seem to be used to build a reputation or to attract mates. Some food calls signal ownership of a resource and function to reduce competition. Thus, whereas alarm calls may be referential (or not), most food calls are not referential.

## Intraspecific Communication

Individuals may communicate with conspecifics for a variety of reasons. We will explore a few of the contexts that involve intraspecific communication, including the sexually selected signals used in antagonistic and mate attraction contexts, signals under kin selection, and finally social calls. It is important to reiterate that just because the sender and receiver are from the same species, interests need not be aligned because selection acts on the individual, not the group or the species.

As mentioned, antagonistic and mate attraction signals are under sexual selection, which is the evolutionary process that arises from the competition of one sex for the other. In most mating systems, males are competing for females (although there are some interesting polyandrous examples such as jacanas and a more contemporary view of mate choice recognizes that both individuals are making decisions about whom to mate with). In antagonistic contexts, including contests over mates, territories, or rank, the interests of a sender and receiver are opposed.

Therefore, we expect high signaling costs to ensure honesty. Male weapons which are (often exaggerated) structures used to defend territories or females are an excellent example of high costs. Most weapons (such as antlers) are expensive to carry, produce, and/or maintain and not all males have the required nutritional history, genetic quality, or a large enough body size to support growing a weapon (Emlen 2008). These weapons are used as both assessment signals of male fighting condition or quality as well as in combat. In general, the male with the biggest weapon usually wins.

Mate attraction also has diverging interests between males and females because of unequal investment in reproduction (females often, but not always, invest more). There is often a tradeoff between the signal and another function to ensure reliability. Many signals used in mate attraction are often correlated with some sort of information about the male: condition, foraging ability, parental care. Similar to antagonistic signals, these signals may become exaggerated by sexual selection. For example, the satin bowerbird (*Ptilonorhynchus violaceus*) builds an elaborate structure (called a bower) (https://macaulaylibrary.org/video/456303). Research by Stéphanie Doucet and Robert Montgomerie suggests that both a male's bower quality and his ultraviolet coloration are correlated with his condition suggesting that these signals are reliable signals of male quality (Doucet and Montgomerie 2003).

Communication between kin is another common communication context. In general, when kin communicate with other kin or their parents, interests mostly overlap because of genetic relatedness. There are two types of signals that have received the most attention: begging calls by offspring and alarm calls. In birds, begging calls appear to be honest signals of need and parents respond appropriately (Searcy and Nowicki 2005). Due to the genetic relatedness and aligned interests between parents and offspring, there may not need to be heavy costs to ensure signal honesty. In fact, researchers have found only weak support for energetic or predation costs that could maintain honesty. Alarm calls are another area of research where interests, especially between kin, may be aligned. Alarm calling behavior is common in birds and mammals and usually conveys information about the predator to conspecifics (and, as we will discuss later, to heterospecifics). In species that live in family groups, this apparently altruistic behavior is often explained by kin selection: an individual gains a fitness benefit by helping a genetic relative. For example, research by Michael Griesser with Siberian jays (*Perisoreus infaustus*) has shown them to be more vigilant and more likely to give alarm calls in the presence of kin than nonkin (Griesser 2003).

Many species live in groups. Social calls among conspecific group members may facilitate group cohesion, group predator avoidance (alarm calls), and/or group foraging (food calls). Because most individuals will benefit from being in a group when groups form to reduce predation risk, interests are more aligned than opposed and, therefore, costs on signals to retain reliability should be relatively low. Food calls, where an individual attracts others to a food source, are thought to be advantageous to the sender and receiver because the group will have reduced predation and/or the additional individuals will help form a coalition to defend the food source from others. This is thought to be the case in ravens (*Corvus corax*). Raven pairs hold territories and when a nonresident raven discovers a food source on the pair's territory, it will give food calls to attract other nonresident ravens to the food source to help defend it from the resident pair (reviewed in Searcy and Nowicki 2005).

## Interspecific Communication

Individuals from different species (even from different taxa) also communicate. Just like with intraspecific communication, the fitness benefits to both sender and receiver need to be considered as well as the signal reliability. Much interspecific communication involves eavesdropping – the use of a signal intended for another receiver. Eavesdropping by unintended receivers can be an important selective force on signal modality and structure. We might initially assume that the eavesdropping receiver always benefits (otherwise why would they eavesdrop?). However, as with all inter-species interactions, eavesdropping can be positive (+), neutral (0), or negative (−) to the sender. In alarm call signaling systems, the sender generally benefits from having eavesdroppers on their alarm signals because these unintended receivers often assist in mobbing the predator from the area (sender +, receiver +; i.e., social eavesdropping; Peake 2005). When making habitat selection decisions, many species eavesdrop on conspecifics' breeding success to make decisions about territory and nest site location the following breeding season with little to no effect on the sender (sender 0, receiver +; i.e., social eavesdropping; Peake 2005). Some species also eavesdrop on heterospecifics. Finally, eavesdropping receivers can have a negative impact on the sender (sender −, receiver +; i.e., interceptive eavesdropping; Peake 2005), which would select for less conspicuous and more direct signals. For example, formative work by Michael Ryan and colleagues with Túngara frogs has also found that fringed-lipped bats (*Trachops cirrhosis*) use the "whine-chuck" call of male Túngara frogs to localize them. Like conspecific females, the addition of the "chuck" makes it easier for the bats to locate the calling individual. Therefore, there is a cost to producing the female-preferred "chuck" and not all males produce it. It is thought that this predatory cost may in part keep this signaling system reliable (Halfwerk et al. 2014). It is important to note that eavesdropping also takes place within intraspecific communication systems.

As demonstrated in some of the examples we present in this chapter, communication is rarely a private conversation, but rather exists in a communication network with multiple senders and receivers. A communication network is a group of animals (conspecifics, heterospecifics, or both) that are within signaling and receiving distance from one another (McGregor 2005). As with eavesdropping, the costs and benefits of multiple senders and receivers within a communication network will influence the signal. Furthermore, communication networks are not filled with symmetrical contributions across individuals or species. For example, Randler and Vollmer (2013) identified asymmetrical responses across species in a European avian mobbing communication network. Species responded most to conspecific mobbing, but responses to heterospecifics varied across species with chaffinches (*Fringilla coelebs*) having the lowest responses and blue tits (*Cyanistes caeruleus*) having the greatest. Again, the costs and benefits to the sender and receiver must be considered to understand the complex responses that exist within communication networks. Additionally, as with eavesdropping above, communication networks also exist in intraspecific networks as well.

We initially discussed the idea that both sender and receiver should benefit in order for a signaling system to persist, but that these benefits can occur independently of each other (e.g., sender manipulates receiver, receiver gains inadvertent information). However, sometimes the benefits of the sender and receiver are linked, such as in mutualisms where one benefits if the other benefits. For example, in Kenya, Anne Rasa found that dwarf mongooses and various hornbill species have a communicative mutualism. Dwarf mongooses (*Helogale parvula*) rely on two species of hornbills (*Tockus* spp.) to be vigilant of predators and give alarm calls while they forage, and hornbills rely on foraging mongooses to displace insects during their foraging for the hornbill's consumption (Rasa 1983).

Remarkably, predators and their prey often communicate with each other. Aposematic coloration is the bright coloration and patterning that (when not a Müllerian mimic) is associated with unpalatability. Bright coloration (and often accompanying odors) is easier to learn by predators avoiding prey. This is still a sender + receiver + interaction because the prey does not get eaten (+) and the predator does not get harmed trying to eat an unpalatable prey (+).

## Applied Communication

People have been applying knowledge of communication to manipulate animals' behavior for a long time. Waterfowl hunters mimic their prey's calls, carnivore hunters mimic the sounds that carnivore's prey emit, and now, even fishers can use electronic baitfish (https://www.livingstonlures.com/) to attract their prey. But wildlife managers are also using the sounds that animals produce to attract and to potentially repel individuals.

Playbacks of conspecific vocalizations induce preferential settlement in several species of birds (pied flycatchers – *Ficedula hypolecua*, Laysan albatrosses – *Phoebastria immutabilis*) and a grasshopper (*Ligurotettix coquilletti*). These studies, and others, suggest that conspecifics may have an important impact on where animals settle and, more generally, that knowledge of conspecific attraction can help inform conservation and wildlife management.

On the Fort Hood Army base in Texas, the endangered black-capped vireo (*Vireo atricapilla*) was having limited success rearing offspring because their nests were parasitized by brown-headed cowbirds (*Molothrus ater*). Cowbirds lay their eggs in other species' nests and this parasitism has caused the decline of many species that cannot evolve the ability to reject cowbird eggs. Wildlife managers Michael Ward and Scott Schlossberg wanted to see if they could call in birds to settle on areas that were "safe" because the researchers were controlling cowbirds in specific areas. To study this, they conducted a playback experiment. In 2000, they had no call playbacks. In 2001 and 2002, they broadcast the vocalizations of black-capped vireos. They found that vireos were attracted and settled in areas with vireo playbacks and were less likely to do so in years and at locations without vireo playbacks. Thus, for black-capped vireos, it seems conspecifics may be important cues for habitat quality (Ward and Schlossberg 2004).

Knowledge that a species uses conspecifics as cues for settlement decisions can inform conservation programs. For instance, animals could be "seeded" into suitable habitat to attract others, or artificial cues could be broadcast or placed in appropriate habitat as a way to attract others. Ultimately, it may be possible to attract enough individuals to form a sustainable population.

Acoustic repellents have been less successful. Repellents can simply be painful sounds or biologically meaningful sounds used by managers to keep animals away from an area. For instance, to reduce bird strikes on airplanes, managers often shoot blanks to scare away birds from runways. Although painful sounds may work, the meaningful ones – including the sounds of predators – have been less successful. However, a series of studies led by Michael Clinchy and Liana Zanette, in a variety of habitats and locations around the world, have shown that broadcasting the sounds of predators can have remarkable effects on the reproductive success of residents (it goes down), on the foraging behavior of prey (they are more cautious), and on the overall structure of ecological communities (they are changed) through the indirect effect of manipulating perceived predation risk (Zanette et al. 2011). Such manipulations may be an essential tool in reinstalling fear into communities where key predators have been extirpated.

## Conclusions

Animal communication involves some of the most conspicuous behaviors in the animal kingdom. There are numerous ways to communicate as well as numerous contexts for communication. We have provided a brief overview of some of the ways and contexts that animals communicate. We have discussed the importance of signal reliability in maintaining signaling systems. Signals need to be reliable on average in order to be useful and this reliability is often maintained through costs that vary in severity depending on the alignment of interests between sender and receiver. We have discussed how signals evolved and some of the selective pressures that may lead to more complex signaling systems (e.g., multimodal signaling). Animal communication is an active area of research, and there remain many unanswered questions regarding both the evolution and ecology of signaling systems.

## Cross-References

- ▶ Auditory Signals
- ▶ Chemical Signals
- ▶ Graded Signals
- ▶ Honest Signaling
- ▶ Receiver
- ▶ Referential Communication
- ▶ Signaler
- ▶ Species-specific Behavior
- ▶ Vocal Communication

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